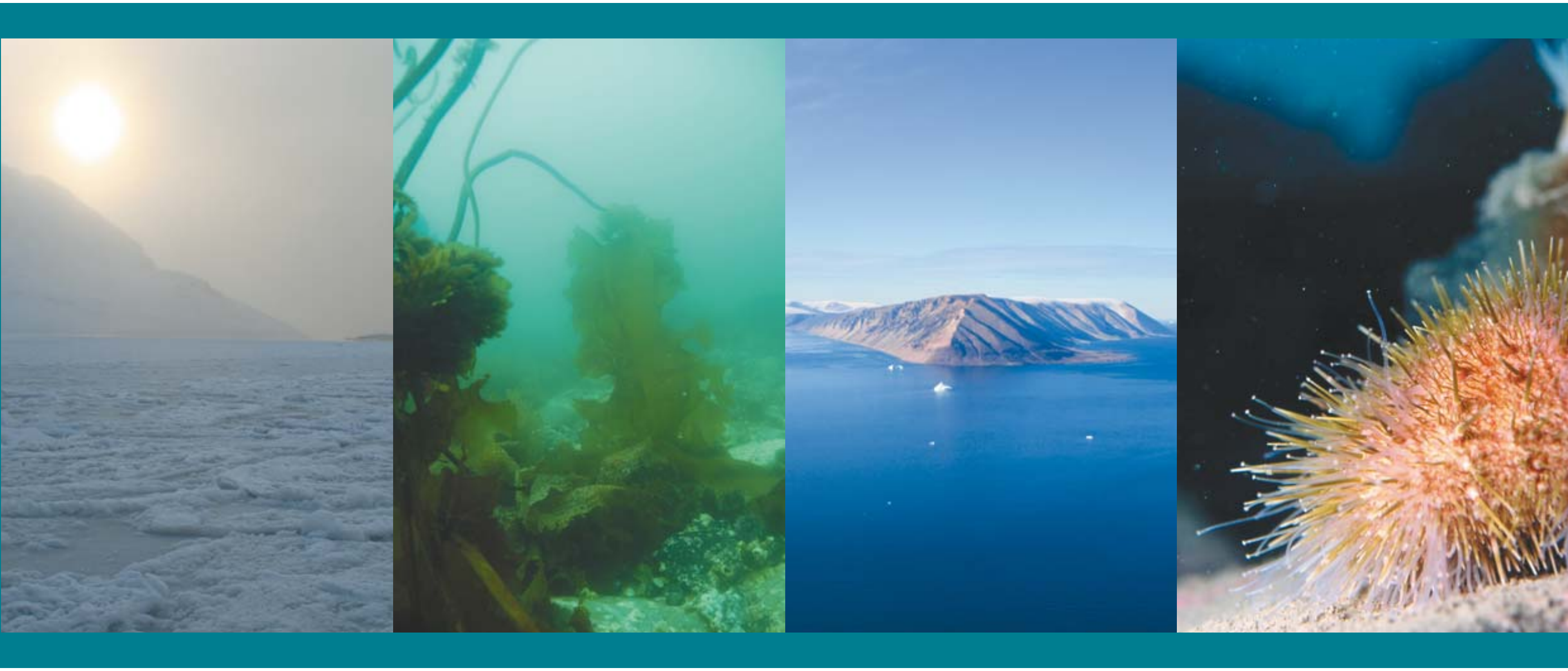
STRUCTURE AND DYNAMICS OF MARINE MACROZOOBENTHOS IN GREENLAND

– AND THE LINK TO ENVIRONMENTAL DRIVERS



Martin E. Blicher

PhD thesis 2010

Greenland Climate Research Centre

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Abstract: The marine ecosystem off Greenland is poorly described. Due to ongoing climate changes and oil explorations in the area there is an urgent need for basic ecological research to be able to document potential changes in the future as well as to identify environmental drivers of ecosystem dynamics.

This PhD study describes macrozoobenthic structure and dynamics on different temporal and spatial scales, and on levels of biological organization ranging from cell to community. Besides providing baseline knowledge on the macrozoobenthic community structure in a number of different biotopes in Greenland, the combined results indicate that benthic fauna play a central role for marine carbon cycling. Further, the study presents novel findings on how temporal and spatial growth variations of benthic macro-invertebrates in Greenland are linked to environmental controls, supporting a general hypothesis of food limitation of Arctic macrobenthos. Variations in temperature, seasonal sea ice distribution and fresh water runoff from land are likely to affect benthic productivity directly and indirectly through its potential effect on primary production and pelagic-benthic coupling. Therefore, the benthic community is expected to be sensitive to environmental change with potential implications for animals on higher trophic levels, such as several bottom foraging bird and fish species.

Keywords: Arctic, sub-Arctic, Greenland, Godthaabsfjord, marine, benthos, sea ice, food availability, temperature, carbon demand, production, shell growth, RNA:DNA, seasonal and annual dynamics, sclerochronology, species richness, spatial patterns, biodiversity, respiration, remineralisation, sea floor photography, eddy correlation, oxygen exchange

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8. Sejr M.K., Włodarska-Kowalczuk M., Legeżyńska J., Blicher, M.E. (2010) Macrobenthic species composition and diversity in the Godhaabsfjord system, SW Greenland. Polar Biology 33:421-431

PREFACE

The ocean and its natural resources has always been at the centre of Greenland and Eskimo culture and plays a dominant role for the economy of modern Greenland. It is remarkable, therefore, that the existing marine ecological structure off Greenland is so relatively incompletely described. From a scientific point of view I have found it inspiring to take part in the exploration of an ecosystem of which so little is known. On the other hand, in the light of the climate forecasts and the ongoing oil explorations in the Arctic region, it has been frustrating to realize the enormous gaps in knowledge regarding the basic structure of the marine ecosystem in Greenland. For this reason, it was, and still is, necessary to carry out descriptive studies to provide the valuable knowledge about basic ecological parameters that makes it possible to ask relevant questions in future research.

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SUMMARY

The Arctic is expected to undergo dramatic climate changes in the coming decades as a consequence of global warming, and effects on both terrestrial and marine ecosystems are considered very likely. However, the existing knowledge of marine ecosystem structure and dynamics in the Arctic, and in Greenland in particular, is limited. The main focus of this PhD study was, therefore: (1) to describe existing patterns in marine macrozoobenthic population dynamics and community structure in Greenland and to assess the importance of macrobenthos in ecosystem carbon cycling, and (2) to increase knowledge about the direct and indirect effects of different environmental drivers on macrozoobenthic production and carbon demand. My co-authors and I conducted a number of studies using several different methodological approaches making it possible to explore dynamics on different scales in time and space, and on different levels of biological organisation. This approach originated partly from the assumption of a trade-off between the level of biological organisation on which dynamics are observed and the likelihood of being able to identify the environmental drivers of these dynamics. Thus, despite the high priority of creating baseline knowledge at ecosystem level, it was necessary to conduct studies of dynamics at lower levels of biological organisation (e.g. organism, population) on relatively short time-scales (i.e. hours, days, months) to effectively identify environmental drivers of ecological dynamics.

Community structure

I studied benthic community structure in the sub-Arctic Godthaabsfjord system, SW Greenland. The sea bed at shallow depths (<60 m) was generally dominated by hard substrates (i.e. rock, stones, gravel, shells). In such areas sea urchins, *Strongylocentrotus droebachiensis*, and scallops, *Chlamys islandica*, dominated the macrobenthic community. However, in the inner and/or deeper parts of the Godthaabsfjord system and in some shallow inlets the sea bed consisted of soft sediments with diverse infauna communities dominated by polychaetes and bivalves. The large variation in benthic species composition found within the fjord system and out to the slope and continental shelf (*c.* 1000 m) was related to differences in depth, substrate, chlorophyll content and physical disturbance. For the shallow inlet, Nipisat Sound, a large fraction of the benthic standing stock was consumed by wintering eiders, and my results indicated that this trophic relationship had a strong impact on the benthic community structure and species composition, supposedly leading to a high turnover.

Altogether, my results indicated that differences in physical characteristics, food availability and predator-prey relationships lead to large local variations in benthic community structure. However, additional research is needed to be able to distinguish between local and large-scale variation in benthic communities in Greenland, and to test the indications of a particularly high species diversity compared to other Arctic regions.

Growth

Growth of bivalves and sea urchins in Greenland was relatively slow compared to other areas in the North Atlantic. Combined results clearly showed that annual growth rates were higher at shallow depths and in geographical areas or years with relatively little seasonal sea ice cover. On a seasonal scale, variations in the mass growth rate, and the growth capacity, of scallops were strongly related to the availability of high-quality food, supporting the indications of a causal relationship in the previous studies. Moreover, the growth of scallops was negatively affected by increasing temperature, indicating that they were not able to compensate for the elevated metabolic cost of maintenance at higher temperature through increased energy assimilation.

Functional importance

Our estimates of carbon demand of macrobenthic communities combined with the few other studies conducted at shallow depths in the Arctic (<200 m) indicate that the amount of carbon channelled through the macrobenthic community corresponds to *c.* 20 % of the annual pelagic primary production. Hence, the spatial differences in productivity seem to be traceable to the benthic environment, indicating a strong and relatively stable pelagic-benthic coupling despite geographical variations in physical characteristics. Further, the benthic fauna in coastal areas is suggested to contribute significantly to total benthic carbon turnover, adding up to >35 % to microbial mineralisation in some areas. Moreover, we addressed the role of macrobenthos in the classical food web. Our results for a wintering habitat for bottom foraging eiders indicate that the interplay between predator and prey can be very strong and central for understanding the dynamics of both.

Conclusions and future perspectives

The different studies in combination revealed large variations in benthic activity at different temporal and spatial scales, and the effect of food availability on benthic activity was visible on all these scales, and on biological levels ranging from cell to community, supporting a general hypothesis of food limitation of Arctic macrobenthos. However, basic ecological parameters such as macrobenthic species composition, species diversity, abundance and biomass were also shown to vary on a relatively small spatial scale (fjord-ocean). Variation in food quality and quantity might be responsible for some of the differences found in parameters at community level. However, extensive investigations are needed to further elucidate local as well as regional variation in benthic communities and to understand how temporal and spatial changes in community structure are linked to the function of the benthic compartment. Ongoing activities along a climatic gradient from 60 to 77°N on the Greenland West coast are expected to provide some answers as to the effect of climate and climate related parameters on biogeography, diversity and function, which is of central importance in the light of future climate change in the Arctic.

DANSK RESUMÉ

Den arktiske region forventes at gennemgå dramatiske klimaforandringer i de kommende årtier som følge af global opvarmning, og effekter på både terrestriske og marine økosystemer anses for meget sandsynlige. Desværre er den eksisterende viden om marine økosystemers struktur og dynamik i Arktis, og i Grønland i særdeleshed, begrænset. Hovedfokus i mit Ph.d. studium var derfor: (1) at beskrive eksisterende mønstre i marin makrozoobentisk populationsdynamik og samfundsstruktur i Grønland og at vurdere makrobentos's rolle i det marine økosystems kulstofomsætning, og (2) at øge den eksisterende viden om direkte og indirekte effekter af forskellige fysiske og biologiske parametre på makrozoobentisk produktion og kulstofoptag. Mine medforfattere og jeg har gennemført en række undersøgelser med flere forskellige metodiske tilgange, som har gjort det muligt at beskrive dynamikker på forskellige skalaer i tid og rum, og på forskellige biologiske organisationsniveauer. Denne strategi blev til dels valgt ud fra en antagelse om en trade-off mellem det biologiske organisationsniveau, hvor dynamikker observeres, og sandsynligheden for at være i stand til at identificere de miljømæssige parametre, som kontrollerer disse dynamikker. På trods af at baseline studier på økosystemniveau havde høj prioritet, var det nødvendigt at gennemføre undersøgelser af dynamikken på lavere biologiske organisationsniveauer (f.eks. organisme, population) på forholdsvis korte tidsskalaer (dvs. timer, dage, måneder) for effektivt at identificere hvilke miljømæssige parametre, som er i stand til at forårsage økologisk variation.

Samfundsstruktur

Jeg studerede den bentiske samfundsstruktur i det sub-arktiske Godthaabsfjord-system i Sydvestgrønland. Havbunden på lave dybder (<60 m) var generelt domineret af hårdbund (dvs. klippe, sten, grus, skaller). I sådanne områder dominerede søpindsvin, *Strongylocentrotus droebachiensis* og kammuslinger, *Chlamys islandica*, det makrobentiske samfund. Men i den indre og/eller dybere dele af Godthaabsfjord-systemet, og i lavvandede vige, bestod havbunden af bløde sedimenter med en divers infauna domineret af børsteorme og muslinger. Den store variation i den bentiske artssammensætning, som fandtes inden for fjordsystemet og ud til kontinentalsoklen (ca. 1000 m), var primært relateret til forskelle i dybde, sediment, klorofylindhold og fysiske forstyrrelser. I den lavvandede vig Nipisat Sund blev en stor del af den bentiske biomasse konsumeret af overvintrende edderfugle. Mine resultater viste, at denne trofiske kobling havde en stærk indflydelse på den bentiske samfundsstruktur og artssammensætning, formodentlig førende til en høj omsætning. Tilsammen viste mine resultater, at forskellene i fysiske karakteristika, tilgængelighed af føde, og rovdyr-byttedyr relationer fører til store lokale variationer i den makrobentiske struktur. Yderligere forskning er imidlertid nødvendig for at kunne adskille lokal og regional variation i bentiske samfund i Grønland og teste indikationerne af en særlig høj artsdiversitet i forhold til andre arktiske regioner.

Vækst

Væksten af muslinger og søpindsvin i Grønland var forholdsvis langsom sammenlignet med andre områder i det nordlige Atlanterhav. Vores resultater viste klart, at de årlige vækstrater var højere på lave dybder og i geografiske områder, eller år med forholdsvis lille udbredelse af havis. På sæsonskala var de observerede variationer i vækstrate, og vækstkapacitet, hos kammuslinger stærkt knyttet til tilgængeligheden af føde, hvilket synes at støtte indikationerne af en årsagssammenhæng mellem fødetilgængelighed og vækst i de tidligere undersøgelser. Desuden blev væksten hos kammuslinger negativt påvirket af stigende temperatur, hvilket antyder at de ikke var i stand til at kompensere for de forhøjede metaboliske omkostninger ved højere temperatur gennem øget energiassimilation.

Funktionel rolle

Vores estimater af kulstofoptag hos makrobentiske samfund kombineret med de få andre undersøgelser på lave dybder i Arktis (<200 m) viser, at mængden af kulstof som kanaliseres gennem det makrozoobentiske samfund svarer til ca. 20 % af den årlige pelagiske primærproduktion. Således synes de rumlige forskelle i produktivitet at kunne spores til det bentiske samfund, hvilket indikerer en stærk og forholdsvis stabil pelagisk-bentisk kobling trods geografiske forskelle i fysiske karakteristika. Herudover foreslås bundfaunaen i kystnære områder at bidrage signifikant til den samlede bentiske kulstof omsætning og tilføje op til >35 % til den mikrobielle mineralisering i nogle områder. Desuden blev der gjort et forsøg på at kvantificere den funktionelle rolle af makrobentos i den klassiske fødekæde. Vores resultater for et overvintringsområde for bundfouragerende edderfugle tyder på, at den trofiske kobling mellem predator og byttedyr kan være stærk og særdeles vigtig for forståelsen af dynamikken hos begge.

Konklusioner og perspektiver

Resultaterne viste store variationer i den bentiske aktivitet på forskellige tidslige og rumlige skalaer, og effekten af fødetilgængelighed på den bentiske aktivitet kunne spores på alle disse skalaer, og på biologiske niveauer fra celle til samfund, hvilket støtter en generel hypotese om fødebegrænsning af arktisk makrobentos. Grundlæggende økologiske parametre såsom makrobentisk artssammensætning, artsdiversitet, tæthed og biomasse varierede på en relativt lille geografisk skala (fjord-ocean). Variation i fødekvalitet og -kvantitet kan også være ansvarlig for nogle af de forskelle, som findes i andre parametre på samfundsniveau. Der er dog brug for omfattende undersøgelser for yderligere at kunne belyse den lokale såvel som regionale variation i bentiske samfund, og for at forstå, hvordan tidslige og rumlige ændringer i samfundsstruktur er relateret til selve den funktionelle rolle af det bentiske samfund. Igangværende aktiviteter langs den eksisterende klimatiske gradient fra 60 til 77° N på Grønlands vestkyst forventes at øge vores viden omkring effekten af klima og klimarelaterede parametre på biogeografi, diversitet og funktion, som er af central betydning i lyset af de fremtidige klimaforandringer i Arktis.

1 SYNOPSIS

1.1 Focus and aims

Ongoing climate changes in the Arctic have attracted enormous attention in recent years and it is expected that changes in the climatic characteristics of the region will have major ecological effects (e.g. ACIA 2005). In Greenland the marine resources are extremely important economically as well as culturally. However, the existing knowledge about the marine ecosystem is limited. The primary goal of my PhD project was, therefore, to conduct ecological studies that could add to a better understanding of the existing marine ecological structure in Greenland, and, moreover, provide the reference data that are needed to identify and understand future climate-related changes. The Godthaabsfjord system, SW Greenland, and the Young Sound system, NE Greenland, have recently been chosen as key areas for the long-term monitoring of climate-related changes in ecosystem dynamics in a sub- and high-Arctic area, respectively (www.g-e-m.dk). Ecological research in areas of contrasting climates is expected to add to the existing knowledge of potential climate effects in the Arctic. I therefore decided to focus primarily on the Godthaabsfjord and Young Sound systems during my PhD study. I concentrated on the benthic compartment for several reasons. Firstly, reports of high macrobenthic abundance and biomass in Greenland (Vibe 1939, Schmid & Piepenburg 1993, Ambrose & Renaud 1995, Sejr et al. 2000), and in the Arctic in general (Klages et al. 2004, Grebmeier et al. 2006a), indicate that the benthic compartment has a key role in marine carbon cycling, which is supported by the high abundance of several benthic predators (i.e. fish, birds, walruses, seals). Secondly, previous studies have indicated that the benthic macroinvertebrate community in Greenland is dominated by old individuals (up to several decades) (Sejr et al. 2002, Blicher et al. 2007), and therefore reflect environmental conditions integrated over a long time-scale. This makes them ideal for studying long-term or large-scale effects of climate. Thirdly, it has been suggested that roughly 75 % of all animal species in Greenland are marine invertebrates, of which the majority are benthic species (Jensen & Christensen 2003). Thus, macrobenthos add significantly to Arctic biodiversity, and can be considered an important component for the structure and function of the Arctic ecosystem.

Still, very little is known about the spatial variation in benthic community structure and function in Greenland, both on a local and regional scale. Moreover, seasonal and inter-annual dynamics have not been studied. However, there is a general expectation that the climatic differences found on seasonal, inter-annual and geographical scales have a large impact on basic ecological processes. Therefore, my co-authors and I have conducted a number of studies of marine benthos in Greenland using several different methods for assessing the same ecological key parameters, namely structure, production and carbon demand, which are central to the understanding of function and energy flow through an ecosystem. The studies were carried out in different habitat types, on different levels of biological organisation from cell to community, integrating dynamics on different time scales ranging from hours to years, and a variety of spatial scales in order to gain a general insight into the dynamics in the benthic community as well as the underlying processes. Thus, the overall objectives of my PhD project were: (1) to describe existing patterns in marine macrozoobenthic population dynamics and community structure in Greenland and to assess the importance of macrobenthos in ecosystem carbon cycling, (*papers 1, 5, 6, 7, 8)*, and (2) to increase knowledge about the direct and indirect effects of different environmental drivers on macrozoobenthic production and carbon demand *(papers 1, 2, 3, 4)*. Below I will summarize the results and perspectives of eight separate studies conducted in Greenland during my PhD project from 2007 to 2010. However, first of all, I will give a brief introduction to the general physical and ecological characteristics of the marine ecosystem in this high-latitude area.

1.2 Physical characteristics of the marine system in Greenland

Greenland stretches over more than 23 latitudinal degrees (60-83°N) and spans climatically from the sub-Arctic most southern part to the high-Arctic in the North. Thus, the island consists of an extremely long coastline facing the Davis Strait and the Baffin Bay in West, and the Denmark Strait and the Greenland Sea in East. The south-northward coastline is traversed by numerous fjords, many of them acting as direct links between the inland ice sheet and the ocean. Many islands are scattered directly off the coast. Greenland's winding coastline adds up to an estimated 40,000 km perimeter (Daniëls and De Molenaar 1993). A basic understanding of the physical characteristics and environmental parameters that are likely to affect the structure and seasonal dynamics of the marine ecosystem in the Arctic is essential for the approach to marine ecological studies in Greenland.

1.2.1 Solar radiation

The intensity of solar radiation in the Arctic varies extremely over the course of a year ranging from no solar radiation during the high-Arctic winter to a maximum of 700 to 800 Watts m^{-2} in summer (e.g. Iversen & Thorsøe 2009, Sigsgaard et al. 2009). Since solar radiation represents almost all the energy available to a system, this seasonal cycle is fundamental for ecosystem dynamics in the Arctic.

1.2.2 Temperature

The Arctic and sub-Arctic climates offer extreme seasonal variations in surface air temperature: the difference between winter minimum and summer maximum being in the range of 50°C (Iversen & Thorsøe 2009, Sigsgaard et al. 2009). However, the range of temperatures in the marine habitat in the Arctic is much narrower; large areas being close to, and often below, 0°C all year round. The upper few meters of the water column are subject to the largest variations in temperature with an annual range in Greenland waters of up to ~8°C and maximum temperatures of 5 to 7°C (paper 3, Juul-Pedersen et al. 2009, Sejr et al. 2009). Hence, a more or less constantly low temperature is a general feature of the marine habitat in the Arctic. For an ecosystem primarily consisting of ectotherm organisms this is obviously an important characteristic, first of all for the individual energy requirements to cover the costs of basic physiological processes, and ultimately for the biogeography in the region.

1.2.3 Bathymetry and oceanography

The Arctic Ocean is an enormous basin with a maximum depth of >5000 m surrounded by large continental shelves of <50-300 m depth. These shelves represent 53 % of the total area of the Arctic Ocean and 20 % of the shelf areas in the world. The Arctic Ocean has surface currents dominated by the circular Beaufort Gyre and the Transpolar Drift, which are strongly wind-affected. The Bering Sea and the Chukchi Sea, representing the connection between the Pacific Ocean and the Arctic Ocean, are characterized by being shallow (<100 m) upwelling areas (Jacobsson et al., 2004, MacDonald et al., 2004). The primary water exchange (>85 %) occurs with the Atlantic Ocean over a sill (400-800 m deep) stretching from East Greenland to Iceland, the Faroe Islands and Scotland, mainly through the Barents Sea and the Fram Strait. The opening to the Atlantic Ocean has a major impact on the Arctic circulation and is characterized by opposite surface currents: Northbound branches of the Gulf Stream, which transports relatively warm water far north and the southward East Greenland current, which exports water and ice from the Arctic Ocean along the Greenland coast. The boundary between open water and sea ice cover in the Greenland Sea and Barents Sea is determined by the balance between these currents. Off Southeast Greenland the East Greenland current mixes with a branch of the warm Gulf Stream, producing the Irminger Current, which runs south of Greenland along the western coast where it is called the West Greenland current. The West Greenland current gradually mixes with water from the Arctic Ocean, which runs out through the Canadian Archipelago to Baffin Bay, and southward as a cold current along the Canadian coast (MacDonald, 2004). Another important oceanographic feature, which is especially important in coastal areas and fjords, is the seasonal input of freshwater from land and from melting sea ice. The large input of freshwater to the marine system affects the stability of the water column as well as the mixed layer depth, and it is a source of large amounts of allochthonous carbon and nutrients, and terrigenous particles. The largest discharges to the Arctic region occur from the large Eurasian and North American rivers to the Arctic Ocean (Rachold et al. 2004); however, the mechanism is also characteristic of the Greenland fjords (Juul-Pedersen et al. 2009, Sejr et al. 2009). Regional climate in Greenland is affected by these oceanographic characteristics leading to differences in climate between the West and East coast, and the regional and local differences in water mass properties also contribute to differences in another important parameter: sea ice.

1.2.4 Sea Ice

Large areas off Greenland are affected by seasonal sea ice formation. In the most northern areas the period with open water lasts only 2-3 months. Given the fact that Greenland stretches in a North-South direction over 2600 km, the island provides a climate gradient ranging from the high-Arctic to the sub-Arctic. This climate gradient is reflected very well in the geographical differences in the duration of the seasonal sea ice cover (paper 2). In the high-Arctic, the period with sea ice cover continues well into July/August. Because sea ice inhibits photosynthesis by preventing sun light from reaching the water column, most high-Arctic areas are characterised by long, almost unproductive periods interrupted by an intense pulse in productivity during the short open-water period (e.g. Rysgaard et al. 1999). In many areas primary production quickly diminishes due to nutrient depletion in the surface layer. However, nutrient-rich water can enter the photic zone by vertical mixing, which again depends on the stability and the mixed layer depth of the water column (i.e. the fresh water input) (Carmack et al. 2006, Wassmann et al. 2006). The structuring role of sea ice is reduced in sub-Arctic areas with longer open-water periods, where several phytoplankton blooms per season have been observed, leading to a several-fold higher annual pelagic primary production (paper 3, Smidt 1979, Juul-Pedersen et al. 2009).

1.3 Ecological characteristics of Arctic marine systems

The Arctic consists of several regions with distinct physical and biological characteristics. However, there are a number of important features that can be considered more or less general for the Arctic as such, including Greenland. The sea ice as such and especially its margins are inhabited by a number of remarkable mammal species, such as polar bear, bearded seal, ringed seal, walrus, bowhead whale, narwhal and beluga (e.g. Bluhm & Gradinger 2008, Laidre et al. 2008). Likewise, many coastal areas in Greenland are exploited by migratory sea birds (e.g. eiders, arctic tern, thick billed murre and little auk) during short periods of the year, either for foraging, staging, breeding, wintering etc., as an integrated part of their life-history (Henningsson & Alerstam 2008 and references therein). The seasonality and geographical differences in the annual primary production, as mentioned above, might be one of the most important biological drivers of ecosystem structure and dynamics in the marine environment in the Arctic. The timing of the migration of copepods from their deep winter habitat to the photic zone in the spring is a well-described example of this (e.g. Wassmann 1998, Juul-Pedersen et al. 2006, Wassmann et al. 2006, Sejr et al. 2007). Arctic copepods are important prey for several bird, fish and mammal species (Wassmann et al. 2006 and references therein), as well as being important for the pelagic mineralisation and the sedimentation of organic material. Still, it has been suggested that the pelagic-benthic coupling is particularly strong in the Arctic (e.g. Petersen & Curtis 1980, Fortier et al. 2002, Wassmann et al. 2006), which is supported by observations of a general relation between benthic oxygen consumption and the overlying pelagic primary production (Klages et al. 2004). A strong pelagic-benthic coupling would also explain the relatively high biomasses of macrobenthic communities beneath polynias and in upwelling areas compared to less productive areas (Ambrose & Renaud 1995, Grebmeier et al. 2006a). Still, direct proportionality does not necessarily exist between primary production and the supply of carbon to the benthic environment beneath the photic zone. The structure and seasonal development of the pelagic food web has a major influence on the fate of newly produced organic carbon (e.g. Wassmann 1998, Wassmann et al. 2006, Sejr et al. 2007). Hence, Grebmeier et al. (2006b) suggested that the pelagic-benthic coupling in the Northern Bering Sea had weakened in response to a general warming and a reduction in the seasonal sea ice cover in the area. However, the fact that the Arctic is dominated by large, relatively shallow areas (<50-200 m) is likely to facilitate a central role of benthic processes in ecosystem carbon cycling. This is supported by the fact that benthic macroinvertebrates are key prey items for several of the dominant predators in the Arctic, contrary to the deep oceans surrounding the Antarctic, where pelagic food chains are more important (e.g. Grebmeier & Barry 1991). With regard to fish in the Arctic and sub-Arctic the dominant bottom-foraging species are cods (*Gadus* spp.), wolffish (*Anarchis* spp.), Greenland halibut (*Reinhardtius hippoglossoides*) and Atlantic halibut (*Hippoglossus hippoglossus*). Benthic macroinvertebrates are also important prey for walrus (*Odobenus rosmarus*) and bearded seal (*Erignathus barbatus*), as well as several sea duck species (*Somateria* spp., *Clangula* sp.). Moreover, the commercially important species, *Chionocetes opilio* (snow crab) and Greenland shrimp (*Pandalus borealis*) are to some extent linked to the bottom and act both as a predators on macrobenthos and as prey for some of the species mentioned above.

Given the fact that the patterns in basic marine ecological parameters in the Arctic are so strongly linked to the seasonality in light conditions, sea ice and fresh water input, and to the temperature regime, it is expected that the ongoing climatic warming of the Arctic will impact the marine ecosystem in a complex manner (ACIA 2005). Therefore, it is important to identify the existing key drivers of ecosystem dynamics, physical as well as biological. The majority of marine ecological studies in the Arctic have concentrated on the pelagic zone. The results of these studies have led to hypotheses of increased primary production, changes in copepod species abundance and timing, and alterations in the pelagic-benthic coupling in response to climate change in the future (Hansen et al. 2003, Grebmeier et al. 2006b, Wassmann et al. 2006, Helaouet & Beaugrand 2007). To be able to even document climate-related ecological changes, reference studies accurately describing the pre-change conditions and key biological structures are needed. This leads to some considerations about scientific approaches. An ultimate goal of ecological research would be to completely describe ecosystem dynamics in time and space, and to identify the key environmental drivers of these dynamics. However, we expect environmental drivers to work on the organism level, not directly on the ecosystem as such. Ecosystem structure and dynamics integrate a complex array of physical as well as biological processes occurring on different scales in time and space. Thus, documentation of ecosystem structure or change might not be the most efficient way to increase our understanding of key drivers. On the other hand, results of more or less controlled experiments dealing with organism- or population-specific short-term dynamics, which may facilitate identification of some key drivers, cannot be directly extrapolated to the macro-ecological level without ignoring potentially important ecological processes occurring on a higher level of biological organisation. Hence, it might be necessary to conduct studies at several different levels of biological organisation using different methodological approaches, elucidating variations on a wide range of temporal and spatial scales, to effectively identify key ecological structures and processes, and to assess the implications on the ecosystem level.

These considerations were an important element in the planning phase of my PhD project, when a small marine ecological research group had just been established at the Greenland Institute of Natural Resources and very little was known about the benthic ecology in the sub-Arctic Godthaabsfjord system and in Greenland in general. I found it extremely important to initiate basic descriptions of the benthic community structure, i.e. abundance, biomass, species composition and diversity, to provide reference studies needed in future research and to try and understand the relation to habitat characteristics. I conducted two such studies of community structure in the Godthaabsfjord system covering habitats from the shallowest (paper 5) to the deepest part of the fjord along a fjord-ocean transect (paper 8). Oxygen consumption, growth, production and carbon demand of macrobenthos were central elements, firstly, in order to understand the role of macrobenthos in ecosystem carbon cycling, i.e. both as consumers (papers 1, 6, 7) and as prey for dominant predators (paper 5), and secondly, to learn more about the effect of different environmental parameters on macrobenthic growth dynamics (papers 2, 3, 4). The studies focusing on identification of key drivers were species-specific, and with reference to the ecological characteristics described above, I concentrated on (1) the potential effect of regional (64 to 77°N) and inter-annual (>20 yr) variation in seasonal sea ice cover (paper 2), and (2) the importance of variations in food availability and temperature for the seasonal and depth-related differences in macrobenthic growth (papers 3, 4). During my work I used a number of more or less applied techniques and tested two new techniques for its applicability for describing variation in benthic activity, namely the use of the RNA/DNA ratio of bivalve tissue as a proxy for their growth rate (paper 4), and the Eddy correlation technique, which measures total benthic community oxygen consumption in-situ across an area of several m^2, and makes it possible to study the short-term dynamics of the entire benthic compartment across heterogeneous habitats (paper 6). Hence, with this array of different approaches I hoped to contribute to answering some of the central questions concerning the marine ecosystem off Greenland.

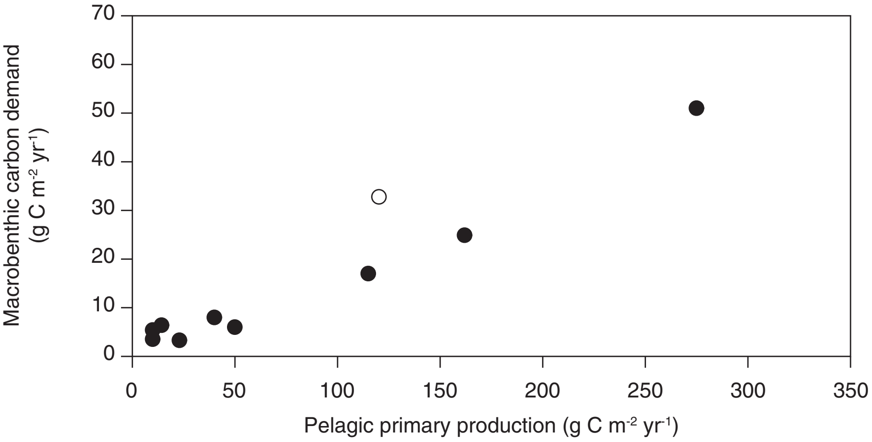
1.4 Annual production of sea urchins and scallops in a sub-Arctic fjord

I wanted to quantify the amount of carbon being consumed annually by the sea urchin, *Strongylocentrotus droebachiensis*, and the scallop, *Chlamys islandica,* which constituted the bulk (>90 %) of the macrobenthic biomass at shallow depths (<60 m) in Kobbefjord, a fjord branch in the Godthaabsfjord system (64° 09′ N, 51° 36′ W). The study was initiated concurrently with the Nuuk-Basis Monitoring Programme (www.g-e-m.dk) and the results supplemented the description of pelagic key structures and dynamics in the Godthaabsfjord system (e.g. Mikkelsen et al. 2008a, Arendt et al. 2010). Densities of sea urchins and scallops were estimated from seafloor photographs covering a total area of 141 m^2 along three depth transects. Annually formed growth bands in the interambulacral plates of *S. droebachiensis* and in the ligament of *C. islandica* were used to estimate individual age (Jensen 1969, Johannessen 1973, Brey 1991, Robinson & MacIntyre 1997) and establish growth functions. Growth and abundance data combined with size frequencies, size-mass relationships

Fig. 1. Sea urchin barren at shallow depth in the Godthaabsfjord system.

Foto: Søren Rysgaard

Fig. 2. Previously published estimates of annual macrozoobenthic carbon demand (●) and the estimate in paper 1 (○) plotted against annual pelagic primary production. Modified from Blicher et al. (2009, paper 1).



of somatic and reproductive tissue, and fjord bathymetry were used to estimate annual production and carbon demand of the two species in order to assess their ecological importance on a fjord scale. Somatic growth of both species was relatively slow and they did not reach sexual maturity until an age of >5 years (~40 mm diameter/shell height). However, the populations in Kobbefjord were dominated by relatively large/old specimens and their reproductive output constituted the majority (62-73%) of their total annual production. Maximum age of *S. droebachiensis* and *C. islandica* was estimated at 24 and 39 years, respectively. Mean annual production in the fjord was estimated at 3.2 g ash-free dry weight (AFDW) m^{-2} for *S. droebachiensis* and 2.5 g AFDW m^{-2} for *C. islandica*. Sea urchins and scallops had total production-to-biomass ratios (P/B) of 0.31-0.37 (deep and shallow) and 0.21, respectively. However, the somatic production-to-biomass ratios (P_s/B) were rather low (0.06 to 0.14), suggesting the instantaneous rate of mortality, Z (yr^{-1}), to lie in the range of 0.13 to 0.21 (Brey 1999). This is in the low end compared with other estimates of P_s/B and mortality of unexploited benthic invertebrate populations in boreal regions and the Antarctic; but in a range similar to the few available estimates from the Arctic (Petersen 1978, Brey & Clarke 1993, Brey 1999, Sejr et al. 2002) The total annual carbon demand of the two species was estimated at 30.6 g C m^2, corresponding to 21-45% of annual pelagic primary production in this area (Mikkelsen et al. 2008a, Mikkelsen et al. 2008b, Rysgaard et al. 2008). Hence, *S. droebachiensis* and *C. islandica* play important roles in the overall carbon budget of Kobbefjord and can be regarded as central species of this shallow benthic community, despite relatively slow individual growth rates.

The joint estimate of annual macrobenthic carbon demand in Kobbefjord was higher than total macrobenthic carbon requirements in most high-Arctic habitats, and in a range comparable to that of the macrozoobenthic community in the highly productive part of the North Bering and Chukchi Seas (Table 3 in paper 1). The combined data indicated that the activity of shallow macrobenthic communities can vary several-fold despite the relatively low temperatures in the Arctic. Overall, the available estimates of annual carbon requirements, although limited, seemed to reflect the level of annual pelagic primary production, which may be regarded as a proxy for the overall availability of food to secondary producers (Fig. 2). These data gave rise to some speculations regarding the effect of a potential increase in primary production as a response to an ongoing reduction in the seasonal sea ice cover in the Arctic (Arrigo et al. 2008, Pabi et al. 2008). However, given the nature of data, they could only give an idea of the underlying processes, and more detailed work was clearly needed to further elucidate this.

1.5 Inter-annual and geographical variation in growth of the Arctic cockle

By analysing annual growth increments in the shell of bivalves we wanted to reconstruct past growth conditions and produce the time-series needed to test the hypothesis of a link between variations in seasonal sea ice cover and annual growth rates of macrobenthos in shallow areas in the Arctic. A reduction in sea ice area distribution and thickness is one of the most significant effects of the recent warming of the Arctic. Data from 1979 to 2008 show a negative trend in Arctic sea ice extent with a reduction of 2.8 % per decade in March and 11 % per decade in September (Richter-Menge et al. 2008). However, the general lack of pre-change data or long time-series of biological parameters makes it difficult to assess the potential ecological consequences of a sea ice reduction. However, it is well-established that sea ice has a major influence on the onset of the spring phytoplankton bloom as well as the total amount of light reaching the water column and, thus, potentially the level of primary production (Carmack et al. 2006, Rysgaard & Nielsen 2006, Wassmann et al. 2006). Variation in primary production is likely to affect the amount of food available to macrobenthos. Thus, it may be expected that spatial and temporal variability in Arctic sea ice cover influencing primary productivity could translate to the next trophic level: the benthic secondary producers. To test whether sea ice cover is coupled to the annual production of Arctic benthos, we measured annual growth increments in the shell of the bivalve *Clinocardium ciliatum* to (1) compare average individual growth rates along a climate gradient from sub-Arctic to high-Arctic Greenland (64 to 76°N), and (2) produce time series of inter-annual variation in bivalve growth at sites with different sea ice conditions. A significant difference in average individual growth rates between the different sites was found. This geographic variation in growth performance was correlated to the average productive open-water (ice-free) period estimated from sea ice data obtained from satellites between 1979 and 2003. At locations with low to moderate sea ice cover, growth rates ranged from 80 to 100 % of the fastest growing sites. At sites with pronounced sea ice cover, bivalve growth was reduced to 35 to 45 % of the maximum growth rates. At these 2 sites the year-to-year variation in bivalve growth correlated negatively with inter-annual variation in local sea ice cover (Fig. 4).

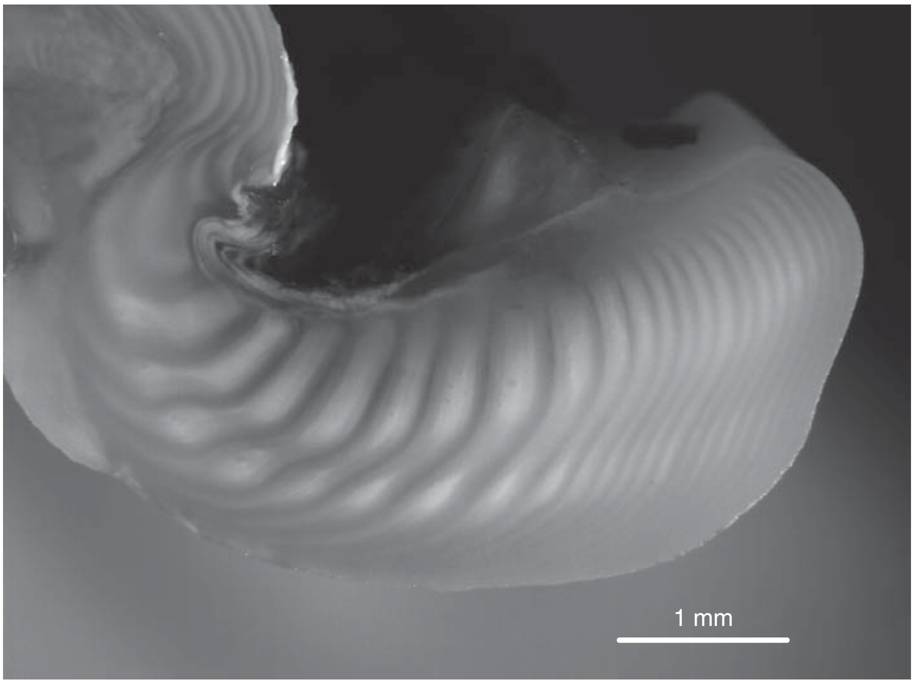


Fig. 3. Photo showing annual growth increments in the chondrophore section of the shell of the Arctic cockle *Clinocardium ciliatum* (Paper 2).

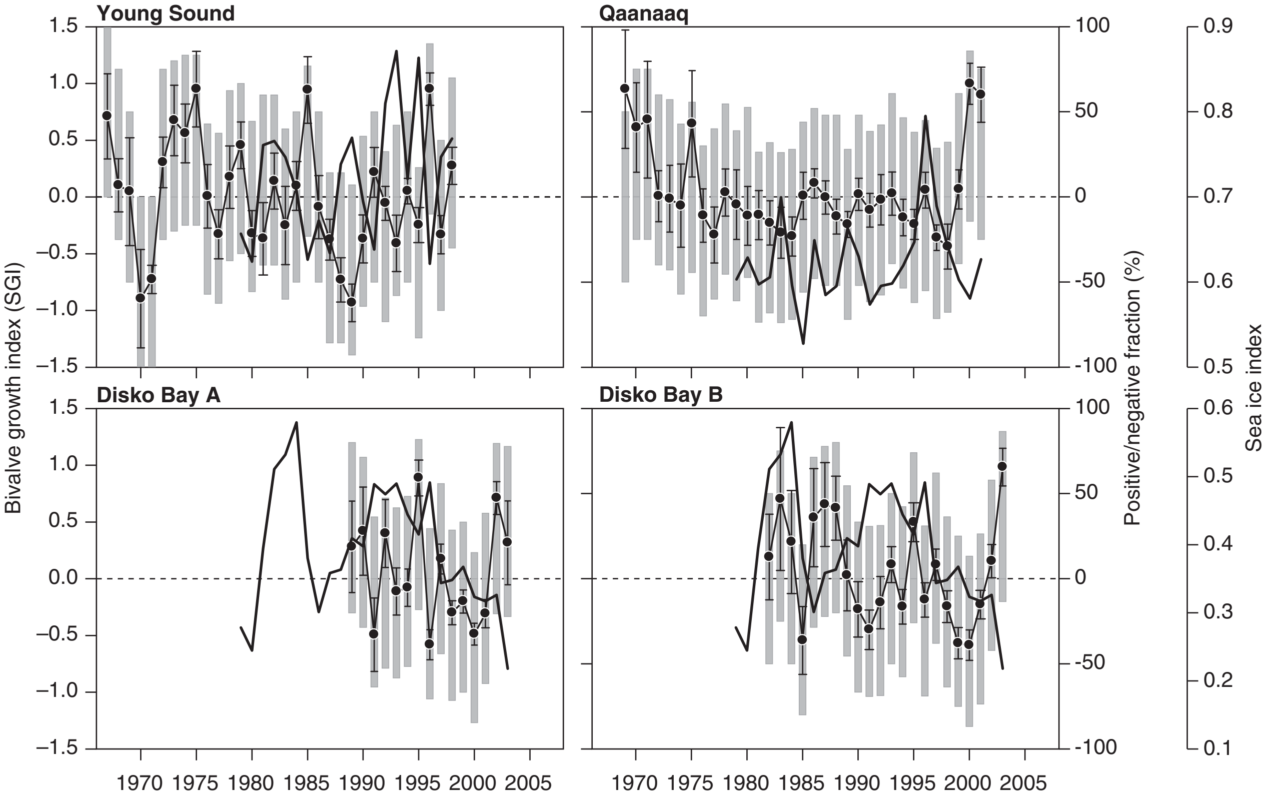


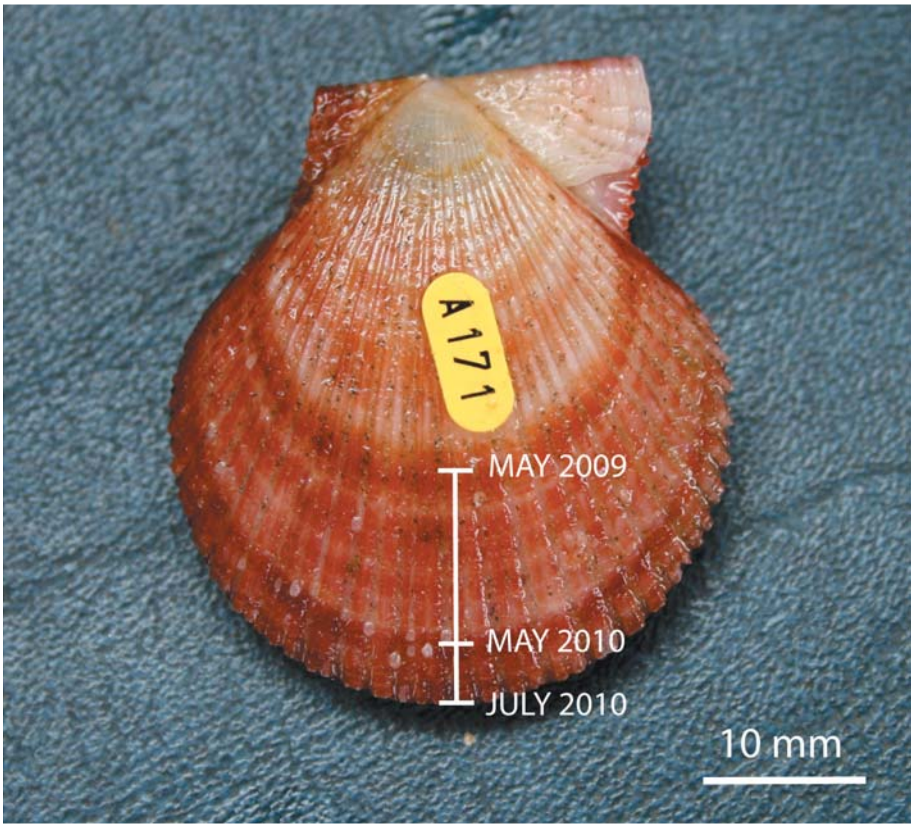
Fig. 4. Reconstructed time-series of variation in annual shell growth of arctic cockles (●) at 4 locations in Greenland. Average (± SE) and percentage of the collected specimens with positive/negative index values (grey bars). Inter-annual variation in summer sea ice index (full line) at 3 locations in Greenland. Data from the fifth sampling site (Nuuk) was left out in this figure due to the general absence of sea ice. Modified from Sejr et al. (2009, paper 2).

Thus, the combination of inter-annual and geographical growth variations of *Clinocardium ciliatum* supported our hypothesis of sea ice playing a central role for bivalve production. At sites with pronounced sea ice cover, food availability may be strongly linked to sea ice dynamics through the bottom-up regulation exerted by sea ice on phytoplankton production. We suspected that much of the unexplained variation in bivalve growth might be attributed to the seasonal dynamics of abiotic (e.g. nutrients, wind-mixing) and biotic (e.g. copepod abundance) parameters in the water column leading to differences in phytoplankton production and/or pelagic-benthic coupling, potentially hampering a simple relation between sea ice cover and food availability to benthos. Indeed, studies of the seasonal dynamics in macrobenthic production were likely to provide more detailed information on the direct effect of different environmental drivers.

1.6 Seasonal dynamics in individual production of suspended scallops

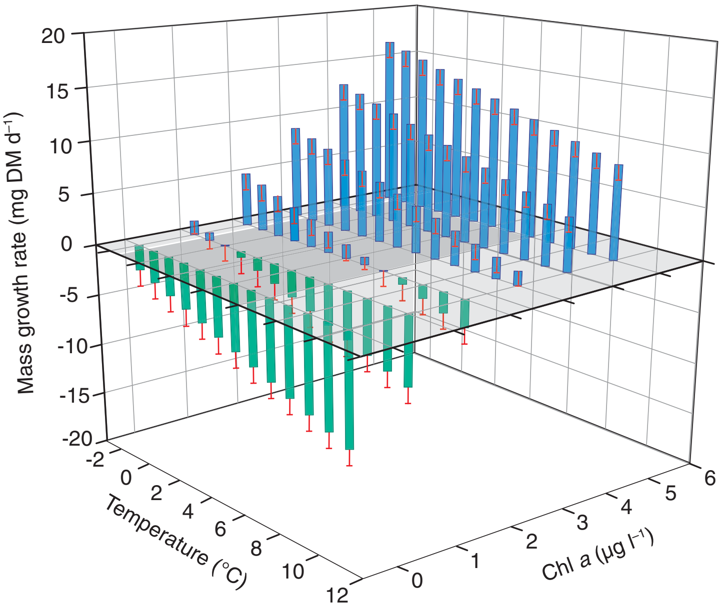
There is almost no information on seasonal dynamics of secondary producers in the sub-Arctic even though such high-resolution data could be important for the identification of key environmental drivers. Hence, I studied the seasonal variation in individual production of somatic and reproductive tissues of scallops, *Chlamys islandica*, suspended in culture nets at two different depths in Kobbefjord, SW Greenland. Scallops were tagged individually with shellfish tags and size and biomass were measured monthly during 17 months. Mass growth varied both seasonally and

Fig. 5. Scallop tagged in May 2009 for a growth experiment (papers 3, 4). Growth rate was measured monthly. Growth checks in the shell were registered at the onset of the experiment and again in May 2010.



between depths with minimum and maximum observed from November to February and in April-May, respectively, and was overall much faster than in the wild population of scallops found at greater depths (paper 1). Based on simultaneous monitoring of biotic and abiotic parameters in the water column we established a growth model relating variation in mass growth rate to variation in environmental conditions. The best-fit model indicated that total mass growth rate depended on chlorophyll *a* concentration, carbon-to-nitrogen ratio of seston, and water temperature. While availability of high-quality food items affected growth positively, the growth model indicated a negative effect of increasing temperature on the mass growth rate of *C. islandica* (Fig. 6).

Fig. 6. Absolute mass growth rate of a scallop, *Chlamys islandica*, of 1 g DW (42 mm SH) plotted against temperature and chl *a* at C:N = 6.6 (Redfield ratio) as estimated from the growth model in paper 3. Error bars indicate the negative effect of the C:N ratio increasing to 14. The grey area shows the range of environmental parameters in the study area during 2007 and 2008. Modified from Blicher et al. (2010, paper 3).



First of all, the high-resolution data supported previous indications of macrobenthic production in Greenland being controlled by the productivity regime of their habitat (papers 1, 2) and provided more details on this causal relationship. The negative effect of elevated temperature on the mass growth rate indicated that scallops were unable to compensate for the elevated metabolic cost of maintenance through increased energy assimilation, thus affecting their growth efficiency. Once again, this indicated food limitation. Hence, we found it most likely that the growth capacity of *C. islandica* in SW Greenland is either never realized or only attained for short periods of time under the present conditions, and that scallops profit from low temperatures in winter and spring by minimizing metabolic costs of maintenance and maximizing growth efficiency. The results of this seasonal study added more evidence to the suggestion that macrobenthic production in the Arctic and sub-Arctic is governed by food availability. Furthermore, the improved understanding of ecological dynamics occurring on a seasonal scale might be crucial to be able to interpret large-scale variations.

1.7 RNA:DNA ratios as indicators of growth in scallops

Traditional approaches to studying growth of bivalves (e.g. papers 1, 2, 3) are time-consuming and elaborate. Moreover, the logistical challenges in Greenland make it a difficult task to study temporal and spatial growth variations of macrofauna in general. Therefore, the validation of an easily obtained proxy for the growth rate of Arctic marine fauna would be of great value in studies of population dynamics. The RNA:DNA ratio (RD) of animal cells is a measure of the capacity for protein synthesis (Wright & Hetzel 1985, Dahlhoff 2004). RD has been widely used in studies of fish larvae where it has been validated as a proxy for the mass growth rate or the physiological condition (Buckley 1984, Clemmesen & Doan 1996, Grønkjær et al. 1997, Caldarone et al. 2003, Buckley et al. 2008). Hence, we examined the RNA and DNA concentration in muscle tissue of field-caught scallops, *Chlamys islandica*, maintained in suspended cultures at 15 and 30 m depth (paper 3), and scallops from a wild population at 50 to 60 m in Kobbefjord in SW Greenland. During an experimental period of 14 months we observed a pronounced seasonal pattern in RD and mass growth, and differences between depths. Even though the period with high levels of RD reflected the growth season relatively well, RD was a poor predictor of individual mass growth rates of *C. islandica*.

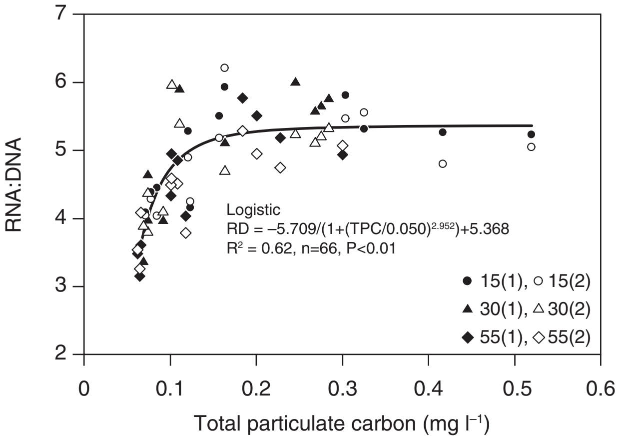


Fig. 7. Plot of the average RNA:DNA ratio against total particulate carbon (TPC). Depths (15, 30 and 55 m) and size groups (1 and 2) are illustrated with different symbols. Modified from Blicher et al. (2010, paper 4)

Despite the negative result, the question of what controlled the protein synthetic capacity in *C. islandica*, and what it reflected, remained important to our ecological understanding. In other studies of invertebrate taxa it has been suggested that variations in nucleic acid ratios related to metabolic activity, physiological robustness, reproductive state, food availability or temperature (Robbins et al. 1990, Lodeiros et al. 1996, Buckley & Szmant 2004, Dahlhoff 2004, Kim et al. 2005, Norkko et al. 2005, Norkko et al. 2006, Fraser et al. 2007). We studied the relation of scallop RD to body condition, temperature and food availability, and found a strong sigmoid relation between RD and food concentration (Fig. 7). Thus, RD was being up- and down-regulated at the beginning and end of the productive summer season, respectively, in response to variations in food availability. This implies that short-term dynamics in the actual mass growth rate is controlled through regulation of ribosome activity rather than ribosome number. This adaption would allow scallops to up-regulate protein synthesis more rapidly ensuring efficient utilization of the intense peaks in food availability in coastal areas in the Arctic, which agrees with the suggestion that the scallops had a higher capacity for growth than actually realized (paper 3).

Even though the study showed that RD cannot be applied as a proxy for the mass growth rate of *C. islandica*, it contributed significantly to the understanding of the physiological mechanisms behind dynamics observed on a higher level of biological organisation (papers 1, 2, 3).

1.8 Trophic coupling between macrozoobenthos and wintering eiders

The previous studies (papers 1-4) clearly indicated an effect of food availability on macrobenthic dynamics (bottom-up effect). However, the potential influence of benthic predators (top-down) was unknown. The Southwest Greenland Open Water Area is an internationally important wintering area for eiders feeding on benthic macroinvertebrates (Merkel et al. 2002). The number of wintering northern common eider (*Somateria*

Fig. 8. Wintering eiders in Nipisat Sound, SW Greenland (paper 5).
Photo: Lars M. Rasmussen

Fig. 9. Macrobenthos from Nipisat Sound collected with a van Veen grab sample and sieved through a 1-mm sieve (paper 5).
Photo: Lars M. Rasmussen

mollissima borealis) in West Greenland has been rapidly declining, presumably because of human activities (i.e. hunting, gillnet fishing) (Merkel 2004, Gilliland et al. 2009). However, the role of naturally occurring variations in weather conditions, food availability, or diseases is poorly studied. It therefore seemed urgent to initiate studies making it possible to assess the trophic relationship between eiders and their macrobenthic prey.

During 2008-10 the seasonal variation in the number of eiders (*Somateria* spp.) was monitored in Nipisat Sound; a key wintering habitat in the Southwest Greenland Open Water Area (Merkel et al. 2002). We observed a distinct wintering season with dense concentrations of eiders lasting from late October to May. To assess the availability of prey items for eiders we studied the macrobenthic species abundance and biomass at 15 stations in Nipisat Sound. Annual production was estimated by an empirical model including environmental characteristics, fauna composition, and individual biomass (Brey 2001). Average macrozoobenthic abundance and biomass were 6912 ind. m^{-2} and 28.4 g ash free dry mass (AFDM) m^{-2}, respectively, in Nipisat Sound. Annual production was estimated at 13.9 g AFDM m^{-2} yr^{-1}. Compared to other high-latitude localities, the estimate of total somatic production of macrobenthos was relatively high (paper 1, Grebmeier et al. 1989, Nilsen et al. 2006, Sejr & Christensen 2007) primarily resulting from a high turnover ratio (production-to-biomass = 0.49). Several of the dominant infauna species found in this study were reported as being dominant at some shallow sites in Disko Fjord, West Greenland (Schmid & Piepenburg 1993). However, the uniqueness of the area might lie in its physical properties, namely several km^2 of shallow depth and soft sediments in a region generally characterized by steep slopes, and gravelly or rocky bottom habitats (paper 1, M. Blicher pers. obs.), causing the macrobenthic community in Nipisat Sound to contain relatively large numbers of polychaetes and bivalves (>80 % of total abundance) within reach of bottom-foraging birds.

In combination with estimates of the energetic requirements of eiders we estimated that wintering eiders consumed 17 to 33 % of the autumn biomass and 58 to 90 % of the total annual production of macrobenthos. Thus, eiders have a strong impact on the macrobenthic community structure, and our data suggest that they are capable of depleting their preferred prey species and keep the community in an early stage of succession. Hence, it is likely that eiders wintering in Nipisat Sound to some extent must rely on non-preferred prey species to be able to cover their cost of living, and that they will have to build up body reserves for the breeding season elsewhere. This agrees with studies of the body condition of eiders in the area (Jamieson 2003, Jamieson et al. 2006). Our results indicated a strong trophic coupling between eiders and macrobenthos in Nipisat Sound, and suggested that food availability is an essential parameter to be able to fully understand the dynamics of migrating sea birds in the Arctic.

1.9 Benthic oxygen exchange across heterogeneous substrates

Estimates of the benthic O_2 exchange rate have been used as an effective tool to quantify short-term variations in carbon turn-over at or within the seabed. However, technical limitations have restricted measurements of benthic community oxygen exchange to sedimentary areas and few assessments of the activity in consolidated sand, on stones, cliffs or rocks have been made. Yet, such biotopes are frequent along the coastline of many Arctic and sub-Arctic regions. The introduction of the aquatic eddy correlation approach (Berg et al. 2003, Kuwae et al. 2006, Berg and Huettel 2008, McGinnis et al. 2008) has made it feasible to quantify the benthic O_2 exchange of such areas. The eddy correlation approach derives the ben-

Fig. 10. Illustration of the Eddy correlation frame used for measuring oxygen exchange across heterogeneous substrates in the Godthaabsfjord system (paper 6). Graphic: Luke Cole, University of Virginia.

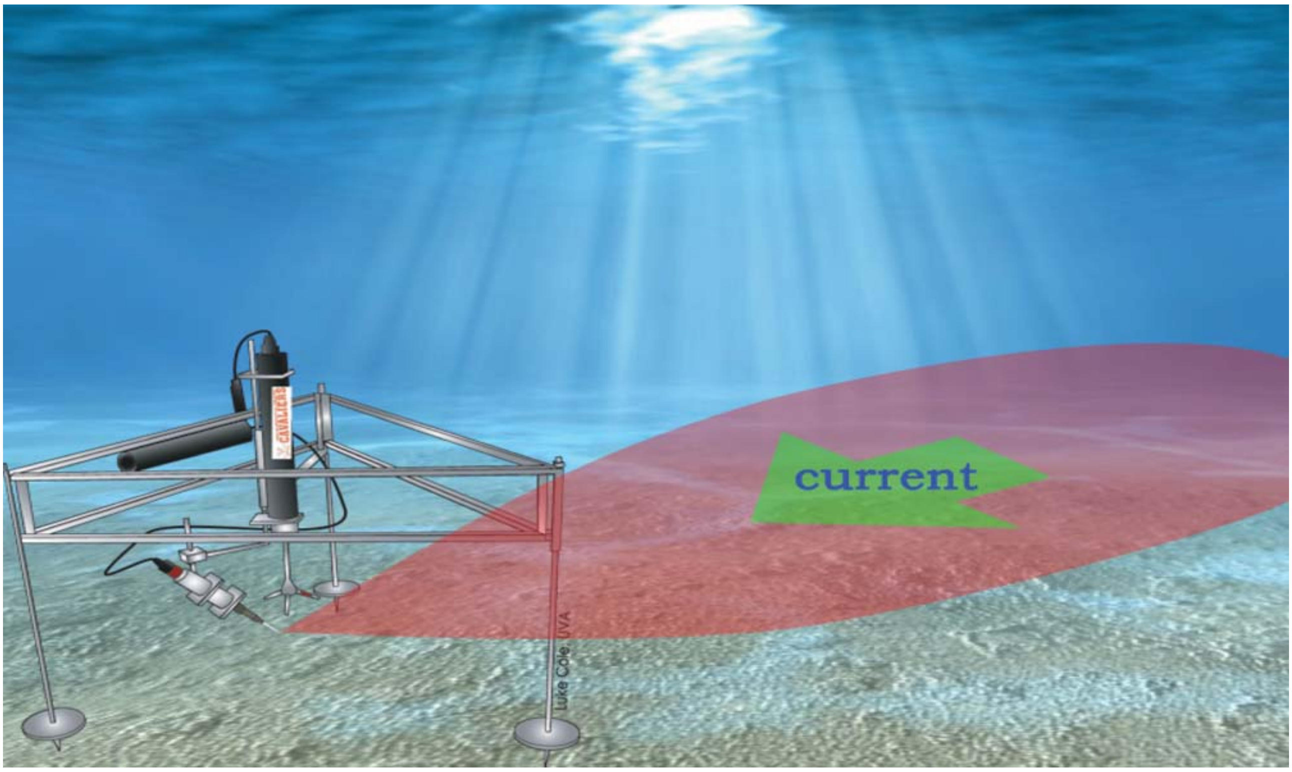
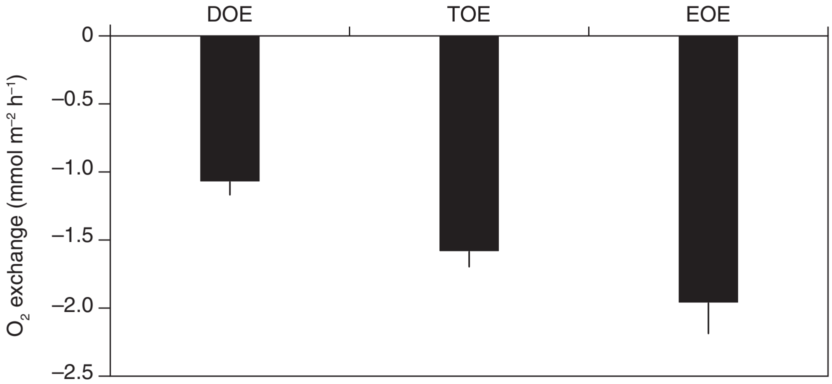


Fig. 11. Average O_2 exchange rates at a station in Nipisat Sound in the Godthaabsfjord quantified in darkness (PAR <10 photons m^{-2} s^{-1}) from microelectrode profiles (DOE), total core incubations (TOE) and in situ eddy correlation (EOE). Error bars indicate the SE, n = 15, 5, 61 for DOE, TOE and EOE, respectively. The difference between DOE and EOE indicates the fauna-mediated oxygen uptake (paper 6).



thic O_2 exchange rate at true in situ conditions from simultaneous recordings of the vertical flow velocity and the O_2 concentration at a given point within the benthic boundary layer and works equally well over soft and hard bottom substrates (Berg and Huettel 2008). Further, it integrates the activity of a much larger area (i.e. 10-50 m^2; Berg et al. 2007) and therefore encompasses a large fraction of the natural variability in a habitat and can be regarded as a true community-oriented approach.

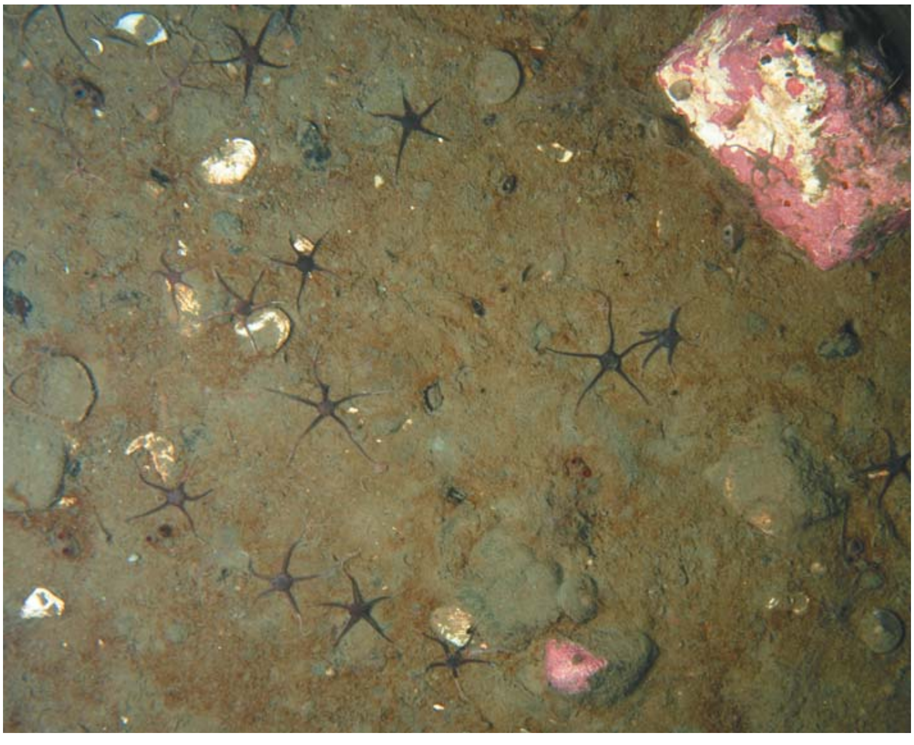
In spring 2009 we used the eddy correlation technique to quantify the in situ nocturnal and diurnal O_2 exchange rate across 3 typical benthic substrates at shallow depths along the coast of the Godthaabsfjord, SW Greenland: (1) In soft sediments the O_2 exchange in darkness as derived by eddy correlation on average amounted to 2.0 ± 0.2 mmol m^{-2} h^{-1}. Encompassing the activity of mega-fauna and a large footprint of the natural variability the rate exceeded the O_2 exchange as quantified by traditional core incubations and microprofile measurements by 24 % and 80 %, respectively (Fig. 11). (2) Measurements across shells, stones and gravel revealed a surprisingly high activity with average O_2 exchange rates comparable with those of sedimentary areas. Carbon fixed by benthic diatoms and coralline red-algae was efficiently recycled by microbes and grazed intensively by an abundant epifauna dominated by sea-urchins, which alone were estimated to account for 19-35 % of total oxygen consumption, and assumed to fuel the microbial community through an intense faeces production. (3) A vertical cliff was covered with sea-cucumbers grazing on phytoplankton and these areas also reflected high O_2 consumption rates (1.2 ± 0.2 mmol m^{-2} h^{-1}). The O_2 exchange derived from the eddy correlation approach exhibited a high short-term variability reflecting the interplay of several dynamic controls, most importantly short-term variations in the local hydrodynamics. Overall, measurements across hard bottom substrates revealed a highly active benthic community efficiently mediating carbon turn-over rates comparable to that of soft bottom sediments.

1.10 Functional importance of brittlestars in NE Greenland

Brittle stars (Echinodermata; Ophiuroidea) are known to form dense assemblages in several marine habitats and in the deep sea around the world (Tyler 1980, Smith 1983, Brey & Clarke 1993, Quiroga & Sellanes 2009). Despite their widespread occurrence in coastal areas in the Arctic (Piepenburg 2000) few studies have focused on the ecology of brittle stars and, therefore, little is known about the significance of brittlestars in ecosystem carbon cycling.

Fig. 12. The underwater camera system used for photographic surveys of epibenthic fauna (papers 1, 6, 7).

Fig. 13. UW image of the sea bed at 30 m depth in Young Sound, NE Greenland. We found distinct patterns in the distribution of brittle stars. *Ophiocten sericeum* was the most abundant species (paper 7).



We measured individual oxygen consumption of the three dominant species in Young Sound, NE Greenland, in incubation chambers using a fiber-optic oxygen sensor enabling continuous measurements. A general relation between individual disc diameter and oxygen consumption was established, which facilitated the estimation of community respiration and carbon demand from sea floor images.

We found distinct patterns in the density and species distribution of brittlestars from sea floor photos spanning a depth range from 20 to 310 m in Young Sound and the adjacent Greenland Sea. The maximum abundance was up to several hundred individuals per square meter. Brittle stars were estimated to add 1-25 % (average = 8 %) to previous estimates of benthic mineralisation during the high-Arctic summer. Overall, our results demonstrate that brittle stars, despite very low individual energy requirements, contribute significantly to marine carbon cycling in Young Sound as well as in the shelf areas off Northeast Greenland.

1.11 Variations in macrobenthic community structure along a fjord-ocean gradient

So far I have primarily focused on growth, production and carbon demand of macrobenthos, and the identification of key environmental drivers in Greenland. In some of my research I have concentrated on the existing climate gradient in Greenland from the sub-Arctic to the high-Arctic. Along this gradient, bivalves and sea urchins show large differences in annual growth rates. (paper 2, Blicher et al. 2007). However, at present, no information is available on how macrobenthic biomass, species composition and diversity vary along this climatic gradient. The need for baseline information on the level of communities is increasing. Climate change, oil exploration and commercial fishery are all factors expected to affect species composition and diversity of Greenland benthos in the coming decades, with potential consequences for the functional role of benthic communities.

This study was the first to contribute to baseline information on benthic diversity along the climatic gradient along the West Greenland coast. Additional cruises were conducted in 2008 and 2009 covering the coastal zone from approximately 66 to 77°N. In 2010, another benthic cruise will cover the southernmost part of the West coast (60-66°N).

We explored patterns of macrobenthic diversity, species composition, abundance and biomass at nine stations along a transect spanning from the inner Godthaabsfjord influenced by glaciers, across the shallow Fyllas Bank and out to the slope of the continental shelf at approximately 1,000 m depth (distance >150 km). The sampled stations were very different in terms of environmental variables, resulting in large differences in species composition primarily related to differences in depth, silt–clay fraction and chl *a* content of the sediment. Habitat differences also reduced species spatial ranges and the majority of species were found at only one (49 %) or two (20 %). Species richness and diversity were lowest in sites exposed to sediment disturbance: near the glaciers in the inner fjord (physical disturbance by mineral sedimentation) and at selected stations on the shelf (bioturbation by burrowing sand eel).

The dominant species in the area were similar to reports from other fjords in Greenland and in Svalbard (Schmid & Piepenburg 1993, Sejr et al. 2000, Hop et al. 2002, Wlodarska-Kowalczuk & Pearson 2004). However, in combination with one other available study from the West Greenland shelf (Anonymous 1978) this study indicated that species richness was in the upper range of values reported from the Norwegian and Canadian shelf (Ellingsen & Gray 2002, Cusson et al. 2007). However, additional studies are needed before the benthic diversity of the coastal areas in West Greenland can be properly compared to other regions.

2 Conclusions and perspectives

My co-authors and I conducted benthic research in a variety of coastal habitats ranging in depth from the shallowest sub-tidal zone to 1000 m depth, in a geographical range from 64°N to 77°N in East and West Greenland. The temporal dynamics of benthos were studied on scales ranging from hours to years on several levels of biological organisation.

Several distinct habitats existed within the Godthaabsfjord system in terms of sea bed characteristics, ranging from dominance of rock, stones and shells (papers 1, 6) to soft sediments consisting of silt and clay near glaciers and rivers (papers 5, 8). These differences in physical characteristics, together with variations in food availability, strongly contributed to local differences in benthic species composition and a high overall diversity. Further studies are needed to test the indications of particularly high species diversity in West Greenland compared to other Arctic regions.

Regarding the functional role of shallow macrobenthic communities our estimates of carbon demand combined with the few other studies conducted in the Arctic indicate that the amount of carbon channelled through the macrobenthic community corresponds to *c.* 20 % of the annual pelagic primary production (paper 1). Even though it is clear that benthic primary producers, advection and inputs from land may contribute significantly to the ecosystem carbon budget and to the food availability in coastal areas (Rysgaard & Nielsen 2006), the pelagic primary production is expected to be a reliable proxy for the overall productivity and food availability in an area. Hence, the spatial differences in productivity seem to be traceable to the benthic environment, indicating a strong and relatively stable trophic coupling despite geographical variations in physical characteristics. In any case, the benthic fauna in coastal areas is suggested to be important for the total benthic carbon turnover, potentially adding up to >35 % to the microbial mineralisation (papers 6, 7). Only a few nonspecific attempts have been made to quantify the functional coupling of macrobenthos to higher trophic levels in the Arctic (Sejr et al. 2002, Nilsen et al. 2006). The results for a wintering habitat for bottom-foraging eiders indicate that the interplay between predator and prey can be strong and central for understanding the dynamics of both (paper 5), and although the case study may not be representative on a larger scale, it clearly illustrates the potential importance of supplementing research focusing on specific ecological compartments with cross-disciplinary ecosystem-oriented approaches.

With respect to individual growth patterns we found the growth rate of bivalves and sea urchins in Greenland to be relatively slow compared to other areas in the North Atlantic (paper 1), however annual growth rates were higher at shallow depths (paper 1) and in areas or years with relatively little seasonal sea ice cover (paper 2). On the community level, differences in annual carbon demand of macrobenthos reflected pelagic primary production (paper 1). This suggested food availability to be a key driver of benthic activity. On a seasonal scale, variations in mass growth (and RNA:DNA) of scallops was strongly related to the availability of food (papers 3, 4), supporting the indications of a causal relationship in previous studies. Moreover, scallops had highest growth rates at low temperature, indicating that they were not able to compensate for the elevated metabolic cost of maintenance at higher temperature through increased energy assimilation. Hence, the apparent effect of food availability on the benthic activity was visible on several temporal and spatial scales, and on biological levels ranging from cell to community, supporting a general hypothesis of food limitation of Arctic macrobenthos.

From a macro-ecological point of view, and in the context of expected climate change in the Arctic, there is an apparent lack of knowledge in terms of biogeography (and the factors determining species distributions), long-term and large-scale dynamics in species diversity, biomass, production, carbon demand of benthic communities and variations in their functional role. The recently initiated ecological monitoring programmes in SW and NE Greenland will provide the reference data and long time-series needed to better understand the long-term dynamics of the marine ecosystem in a sub- and high-Arctic area (www.g-e-m.dk). However, Greenland presents a unique opportunity to study changes in coastal ecosystems along a climate gradient from the sub-Arctic to the high-Arctic. The existing geographical gradient may contain important information on how and why ecosystems in the Arctic will be affected by future climate change. Regarding macrobenthos, a number of activities are ongoing, aimed at providing a baseline description of community structure at depths <200 m along the entire west coast of Greenland spanning from the sub- to high-Arctic. However, many aspects of the general ecological structure and ecosystem function in high-Arctic vs. sub-Arctic habitats remain unknown. For example, suggestions have been made of a weakened pelagic-benthic coupling in the Northern Bering Sea, apparently in response to a recent warming and reduction in seasonal sea ice cover enabling pelagic grazers and predators to consume a

Fig. 14. Macrobenthic sampling in Baffin Bay, NW Greenland. Photo: Paul Batty.

larger fraction of the new production (Grebmeier et al. 2006b). Understanding such dynamics in ecosystem structure and function is fundamental in order to comprehend the dynamics on higher trophic levels (i.e. fish, birds, whales), which are of direct importance to man and society. Therefore, I am participating in ecological studies of deeper areas (>200 m) in Greenland, which are important habitats for several commercially important species such as snow crab, Greenland halibut and shrimp. These investigations will begin in 2011 at 70 to 72°N off West Greenland. However, for studying examples of the direct coupling between climate and biological structure, other habitats might be suitable. The tidal zone in Greenland is virtually unstudied, but I conducted preliminary investigations in the Nuuk area, which indicate that this habitat is characterized by only a few, but very abundant, invertebrate and macro-algae species. The tidal zone is expected to be directly affected by future climate changes (sea ice, air/ocean temperature, fresh water run-off, pH), and due to the ease of access, we will use it for conducting case studies about the coupling between climate and community structure as well as for studying the relative importance of physical and biological drivers of change.

Thus, despite intense marine ecological research in Greenland in recent years, and in the near future, we are still in the very early phase of establishing baseline data of the existing structure and function of the marine ecosystem off Greenland in general, and the benthic compartment in particular. In a climate change context such baseline knowledge is necessary for being able to document and understand potential ecological changes in the future.

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Paper I

HIGH CARBON DEMAND OF DOMINANT MACROZOOBENTHIC SPECIES INDICATES THEIR CENTRAL ROLE IN ECOSYSTEM CARBON FLOW IN A SUB-ARCTIC FJORD

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High carbon demand of dominant macrozoobenthic species indicates their central role in ecosystem carbon flow in a sub-Arctic fjord

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ABSTRACT: The sea urchin *Strongylocentrotus droebachiensis* and the scallop *Chlamys islandica* dominate the shallow macrobenthic community in Kobbefjord, southwest Greenland (64° 09′ N, 51° 36′ W). Densities were estimated from seafloor photographs along 3 depth transects (0 to 120 m). Annually formed growth bands in the interambulacral plates of *S. droebachiensis* and in the ligament of *C. islandica* were used to establish growth functions. Growth data combined with size frequencies, size–mass relationships and fjord bathymetry were used to estimate annual production and carbon demand of the 2 species in order to assess their ecological importance. Distributions of the 2 species were strongly related to depth and partially separated. Averaged over all depths, the densities were estimated at 4.9 ind. m^{-2} (range: 0 to 38 ind. m^{-2}) and 5.6 ind. m^{-2} (range: 0 to 57 ind. m^{-2}) for *S. droebachiensis* and *C. islandica*, respectively. Maximum ages of *S. droebachiensis* and *C. islandica* were estimated at 24 and 39 yr, respectively. Somatic growth of both species was relatively slow, and their reproductive output constituted the bulk (62 to 73 %) of their total annual production. Mean annual production in the fjord was estimated at 3.2 g ash-free dry weight (AFDW) m^{-2} for *S. droebachiensis* and 2.5 g AFDW m^{-2} for *C. islandica*. The total annual carbon demand of the 2 species was estimated at 30.6 g C m^{-2}, corresponding to 21–45 % of annual pelagic primary production in this area. In conclusion, *S. droebachiensis* and *C. islandica* play important roles in carbon cycling of Kobbefjord and can be regarded as central species of the shallow benthic community. A comparison with literature estimates of annual macrozoobenthic carbon demand in Arctic and sub-Arctic habitats revealed that the macrozoobenthic carbon demand in Kobbefjord is relatively high and that annual carbon requirements of macrozoobenthos in the Arctic seem to reflect the level of pelagic primary production.

KEY WORDS: Macrobenthos · *Strongylocentrotus droebachiensis* · *Chlamys islandica* · Production · Carbon demand · Kobbefjord · Greenland · Climate

INTRODUCTION

Of all oceans the Arctic Ocean contains the largest shelves (<50 to 300 m), which make up more than ~50 % of the Arctic Ocean area and ~20 % of all shallow continental shelves in the world (Menard & Smith 1966). Thus, benthic communities in the Arctic have traditionally been considered important for overall ecosystem carbon cycling, but there are still only a few estimates of the production and carbon requirements of macrobenthos (Grebmeier et al. 1989, Rysgaard & Nielsen 2006), and several studies of Arctic macrobenthos have considered biomass as a proxy for production and carbon demand (e.g. Grebmeier et al. 2006a). However, this interpretation is supported by the fact that macrobenthic biomass in parts of the Arctic to some degree reflects the spatial variation in primary production in the overlying water column or the amount of sediment chlorophyll (Grebmeier et al. 2006a), which, in combination with physiological and theoretical studies (e.g. Clarke 1988, Clarke & Fraser 2004, Sejr et al. 2004), suggests that the activity of mac-

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robenthic communities in polar areas is primarily limited by food availability and to a lesser extent by low temperature. The relation between macrobenthic carbon demand and standing stock is not necessarily straightforward, however. It is influenced by species composition, age structure of populations, growth rate, reproductive output and rate of metabolism and, indirectly, by temperature, habitat structure and disturbance level. Estimates of macrobenthic production and carbon demand in the Arctic are therefore essential for at least 2 reasons. (1) They generate baseline studies that describe population dynamics and quantify the role of macrobenthos in marine carbon cycling under the present environmental and climatic conditions. This is important for both the existing and future understanding of ecological structures in Arctic marine ecosystems. (2) They allow evaluation of the importance of different environmental parameters, biotic as well as abiotic, for benthic production in polar areas. Both perspectives are important in the light of future global warming, which is predicted to be particularly intense in the Arctic (e.g. ACIA 2005). Future atmospheric warming will reduce the sea ice cover and consequently increase the amount of light reaching the water column. Increased irradiation has the potential to positively affect primary production in large areas, especially in the high-Arctic (Rysgaard et al. 1999, Wassmann et al. 2006, Arrigo et al. 2008) and thus potentially extending the growth season for benthic secondary producers. A study of individual growth of the sea urchin *Strongylocentrotus droebachiensis* along an existing climate gradient in Greenland revealed a positive correlation between individual growth performance and the length of the sea ice–free period during summer. This trend in secondary production was suggested to be a result of geographical differences in marine primary production and, hence, food level, which might correspond to the temporal development in a global warming scenario (Blicher et al. 2007). Still, a more detailed understanding of the relationship between primary production and benthic secondary production at the community level is necessary, and may have important implications for predictions of future ecosystem structure in the large shallow areas in the Arctic.

Kobbefjord, one of the numerous fjords in Southwest Greenland, is a part of the Godthåbsfjord system, which has been chosen as a study area in a recently initiated long-term climate-monitoring program focusing on ecosystem structures and dynamics in the sub-Arctic (www.nuuk-basic.dk). Dredge collections conducted in an earlier pilot study in Kobbefjord indicated that the sea urchin *Strongylocentrotus droebachiensis* (O. F. Müller) and the scallop *Chlamys islandica* (O. F. Müller) dominate the shallow macrozoobenthic community in terms of biomass (M. E. Blicher unpubl. data). The objective of the present study was to quantify the density and biomass of these 2 epifaunal species and estimate their annual production and carbon demand in Kobbefjord, and compare it to other estimates of macrozoobenthic carbon demand in the Arctic region. Annual pelagic primary production in Kobbefjord is within the range of 75 to 160 g C yr^{-1} (Smidt 1979, Mikkelsen et al. 2008a,b, Rysgaard et al. 2008), which is high compared to in other regions of Greenland and in the Arctic in general (Rysgaard et al. 1999). Production and carbon demand of macrozoobenthos in Kobbefjord was expected to reflect the pattern in primary production. We therefore hypothesized that carbon demand of the dominant macrozoobenthic species in Kobbefjord is high compared to other estimates of macrozoobenthic carbon demand in the Arctic region.

MATERIALS AND METHODS

The study was conducted in 2007 and 2008 in the outer region of Kobbefjord, which is a part of the Godthåbsfjord system in sub-Arctic Southwest Greenland (Fig. 1). Kobbefjord is ~17 km long and 0.8 to 2 km wide. The innermost part of the fjord is usually sea ice covered during winter, with extensive interannual variation. Sea surface temperature ranges from –1.5°C during winter to a maximum of ~8°C in late summer. The amount of chlorophyll *a* in the photic zone varies from very low concentrations in winter (<0.1 µg l^{-1}) to maximum values of up to 3–5 µg l^{-1} during blooms, which can occur in both spring and late summer (M. E. Blicher unpubl. data). The present study focuses on the fjord's outer region of ~16 km^2 (Fig. 1b).

Species density. A series of high-resolution digital photographs of the sea floor was obtained along 3 transects in depth intervals of 10 m each, between 0 and 120 m depth (Fig. 1b). Lasers were attached to the system to scale the images. A total of 288 digital photographs, each covering ~0.5 m^2 (~141 m^2 in total), was used to quantify the density of the sea urchin *Strongylocentrotus droebachiensis* and the scallop *Chlamys islandica*.

Collection and processing. *Strongylocentrotus droebachiensis* and *Chlamys islandica* were collected using a triangular dredge (mesh size: 1 × 1 cm) at 50 to 60 m depth in outer Kobbefjord. Sea urchins were also collected at 5 to 15 m depth and included in a biomass analysis. Specimens where frozen (–18°C) immediately after collection and kept frozen until analysis. Maximum diameter of sea urchins and shell height of scallops were measured to the nearest 0.1 mm using Vernier callipers, and wet weight (WW) was determined to the nearest 0.01 g. Specimens were carefully

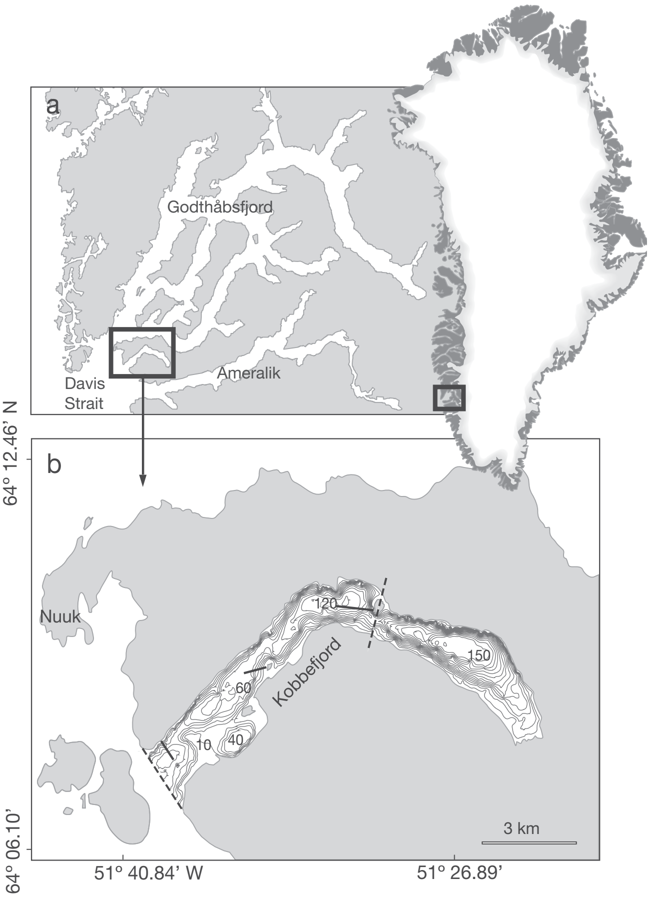

Fig. 1. (a) Location of the study area in Greenland. (b) Enlargement of Kobbefjord. The outer region, where we conducted the dredge collections and underwater photo transects, is bound by dashed lines; 10 m depth curves are shown (see 'Results')

dissected into gonads and somatic tissue to establish relations between biomass and size. Gonad and somatic dry weight (DW) and ash-free dry weight (AFDW), respectively, were determined by drying at 60°C for at least 24 h until constant weight, followed by ignition at 550°C in a muffle furnace for 12 h.

For *Strongylocentrotus droebachiensis* we fitted a power function to gonad mass-at-diameter data:

$$M_{g\,(Sd)} = aD_t^b \tag{1}$$

where $M_{g\,(Sd)}$ is the individual gonad mass (g AFDW) of *S. droebachiensis* at diameter D_t (mm), and a and b are coefficients in the regression. We used the sigmoidal Gompertz function to describe the relationship between gonad mass $M_{g\,(Ci)}$ and shell height SH_t (mm) of *Chlamys islandica*:

$$M_{g\,(Ci)} = M_{g\,(Ci)\infty} e^{-\exp[-K(SH_t - SH*)]} \tag{2}$$

where $M_{g\,(Ci)\infty}$ is the maximum individual gonad mass (g AFDW), K defines the slope and $SH*$ is the shell height (mm) at curve inflexion. As for all non-linear regressions in the present study, we used the iterative Levenberg-Marquardt algorithm (Marquardt 1963).

Age. We determined individual age using separate methods for the 2 species. For *Strongylocentrotus droebachiensis* we used a combination of the methods described by Jensen (1969), Pearse & Pearse (1975) and Brey (1991). Individuals were carefully cut along the ambitus with a scalpel, after which the intestine, gonads and Aristotle's lantern were removed. We bleached the echinoid skeleton in a 5% sodium hypochlorite (NaOCl) solution for 5 to 10 min to remove organic tissue. The skeleton was then dried at 60°C for 12 h and charred in a muffle furnace at 300°C for 5 to 10 min. We carefully polished the interambulacral plates with carborundum paper (800 grit) on the outside of the plates after which they were placed in xylene. In this way, growth zones in the skeletal plates, consisting of alternating translucent winter zones and opaque summer growth zones were made visible. Using a dissecting microscope we counted growth zones in the oldest interambulacral plates closest to the mouth (Nos. 1 to 7), which contain the first year's growth zone and supplemented it with counts in younger plates as described by Blicher et al. (2007).

The age of *Chlamys islandica* was determined by the method described by Johannessen (1973). We carefully removed the dark elastic part of the shell ligament, exposing the underlying hard part, where growth zones, consisting of alternating dark winter lines and pale summer growth increments, became visible. We estimated age by counting the narrow winter growth lines.

Growth patterns. Growth functions were fitted to size-at-age data. To describe the growth of *Strongylocentrotus droebachiensis* collected at 50 to 60 m in Kobbefjord, we chose a flexible Richards' growth model (Richards 1959, Sugden et al. 1981), which has been shown to describe growth of this species particularly well (Blicher et al. 2007):

$$D_t = D_\infty \left[1 - (1-m) \exp\left\{ \frac{-(t - t*)}{Tm^{m/(1-m)}} \right\} \right]^{1/(1-m)} \tag{3}$$

where D_∞ is the asymptotic diameter (mm), t is individual age (yr), $t*$ is an age-at-growth inflexion, T (yr) is the time needed to grow from zero to D_∞ at the maximum growth rate, and m is a shape factor for Richards' curves. In the present study we also included an estimate of growth of *S. droebachiensis* collected at 5 to 15 m in Kobbefjord, which has been published in Blicher et al. (2007): $D_t = 64.35[1 + 0.975\exp(-0.185(t - 10.989))]^{-1.025}$. This was done to compare growth at different depths in Kobbefjord and to include this factor in the further analyses.

Growth of *Chlamys islandica* was described by the specialized von Bertalanffy growth model:

$$SH_t = SH_\infty(1 - e^{-K(t-t_0)}) \tag{4}$$

where SH_t is shell height (mm) at age t (yr), $SH*$ is the asymptotic shell height (mm), t_0 is the age at which shell height would be zero and K is a growth coefficient (yr^{-1}).

Production. We estimated the annual somatic production of average individuals, $\overline{P}_{\mathrm{s(ind)}}$, in the 2 populations by the mass-specific growth rate method (Brey 2001). This method incorporates: (1) the size frequency of a population, (2) the growth function and (3) the size–mass relationship:

$$\overline{P}_{\mathrm{s(ind)}} = \sum_i F_i M_{\mathrm{s},i} G_i \tag{5}$$

where F_i is the fraction of size class i (2 mm intervals) in the population, $M_{\mathrm{s},i}$ is the somatic mass (g AFDW) of an average individual in size class i, and G_i is the mass-specific growth rate (yr^{-1}) of an average individual in size class i. $M_{\mathrm{s},i}G_i$ equals the absolute individual somatic mass growth rate of an individual in size class i, $P_{\mathrm{s(ind)},i}$ (g AFDW yr^{-1}). Thus, $\overline{P}_{\mathrm{s(ind)}}$ is weighted by the frequency of different size classes in the populations. The expression of G_i varies according to growth model used. For *Strongylocentrotus droebachiensis* in the present study the expression is:

$$G_{i(Sd)} = -\frac{b\{D_i - D_i^{\,m} D_\infty^{\,(1-m)}\}}{D_i(1-m)Tm^{m/(1-m)}} \tag{6}$$

where b is the exponent of the size–mass relationship. T, m and D_∞ are parameters from the growth model (Eq. 3), and D_i is the mean diameter of size class i. When using the specialized von Bertalanffy model, as in the case of *Chlamys islandica* in the present study, the expression of the weight-specific growth rate is:

$$G_{i(Ci)} = bK\{(SH_\infty/SH_i) - 1\} \tag{7}$$

where b is the exponent of the size-mass relationship, K and SH_∞ are parameters from the growth model (Eq. 4), and SH_i is the mean shell height in size class i.

Since both species involved in the present study have discrete reproductive cycles and spawn only once per year (Sundet & Vahl 1981, Oganesyan 1998), we estimated the annual gonad production by monitoring the gonad mass of sea urchins and scallops in Kobbefjord in the spring, late summer and winter, i.e. in May and August 2007, and in February 2008. The reproductive output of an average individual of a population, $\overline{P}_{\mathrm{s(ind)}}$, was calculated on the basis of the difference between the observed minimum and maximum individual gonad mass in combination with the size frequency of the population:

$$\overline{P}_{\mathrm{g(ind)}} = \sum_i F_i P_{\mathrm{g(ind)},i} \tag{8}$$

where $P_{\mathrm{g(ind)},i}$ is the reproductive output (g AFDW) of an average individual in size class i estimated from gonad mass-at-size regressions.

At population level, the average annual somatic production, $P_{\mathrm{s(pop)}}$, and gonad production, $P_{\mathrm{g(pop)}}$, per square meter in each 10 m depth interval were calculated on the basis of Eqs. (5) & (8) and the densities of the 2 species. In an attempt to extrapolate these calculations to fjord scale, a bathymetry model of Kobbefjord, based on multi-beam data from the Danish Navy Hydrographic Survey Group, was created using triangular interpolations of the data with a contouring and three-dimensional surface mapping program (Surfer 8). From this model, we estimated the seafloor area of the relevant depth intervals. By multiplying estimates of seafloor area with the average annual production in specific depth intervals, we estimated total production, $P_{\mathrm{(tot)}}$, in the outer fjord region.

Carbon demand calculations. Organic carbon contents of bivalve tissue were determined on 6 replicate individuals. Samples were dried and homogenized and analysed on an elemental analyser (ANCA-GSL, SerCon). For *Strongylocentrotus droebachiensis* AFDW was converted to organic carbon (C) by the following factor (Blicher et al. 2007): C = 0.5 × *AFDW*. Production-to-consumption ratios (*P*:C) of marine invertebrates can vary considerably, and the number of published estimates are limited. For the 2 species involved in the present study, we used the following ratios: *Strongylocentrotus droebachiensis*: *P*/C = 0.1 (Miller & Mann 1973); *Chlamys islandica*: *P*/C = 0.075 (Vahl 1981).

RESULTS

Fjord bathymetry

The available depth data for Kobbefjord allowed us to create a bathymetry model (Fig. 1b, data summarised in Tables 1 & 2). Kobbefjord is a sill fjord, and the outer region (Fig. 1b) has an average depth of ~44 m, with a basin extending down to ~120 m depth. The bathymetry model was used for the calculation of sea urchin and scallop production at a fjord scale.

Densities and size frequencies

As indicated by dredge collections, photographs of the seafloor revealed that *Strongylocentrotus droebachiensis* and *Chlamys islandica* clearly dominated the macrobenthic community <60 m depth (Fig. 2a,b).

Table 1. *Chlamys islandica.* Mean (±SE) somatic (P_s) and gonad (P_g) production on a population level in Kobbefjord. $P_{s(pop)}$ and $P_{g(pop)}$ are the area-specific production values. $P_{s(tot)}$ and $P_{g(tot)}$ refer to the population production values in the given depth intervals. Total production was estimated at 40.5 t ash-free dry weight (AFDW) yr^{-1}

Depth (m)	Density (Ind. m^{-2})	Biomass (g AFDW m^{-2})	$P_{s(pop)}$ (g AFDW yr^{-1} m^{-2})	$P_{g(pop)}$ (g AFDW yr^{-1} m^{-2})	Area (m^2)	$P_{s(tot)}$ (g AFDW yr^{-1})	$P_{g(tot)}$ (g AFDW yr^{-1})
0–10	0	0	0	0	2 712 916	0	0
10–20	0	0	0	0	1 752 558	0	0
20–30	0.32 (0.16)	0.68 (0.34)	0.04 (0.02)	0.11 (0.05)	1 414 558	55 835	149 065
30–40	5.03 (0.90)	10.58 (1.89)	0.61 (0.11)	1.64 (0.29)	1 544 902	949 088	2 533 824
40–50	24.45 (2.34)	51.40 (4.91)	2.98 (0.29)	7.97 (0.76)	1 906 172	5 689 642	15 189 900
50–60	16.46 (2.03)	34.61 (4.28)	2.01 (0.25)	5.36 (0.66)	1 940 695	3 900 709	10 413 902
60–70	1.36 (0.28)	2.87 (0.59)	0.17 (0.03)	0.44 (0.09)	2 151 090	358 305	956 584
70–80	0.79 (0.27)	1.66 (0.57)	0.10 (0.03)	0.26 (0.09)	805 514	77 739	207 544
80–90	0	0	0	0	653 348	0	0
90–100	0	0	0	0	506 591	0	0
100–110	0	0	0	0	737 266	0	0
110–120	0	0	0	0	149 232	0	0
Sum					16 275 214	11 031 319	29 450 819

Table 2. *Strongylocentrotus droebachiensis.* Mean (±SE) somatic (P_s) and gonad (P_g) production on a population level in Kobbefjord. $P_{s(pop)}$ and $P_{g(pop)}$ are the area-specific production values. $P_{s(tot)}$ and $P_{g(tot)}$ refer to the population production values in the given depth intervals. Total production was estimated at 52 t AFDW yr^{-1}

Depth (m)	Density (Ind. m^{-2})	Biomass (g AFDW m^{-2})	$P_{s(pop)}$ (g AFDW yr^{-1} m^{-2})	$P_{g(pop)}$ (g AFDW yr^{-1} m^{-2})	Area (m^2)	$P_{s(tot)}$ (g AFDW yr^{-1})	$P_{g(tot)}$ (g AFDW yr^{-1})
0–10	15.41 (1.30)	26.41 (2.24)	3.76 (0.32)	6.01 (0.51)	2 712 916	10 202 014	16 305 025
10–20	13.40 (1.85)	22.97 (3.17)	3.27 (0.45)	5.23 (0.72)	1 752 558	5 732 521	9 161 809
20–30	4.04 (1.12)	6.93 (1.92)	0.99 (0.27)	1.58 (0.44)	1 414 558	1 395 816	2 230 816
30–40	1.69 (0.38)	2.89 (0.66)	0.25 (0.06)	0.66 (0.15)	1 544 902	382 719	1 015 749
40–50	3.37 (0.65)	5.78 (1.11)	0.50 (0.10)	1.32 (0.25)	1 906 172	944 721	2 507 323
50–60	1.40 (0.38)	2.40 (0.66)	0.21 (0.06)	0.55 (0.15)	1 940 695	399 442	1 060 132
60–70	0.60 (0.24)	1.02 (0.42)	0.09 (0.04)	0.23 (0.12)	2 151 090	188 621	500 607
70–80	0	0	0	0	805 514	0	0
80–90	0	0	0	0	653 348	0	0
90–100	0	0	0	0	506 591	0	0
100–110	0	0	0	0	737 266	0	0
110–120	0	0	0	0	149 232	0	0
Sum					16 275 214	19 245 855	32 781 462

The images also showed that stones, rock, sand and shell gravel were the most abundant substrates at this depth interval and that soft sediment was not typical. The remaining macrobenthic community in this zone consisted primarily of epifaunal taxa such as barnacles, chitons, holothurians, sponges, bryozoans and ascidians (<10% WW), but also the bivalves *Clinocardium* sp., *Hiatella* sp. and *Astarte* spp. were caught sporadically when dredging (data not shown). The density of sea urchins and scallops decreased to zero in concurrence with a gradual change in structure of the sea bed from gravel and stones to soft mud from a depth of ~60 m down to ~120 m. Even though the epifaunal biomass clearly decreased at >60 m, burrows and surface tracks on the sediment surface still indicated macrofaunal activity (Fig. 2c). *S. droebachiensis* and *C. islandica* were, to a large extent, vertically separated in Kobbefjord. The density of sea urchins was highest at <20 m depth (ranging from 2 to 38 ind. m^{-2}), and scallop densities peaked between 30 and 60 m depth (ranging from 0 to 57 ind. m^{-2}). The weighted mean densities (with respect to sea floor area) across all depths were 4.9 ind. m^{-2} (n = 288, SE = 0.40) and 5.6 ind. m^{-2} (n = 288, SE = 0.57) for *S. droebachiensis* and *C. islandica*, respectively (Fig. 3). Mean biomass of *S. droebachiensis* and *C. islandica* at 0 to 120 m was estimated at 20.5 g AFDW m^{-2} (~29 g AFDW m^{-2} at 0 to 60 m), ranging from a minimum of zero at >80 m depth to a maximum

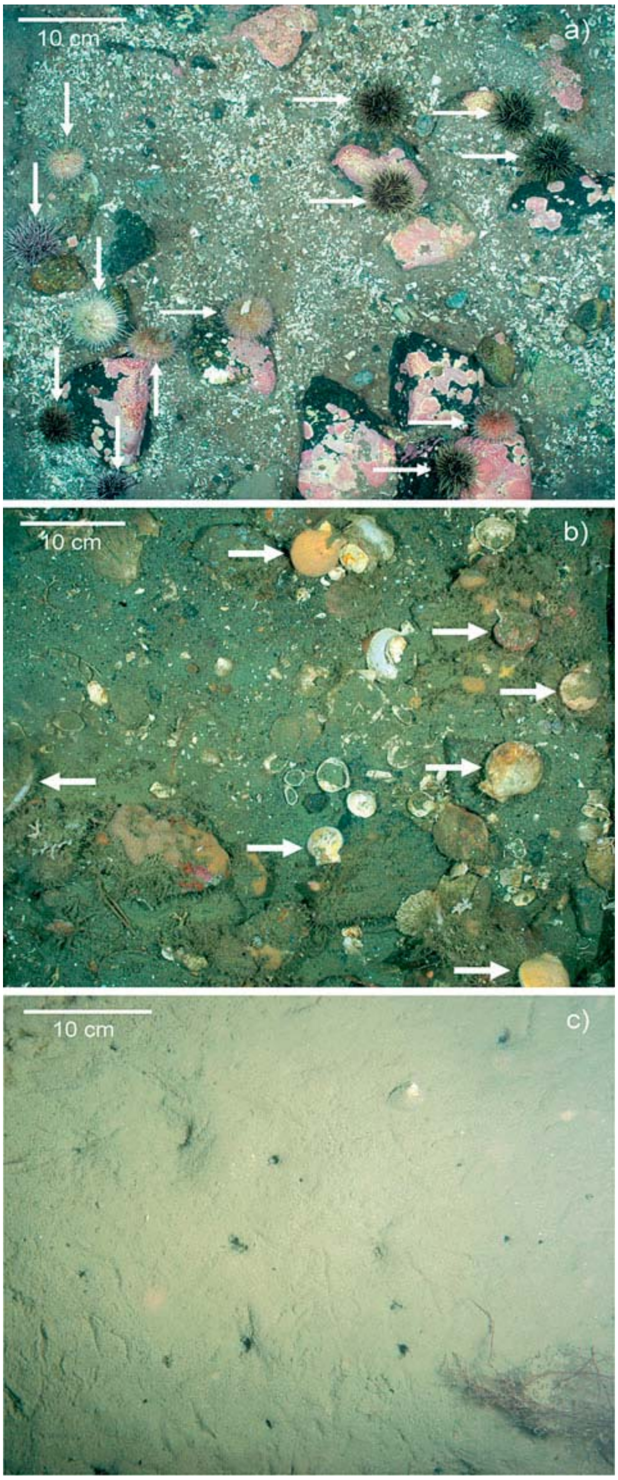

Fig. 2. Underwater photographs of the seafloor at different depths in Kobbefjord. (a) The 10 to 20 m stratum. Dominance of *Strongylocentrotus droebachiensis* indicated by white arrows. (b) The 50 to 60 m stratum. Dominance of *Chlamys islandica* indicated by white arrows. (c) The 80 to 90 m stratum. Soft sediment with burrows and surface tracks. Each photo can be regarded as representative of the given depth interval with respect to characteristic macrofaunal and seafloor structure

of 57.2 g AFDW m^{-2} at 40 to 50 m depth (Tables 1 & 2). The size frequencies, which resulted from a number of dredge collections at 5 to 15 m and 50 to 60 m depths through 2007 and 2008, are illustrated in Fig. 4. The size structure of *S. droebachiensis* was unimodal and dominated by individuals between 40 and 60 mm in diameter. The population of *C. islandica* also had a relatively high frequency of large specimens (55 to 75 mm), but not as distinctly so as sea urchins.

Growth patterns

Growth functions were fitted to size-at-age data for both species collected at 50 to 60 m depth in the outer Kobbefjord (Fig. 5): *Strongylocentrotus droebachiensis*: $D_t = 69.64[1 + 0.005\exp(-0.146(t - 5.558))]^{-200.275}$ ($n = 73$, $R^2 = 0.928$); *Chlamys islandica*: $SH_t = 79.54[1 - \exp(-0.139(t - 0.916))]$ ($n = 80$, $R^2 = 0.927$).

The size-at-age data and growth curve for sea urchins collected at shallower depths (5 to 15 m) in Kobbefjord (Blicher et al. 2007) are also illustrated in Fig. 5.

Individual biomass and production

For a sub-sample of *Chlamys islandica* collected in Kobbefjord in May and August 2007 and February 2008 a relation between somatic mass, M_s (g AFDW), and shell height, *SH* (mm), was established (*SH* ranging from 19.8 to 86.3 mm): $M_s = 7.328 \times 10^{-6}\, SH^{2.988}$ ($n = 134$, $R^2 = 0.96$).

For *Strongylocentrotus droebachiensis* we pooled the size–mass data for sea urchins from 7 different

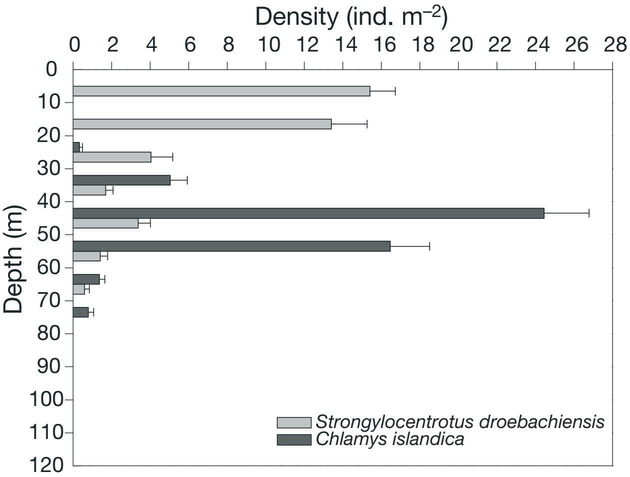

Fig. 3. *Chlamys islandica*, *Strongylocentrotus droebachiensis*. Average densities (ind. m^{-2}) and standard error in 10 m depth intervals in Kobbefjord

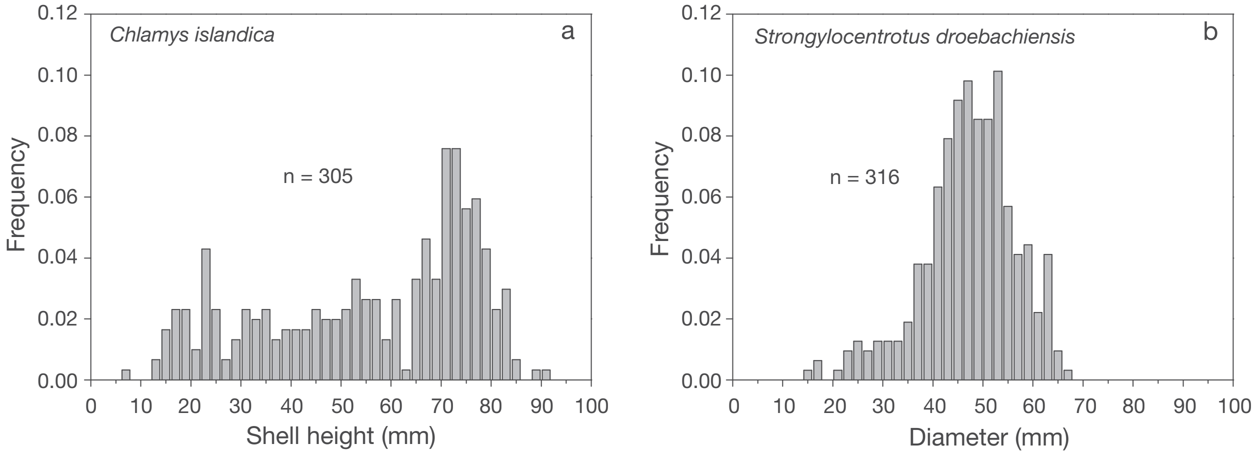

Fig. 4. (a) *Chlamys islandica* and (b) *Strongylocentrotus droebachiensis* size frequencies collected in 2007 and 2008 in Kobbefjord

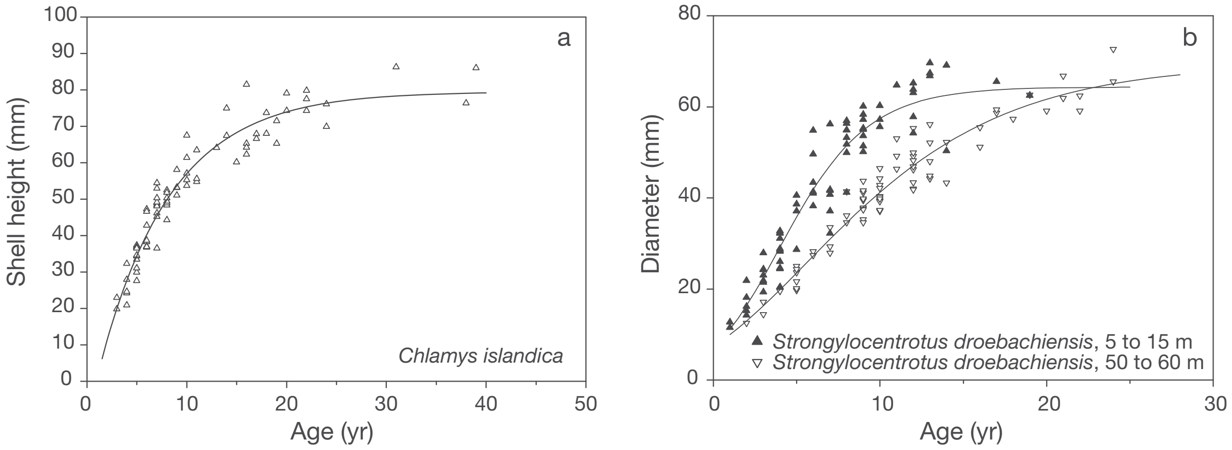

Fig. 5. *Chlamys islandica*, *Strongylocentrotus droebachiensis*. Growth curves fitted to size-at-age data for specimens collected in Kobbefjord. (a) *C. islandica* $SH_t = 79.54[1-\exp(-0.139(t-0.916))]$. (b) *S. droebachiensis* at 5 to 15 m: $Dt = 64.35[1 + 0.975\exp(-0.185(t-10.989))]^{-1.025}$; and at 50 to 60 m: $Dt = 69.64\,[1 + 0.005\exp(-0.146(t-5.558))]^{-200.275}$

Greenland populations (Blicher et al. 2007) to establish a relation between somatic mass, M_s (g AFDW), and diameter, D (mm), which can be considered to be general for this species: $M_s = 3.434 \times 10^{-5}\ D^{2.690}$ (n = 213, $R^2 = 0.95$).

For both species we observed minimum gonad mass in August and maximum in May (Fig. 6). Depth had no effect on the gonad mass of *Strongylocentrotus droebachiensis* at any of the sampling dates, which we tested by comparing gonad indices, GI_{Sd} = gonad DW/total WW (Students' *t*-test, 2-tailed, $p > 0.05$). Consequently, the data from the 2 sampling depths were pooled.

Based on size–mass relations and growth models for the 2 species, the annual individual somatic production, $P_{s(ind)}$, as a function of size was calculated (Fig. 7). For *Chlamys islandica* $P_{s(ind)}$ peaked at 0.22 g AFDW ind.$^{-1}$ yr^{-1} at a shell height of ~55 mm. Maximum $P_{s(ind)}$ for *Strongylocentrotus droebachiensis* was found at a diameter of ~45 mm, but differed slightly between depths. For specimens collected at 5 to 15 and 50 to 60 m, $P_{s(ind)}$ peaked at 0.30 and 0.17 g AFDW ind.$^{-1}$ yr^{-1}, respectively. The observed seasonal variations in gonad status were used to establish relations between size and reproductive output for *C. islandica* and *S. droebachiensis* as illustrated in Fig. 7. We considered the size frequencies (Fig. 4) to be representative for the 2 populations and estimated the average somatic production at 0.122 g AFDW ind.$^{-1}$ yr^{-1} for *C. islandica* and 0.243 and 0.147 g AFDW ind.$^{-1}$ yr^{-1} for *S. droebachiensis* at 5 to 15 and 50 to 60 m depth, respectively. Average individual gonad production was 0.326 g AFDW ind.$^{-1}$ yr^{-1} for *C. islandica* and 0.390 g AFDW ind.$^{-1}$ yr^{-1} for *S. droebachiensis*. In conclusion, reproduction represents a major part of the total annual production (62 to 73%) for the species involved in the present study.

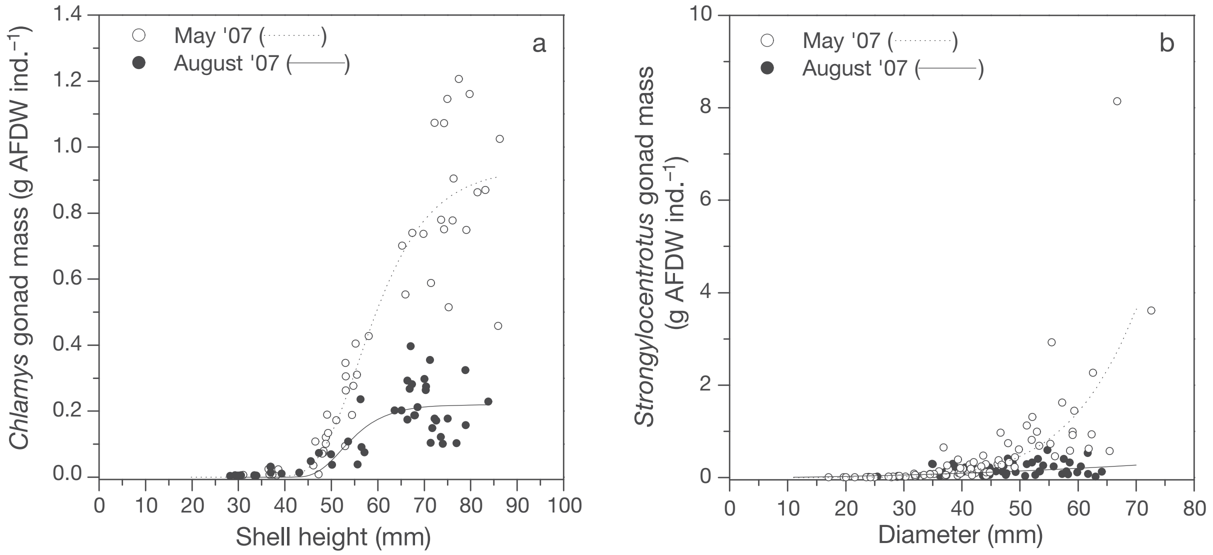

Fig. 6. *Chlamys islandica*, *Strongylocentrotus droebachiensis*. May and August were considered to be the periods of maximum and minimum gonad mass, respectively, for both species. (a) The Gompertz function was fitted to gonad mass-at-size data for *C. islandica*: $M_{g(Ci)}^{May} = 0.936e^{-\exp[-0.118(SHt-55.740)]}$ (n = 60, $R^2 = 0.87$) and $M_{g(Ci)}^{Aug}$ $0.220e^{-\exp[-0.118(SHt-52.090)]}$ (n = 44, $R^2 = 0.63$). (b) A power function was used for *S. droebachiensis*: $M_{g(Sd)}^{May}$ $1.631 \times 10^{-11} D_t^{6.151}$ (n = 82, $R^2 = 0.85$) and $M_{g(Sd)}^{Aug}$ $8.753 \times 10^{-5} D_t^{1.888}$ (n = 53, $R^2 = 0.17$)

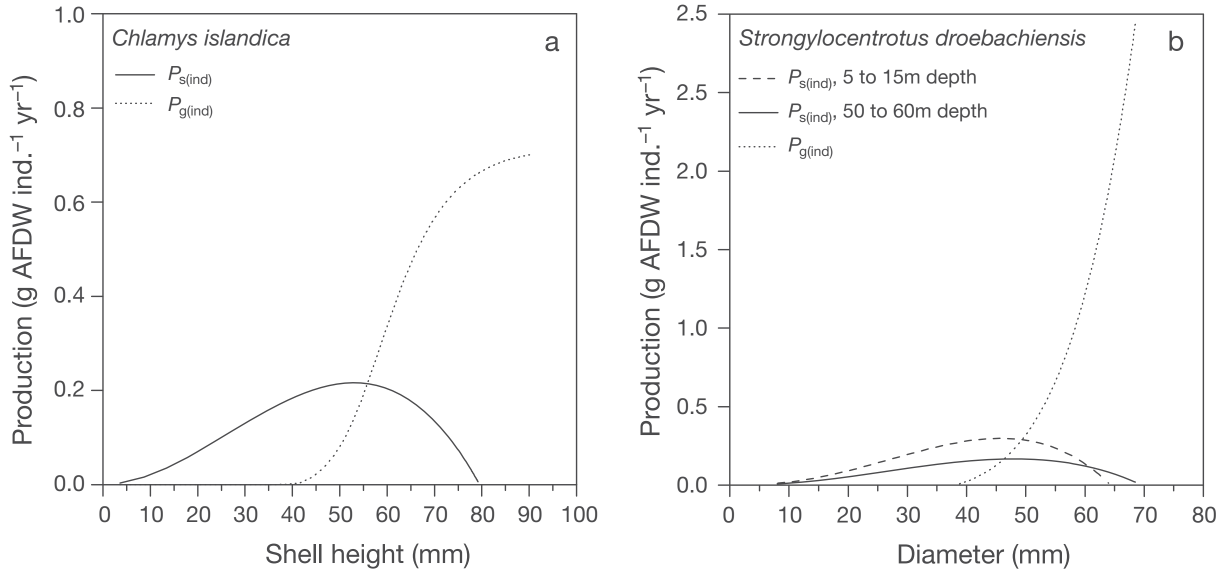

Fig. 7. Annual individual somatic production, $P_{s(ind)}$, and gonad output, $P_{g(ind)}$ (g AFDW) in relation to size of: (a) *Chlamys islandica* and (b) *Strongylocentrotus droebachiensis*in Kobbefjord

Population production and carbon demand

The species densities illustrated in Fig. 3 were considered to be representative of the outer region of Kobbefjord (defined in Fig. 1b), and these data were used to estimate the biomass and production of the 2 populations. The individual production rates for *Strongylocentrotus droebachiensis* collected at 5 to 15 m and 50 to 60 m depth were considered valid in the depth intervals from 0 to 30 m and from 30 to 70 m, respectively. Tables 1 & 2 summarise the calculation of the depth-specific population production, $P_{(pop)}$, of *Chlamys islandica* and *S. droebachiensis*, and total production, $P_{(tot)}$, in which the bathymetry of Kobbefjord is considered. For sea urchins, $P_{(pop)}$ peaked at 0 to 10 m depth at a value of 9.77 g AFDW m^{-2} yr^{-1}, while scallop production was highest at

40 to 50 m depth and reached a value of 10.95 g AFDW m^{-2} yr^{-1}. Averaged over the outer region of Kobbefjord, these values were 3.20 and 2.49 g AFDW m^{-2} yr^{-1} for sea urchins and scallops, respectively. The production-to-biomass ratios were 0.31 and 0.37 for the shallow- and deep-living sea urchins, respectively, and 0.21 for scallops. Total annual production of *C. islandica* and *S. droebachiensis* was estimated at 92.5 t AFDW in the outer region of Kobbefjord.

The average organic carbon content of scallop tissue was measured at 0.44 × AFDW (n = 6, SE = 0.01), which was used for the estimation of carbon demand. Using previously published estimates of production-to-consumption ratios (see 'Materials and methods'), the mean annual carbon demands for *Strongylocentrotus droebachiensis* and *Chlamys islandica* in outer Kobbefjord (~16 km^2) amounted to 16.0 and 14.6 g C m^{-2}, respectively, or ~260 t C for sea urchins and ~237 t C for scallops.

DISCUSSION

Abundance of *Strongylocentrotus droebachiensis* and *Chlamys islandica*

Photographs of the seafloor confirmed that *S. droebachiensis* and *C. islandica* were very abundant in Kobbefjord and that these 2 species clearly dominated the macrobenthic community at depths of <60 m, where the seabed primarily consisted of stones, rock, sand and shell gravel. The density of *S. droebachiensis* in Kobbefjord was high but not extreme in comparison to other observations in coastal areas of the North Atlantic (Himmelman et al. 1983, Hop et al. 2002, Gagnon et al. 2004). *S. droebachiensis* has been observed in high densities in many areas along the Greenland coast, but never in high numbers at >40 m depth, which agrees with our observations in Kobbefjord (Nielsen 1994). *C. islandica* was only found at >20 m depth. At these depths, densities were moderate compared to mean densities of 50 to 70 ind. m^{-2} in a scallop bed in northern Norway, but in the range of observations off Svalbard (Vahl 1981, Rubach & Sundet 1987). The depth distribution of *C. islandica* in Kobbefjord fit well with the general trend of peak abundance between 20 and 60 m depth observed off the West Greenland coast (Pedersen 1994). Both *C. islandica* and *S. droebachiensis* have been registered in numerous areas in fjords and along the Greenland coast and most often in gravelly or rocky habitats (Nielsen 1994, Pedersen 1994), as observed in Kobbefjord. Thus, the degree of dominance of these 2 species is probably not unique for the study area, but is dependent on habitat structure and hydrographic conditions. Although it is still uncertain which parameters are responsible for the distribution patterns and indeed also the vertical separation of the 2 species, it is expected that dominance by *C. islandica* and *S. droebachiensis* of macrobenthic communities is common in many coastal areas of West Greenland. The average densities in Kobbefjord are based on underwater photographs covering a total of 141 m^2 in this relatively small fjord. This area is large compared to that in similar studies using other methods for quantification of benthos (e.g. cayak corer, van veen grab, box corer). Moreover, the underwater images revealed clear depth-related patterns in the distribution of the 2 species. With the given growth patterns and age structures of the 2 populations, we do not expect either densities or size frequencies to vary considerably on a short-term scale. Thus, we find it reasonable to assume that the average densities can be regarded as representative for the outer fjord region.

Individual production

Somatic growth

In Kobbefjord, growth patterns of *Strongylocentrotus droebachiensis* differed between depths. Maximum $P_{s(ind)}$, which can be regarded as an expression of growth performance (Brey 2001) was ~40% lower for the deeper living (50 to 60 m) sea urchins compared to those living at depths of 5 to 15 m. Overall, growth of *S. droebachiensis* in Kobbefjord was slower than in temperate areas, but faster than in high-Arctic populations. The individual growth performances differed by a factor of 2 to 3 between Kobbefjord and the high-Arctic sites of Young Sound and Qaanaaq (Blicher et al. 2007, and references therein). *Chlamys islandica* collected at 50 to 60 m depth in Kobbefjord reached a shell height of 60 mm at an age of 11 yr, compared to 9–10 yr for Svalbard and other West Greenland populations. Populations in northern Norway, Canada and Iceland reached 60 mm shell height in 6 to 7 yr (Pedersen 1994 and references therein), and the population in Kobbefjord can thus be regarded as rather slow growing compared to other North Atlantic populations. Hence, we can consider 2 types of growth variation: (1) local variation, e.g. the depth-related differences in growth of sea urchins reported in the present study and (2) growth variation observed between regions. It is well documented that growth of both *S. droebachiensis* and *C. islandica* is highly affected by food quantity and quality (Wallace & Reinsnes 1985, Meidel & Scheibling 1999), which differ greatly on local, regional, as well as temporal scales. But temperature itself acting on physiological processes can also influence the potential of growth in ectotherms (e.g. Pörtner et al. 2005). During spring and summer, from May to September, when we expect the highest growth rates, the average temperatures at 5 and 50 m depth in the entrance to Kobbefjord were 3.8 and 1.9°C, respectively, in 2008, i.e. they reflected a difference of 1.9°C (M. E. Blicher unpubl. data). Obviously, temperature regimes also differ on a regional scale in the Arctic. For comparison, the average temperature in the high-Arctic fjord Young Sound is ~2°C at 5 m depth and –1.5°C at 50 m depth in the productive summer period (Rysgaard et al. 1999). Thus, the regional difference in temperature between the sub-Arctic and high-Arctic is within 2 to 4°C, depending on depth and season. Pectinids, as well as echinoids, have been subject to investigations concerning the effect of temperature on individual growth and metabolism. Studies of polar species generally agree that temperature alone cannot explain either the temporal or spatial variation in metabolism or growth (e.g. Vahl 1978, Brockington & Clarke 2001, Heilmayer et al. 2004, Sejr et al. 2004). These results in combination suggest that the difference in temperature regime between sub-Arctic and high-Arctic areas, and between different depths, may be of secondary importance for marine macrobenthic production. It seems more likely that the geographical variation in primary production, which can differ by a factor of 10 to 20 as in the case of Kobbefjord and Young Sound, affects food availability for secondary producers and to a large extent is responsible for regional differences in the growth of sea urchins, which has previously been reported (Blicher et al. 2007). Hence, the depth-related growth variation of *S. droebachiensis* reported in the present study is most likely related to differences in food quantity and quality, in this case, between the shallow photic zone (potential food: macroalgae, benthic microalgae and pelagic phytoplankton) and the aphotic zone (sedimentary phytoplankton and detritus, encrusting algae and drifting macroalgae), more than to differences in temperature. Growth of *C. islandica* in Kobbefjord was not compared across depths, but depth has been shown to affect the growth of this species due to its effect on food availability (Wallace & Reinsnes 1985) and other studies indicate local growth variations (Engelstoft 2000). Thus, the relatively slow growth of *C. islandica* reported here compared to the results of other West Greenland and North Atlantic studies may be a consequence of sampling depth and other local conditions as of regional differences as well.

In conclusion, the primary reasons for variations in the individual growth patterns of *Chlamys islandica* and *Strongylocentrotus droebachiensis* presumably lie in variations in the food availability on both local and regional scales.

Reproduction

High allocation of resources to reproductive tissue was characteristic of both *Chlamys islandica* and *Strongylocentrotus droebachiensis*, and reproduction accounted for more than half of total annual production. These results agree with other estimates indicating that polar macrobenthic populations might invest more energy in reproduction, relative to somatic growth, than populations from warmer climates (Brey et al. 1995, Blicher et al. 2007). This may either be an adaptation to life in the polar environment (e.g. low temperature, low food supply, low recruitment success), or a consequence of the age and size structure, which could be right-skewed in undisturbed and, often, slow-growing polar populations (e.g. Sejr et al. 2002, Heilmayer et al. 2003), and thus indirectly related to the polar environment. Regardless of the ecological reasons for the tendency towards high reproductive output relative to somatic production in some polar macrobenthic populations, our results highlight the importance of including reproduction in estimates of population production in any study concerned with ecosystem carbon flow.

Role of macrobenthos in Kobbefjord carbon cycling

The estimate of an annual carbon demand of ~498 t C for *Chlamys islandica* and *Strongylocentrotus droebachiensis*, which almost exclusively originated from <60 m depth, corresponds to 30.6 g C m^{-2} yr^{-1} (ranging from 0 to 73 g C m^{-2} yr^{-1} depending on depth) averaged across the entire outer fjord sea floor area (~16 km^2), or 21 to 45% of total pelagic primary production in the entire outer fjord region. The role of macroalgae and benthic microalgae as food for sea urchins might be considerable at the shallowest depths. Unfortunately, we do not know the amount of organic carbon produced by benthic primary producers, and thus we cannot include this in our comparison for the time being. No estimates of advection and inputs from land are available either. Still, we believe that the level of pelagic primary production generally gives an indication of the overall productivity and food availability in shallow systems.

Keeping in mind that our estimate of the macrobenthic carbon demand includes only 2 species, albeit the dominant ones, and that our knowledge of several potentially important contributors to the carbon source of the macrobenthic community is limited, it is evident that a complete quantification of the role of macrobenthic organisms in the Kobbefjord carbon cycling is difficult. However, it was evident from the sea floor photographs of the soft bottom at >60 m that infaunal activity may be considerable (Fig. 2c). In an attempt to roughly estimate the infaunal activity at these depths, we supplemented our estimate with the results from oxygen incubations of sediment cores (22 cm^2 each) sampled at a single station in the deepest part of Kobbefjord (Mikkelsen et al. 2008b). The difference between the total oxygen uptake and the diffusive oxygen uptake, which we considered as an approximate estimate of infaunal activity (excluding the largest fauna), was converted to an average carbon demand of 7.7 g C m^{-2} yr^{-1} (seasonally varying from 16.8 to 25.2 mg C m^{-2} d^{-1}), assuming a respiratory quotient of 0.8 (Hatcher 1989). Extrapolated to the seafloor area between 60 and 120 m depth, where soft sediment dominates, this amounts to an annual carbon demand of 39 t C or 2.4 g C m^{-2} averaged across the entire outer fjord region. Combined with the estimate for *Chlamys islandica* and *Strongylocentrotus droebachiensis*, the macrobenthic carbon demand in Kobbefjord adds up to 33 g C m^{-2} yr^{-1}. This estimate gives some important indications of a macrobenthic community that requires a considerable amount of carbon compared to the pelagic primary production of 75 to 160 g C yr^{-1} of the specific area. The proportion of the consumed organic matter that is excreted as either dissolved organic matter or faeces is in the range of 60 to 80% for *C. islandica* and *S. droebachiensis* (Miller & Mann 1973, Vahl 1981). This contribution of fractionated organic matter to the benthic environment may indeed stimulate bacterial mineralisation (Mamelona & Pelletier 2005). In addition, the high reproductive outputs show that large amounts of eggs are released into the water column. However, we cannot even guess at the proportion of eggs that survive and develop into actively feeding planktonic larvae, or at how many may reach metamorphosis. In any case, spawning seems to represent a potentially important coupling between the benthic and pelagic communities.

Given the dominance and high production of *Chlamys islandica* and *Strongylocentrotus droebachiensis* in the shallow (<60 m) and presumably most productive areas of Kobbefjord, it is reasonable to conclude that the 2 species in the present study, and the macrobenthic community as such, play an essential role in the carbon cycling of the fjord, and that a large fraction of the total macrobenthic carbon demand is included in our combined estimate. However, there are several basically unstudied parameters in the Kobbefjord ecosystem, such as pelagic secondary production, benthic primary production, sedimentation and bacterial mineralisation. These obvious gaps in our knowledge make it difficult to draw any conclusions on the exact routes of carbon through the Kobbefjord ecosystem.

Comparison of macrobenthic activities in the Arctic

Production of *Strongylocentrotus droebachiensis* in Kobbefjord was high compared to another estimate from the Arctic. The sea urchin population in Kobbefjord produced 15 times more biomass (AFDW m^{-2} yr^{-1}) than *S. droebachiensis* in the high-Arctic fjord Young Sound in a comparable depth range (0 to 60 m) (Blicher et al. 2007). The difference in individual growth rates was only a fraction of the overall difference in secondary production at the population level, which we demonstrated in the present study. The higher production of the Kobbefjord population was a consequence of faster individual growth rates, higher reproductive output and higher density of sea urchins.

The joint estimate of annual macrobenthic carbon demand in Kobbefjord was higher than total macrobenthic carbon requirements in most high-Arctic habitats, and was in a range comparable to that of the macrozoobenthic community in the highly productive part of the North Bering and Chukchi Seas (Table 3, Fig. 8). Even though the estimates in Table 3 have been calculated by different methods and not all temporal and spatial variations have been captured, the scale of differences in carbon demand between Arctic sites are remarkable given the fact that the compared communities are in similar depth and temperature ranges (see subsection of 'Individual production' for details on temperature). Hence, the existence of areas with low macrobenthic activities in the Arctic may not be related directly to temperature. Instead, the available data, although limited, support the expectation that variations in ecosystem primary production and thus food availability for secondary producers are reflected in macrozoobenthic production and carbon demand in the Arctic region. However, benthic primary producers (micro- and macroalgae), advection and inputs from land might contribute significantly to food availability in coastal areas independent of pelagic primary production (e.g. Rysgaard & Nielsen 2006). Hence, the apparent relation between macrozoobenthic carbon demand and pelagic primary production is only suggestive with respect to the underlying processes.

Given the reductions in seasonal sea ice cover in the Arctic in recent years (Serreze et al. 2007), one of the primary ecological effects is the changed light regime in the water column, leading to a longer productive season and higher level of primary production (Rysgaard et al. 1999, Wassmann et al. 2006, Arrigo et al. 2008). Hence, it has been argued that reductions in sea ice cover have the potential to reorganize benthic-oriented ecosystems towards a higher dominance of pelagic processes (Grebmeier et al. 2006b). However,

Table 3. Summary of available estimates of macrobenthic carbon demand and pelagic primary production from coastal and shelf areas in the Arctic and sub-Arctic. Superscript letters indicate the source of the estimate of primary production. No superscript indicates that estimates of both macrobenthic carbon demand and pelagic primary production are given in the same study. See illustration in Fig. 8

Location	Macrobenthic carbon demand (g C m^{-2} yr^{-1})	Depth (m)	Pelagic primary production (g C m^{-2} yr^{-1})	Source
North Bering & Chukcki Seas	51	19–53	250–300	Grebmeier et al. (1989)
Kobbefjord, West Greenland	33	0–120	75–160[b,i,j]	Present study
Bering Sea	25	6–161	150–175[e]	Klages et al. (2004)
Sørfjord, North Norway	17[a]	18–128	105–132[c]	Nilsen et al. (2006)
North Bering & Chukcki Seas	4–8	19–53	50	Grebmeier et al. (1989)
Kara Sea	1–16	10–68	30–50[h]	Klages et al. (2004)
NW Barents Sea	3.3	80–240	8–38[d,f]	Piepenburg et al. (1995)
Young Sound, NE Greenland	5.4	0–40	10[g]	Rysgaard & Nielsen (2006)
Young Sound, NE Greenland	3.5	40–160	10[g]	Rysgaard & Nielsen (2006)
Laptev Sea	3–10	0–50	7–25	Schmid et al. (2006)

[a]Values were calculated assuming 40.77 KJ g^{-1} C and a production-to-consumption ratio of 0.27 (Brey 2001), [b]Smidt (1979), [c]Eilertsen & Taasen (1984), [d]Wassmann & Slagstad (1991, 1993), [e]Walsh & Dieterle (1994), [f]Hegseth (1998), [g]Rysgaard et al. (1999), [h]Sakshaug (2004), [i]Mikkelsen et al. (2008a, b), [j]Rysgaard et al. (2008).

the combination of data listed in Table 3 and illustrated in Fig. 8 indicate that the carbon requirements of macrobenthic communities in shallow ecosystems in the Arctic have the potential of increasing in concurrence with the level of primary production despite variations in physical characteristics. Thus, macrobenthic production, and carbon demand, on the shelves and in coastal areas in the high-Arctic may be expected to increase as a consequence of future reductions in seasonal sea ice cover.

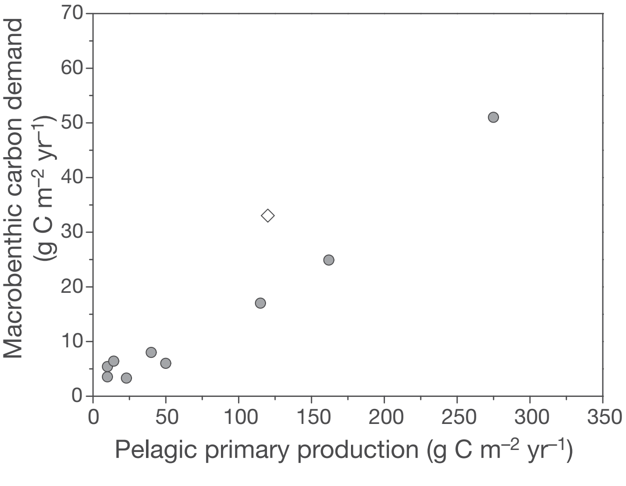

Fig. 8. Illustration of data presented in Table 3. Previously published estimates of annual macrozoobenthic carbon demand (●) and the estimate in the present study (◇) plotted against annual pelagic primary production. See Table 3 for references

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Paper II

SEA ICE COVER AFFECTS INTER-ANNUAL AND GEOGRAPHIC VARIATION IN GROWTH OF THE ARCTIC COCKLE *CLINOCARDIUM CILIATUM* (BIVALVIA) IN GREENLAND

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Sea ice cover affects inter-annual and geographic variation in growth of the Arctic cockle *Clinocardium ciliatum* (Bivalvia) in Greenland

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ABSTRACT: Sea ice exerts a strong influence on Arctic marine primary production, thereby influencing food availability for secondary producers. Food availability is recognized as one of the primary constraints on macrobenthic growth and production. Thus, it may be expected that spatial and temporal variability in Arctic sea ice cover influencing primary productivity could translate to the next trophic level: the benthic secondary producers. To test whether sea ice cover is coupled to the annual production of Arctic benthos, we measured annual growth increments in the shell of the bivalve *Clinocardium ciliatum* to (1) compare average individual growth rates along a climate gradient from sub-Arctic to high-Arctic Greenland, and (2) produce time series of inter-annual variation in bivalve growth at sites with different sea ice conditions. A significant difference between average individual growth rates between the different sites was found. This geographic variation in growth performance was correlated to the average productive open-water (ice-free) period estimated from sea ice data obtained from satellites between 1979 and 2003. At locations with low to moderate sea ice cover, growth rates ranged from 80 to 100% of the fastest growing sites. At sites with pronounced sea ice cover, bivalve growth was reduced to 35 to 45% of the maximum growth rates. At these 2 sites the year-to-year variation in bivalve growth correlated negatively with inter-annual variation in local sea ice cover. We suggest that, in the Arctic, bivalve growth is governed by food availability. At sites with pronounced sea ice cover, food availability may be linked to sea ice dynamics through the bottom-up regulation exerted by sea ice on phytoplankton production, which renders such areas especially susceptible to future climate change.

KEY WORDS: Bivalve · Annual growth · Arctic · Sea ice · Sclerochronology · Marine · Climate

INTRODUCTION

Reduction in sea ice area distribution and thickness is one of the most significant effects of the recent warming of the Arctic. Data from 1979 to 2008 show a negative trend in Arctic sea ice extent with a reduction of 2.8% per decade in March and 11% per decade in September (Richter-Menge et al. 2008). In September 2007, a record low sea ice cover was observed, which was 39% below the September mean from 1979 to 2000 (National Snow and Ice Data Center 2007). Outputs from atmosphere-ocean general circulation models predict a 15 and a 61% reduction in sea ice extent (average of 14 model outputs) in March and September, respectively, in the Arctic at the end of this century. Additionally, 7 of 14 models predict that the Arctic Ocean will be ice-free in late summer at the end of the 21st century (Arzel et al. 2006). In Arctic marine ecosystems, an important influence of sea ice is that it impedes light penetration into the water column and hence controls primary production, especially during spring. Sea ice thereby determines the timing of the spring bloom and the length of the productive open-water period and, thus, potentially the size of the

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annual primary production (Rysgaard et al. 1999, Arrigo et al. 2008).

On the Arctic sea floor, the biomass of macrobenthos often reflects the productivity of the overlying water column (Grebmeier et al. 1989, Renaud et al. 2007) and benthic growth and production are generally considered to be regulated by food availability (Clarke 1988, Clarke & Fraser 2004, Sejr et al. 2004); thus, it may be expected that patterns of Arctic sea ice cover not only affect primary production, but may also affect benthic secondary production. That geographical variation in ice cover can affect annual growth rates of macrobenthos was recently shown in sea urchin *Strongylocentrotus droebachiensis* collected around Greenland (Blicher et al. 2007).

The aim of this study was to test the proposed coupling between sea ice and growth rates of macrobenthos. We attempt to do this by measuring annual shell growth in the Arctic cockle *Clinocardium ciliatum* (Fabricius, 1780) and comparing it to information on sea ice cover derived from satellites. Two aspects of the potential coupling between sea ice and benthos were tested: (1) Whether spatial variation in average individual growth between different sites could be related to differences in the extent of seasonal sea ice cover. This was tested by comparing bivalve growth along a climatic gradient in Greenland (64° N to 76° N). (2) Whether inter-annual variation in bivalve growth at 5 different locations could be related to local sea ice conditions from 1979 to 2003. This was tested by reconstructing past variation in bivalve growth from shell increment analysis.

MATERIALS AND METHODS

Study sites. The study was conducted at sites representing a gradient of increasing sea-ice cover from the sub-Arctic to the high-Arctic (Fig. 1). Sites were visited between 1998 and 2007. Geographic positions and sampling depths are given in Table 1.

Ice data and climatic indices. Site-specific ice cover was based on satellite data from 1979 to 2003 extracted from Gloerson et al. (1990) and Maslanik & Stroeve (2004). Data are presented as a sea ice index (range: 0 to 1), with low values indicating little or no sea ice and high values indicating full ice cover. Data were extracted on a local scale at the position of bivalve collection in an area covering 4 pixels with each pixel covering 25 × 25 km. To make sure that reasonable ice data could be extracted from just 4 pixels, data were compared to regional data extracted from 18 (Disko Bay) and 54 pixels (Greenland Sea off Young Sound). For each site, the productive open-water period was calculated as the average number of days with open water and more than 6 h of daylight, below which primary production was assumed to be ~0 due to light limitation at these high latitudes (Rysgaard et al. 1999).

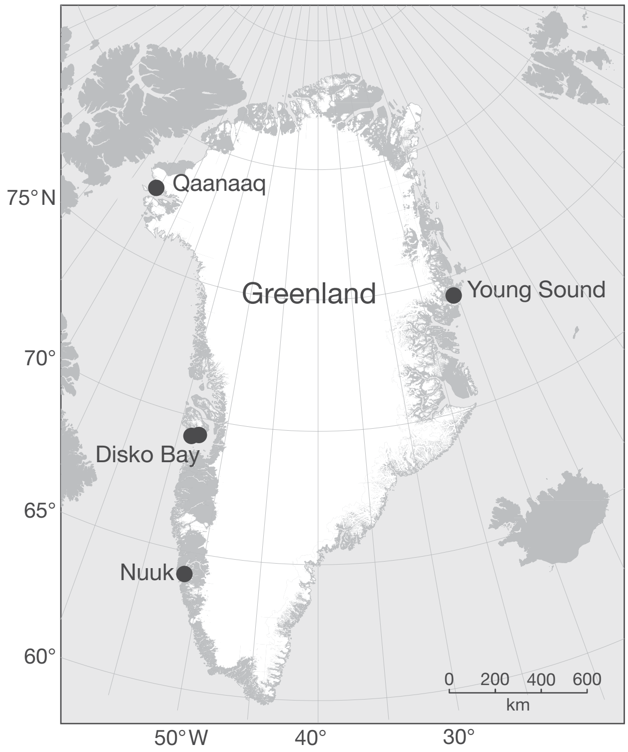

Fig. 1. *Clinocardium ciliatum*. Location of the different sampling sites

Table 1. *Clinocardium ciliatum*. For each sampling site: position; depth; growth performance (G_{max}) estimated as the maximum annual shell growth of the chondrophore region; duration of the productive open-water period (POWP)

Site	Position		Depth	n	G_{max}	95% CI	G_{max}	POWP
	N	W	(m)		(µm yr^{-1})		(% of max)	(d)
Qaanaaq	76° 32′	68° 45′	25–40	29	166.9	22.4	43	90
Young Sound	74° 18′	20° 15′	20–35	29	136.3	9.9	35	85
Disko Bay A	69° 15′	53° 34′	25–45	39	347.9	36.1	89	186
Disko Bay B	69° 14′	53° 33′	25–45	35	314.8	23.4	81	186
Nuuk	64° 07′	51° 38′	50–60	27	389.4	40.9	100	290

Open water was defined as <50% sea ice cover (see Blicher et al. 2007). To describe the inter-annual variation in sea ice cover for each site, we calculated, for both local and regional data, the summer mean index defined as mean sea ice index (1979 to 2003) during the period with a minimum of 6 h of daylight.

The relation between the inter-annual variation in bivalve growth and the annual means of the Arctic Oscillation (AO) index and the Arctic Climate Regime Index (ACRI) was also tested. As in the study of Ambrose et al. (2006), we used 2-yr running means of climatic indices as well as a 1-yr lag to account for the time necessary for physical processes to be reflected in shell growth. Data on AO were obtained from www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html and ACRI from Proshutinsky & Johnson (1997) and A. Proshutinsky (pers. comm. for updated index).

Bivalve collection, preparation, and measurements. Upon collection, cockles were washed and stored in the freezer and transported to the lab for further analysis. This species produces clearly separated growth increments, which are assumed to represent annual growth based on the strong seasonal influence on food availability in the Arctic and previous studies from other Arctic species (Sejr et al. 2002a, Ambrose et al. 2006) and from the same genus (Goshima & Noda 1992). Both externally on the shell and internally in the hinge region, narrow dark bands ('winter rings') are formed during the winter. In between the winter rings there are wider increments representing the summer shell growth. The widths of the summer increments in the chondrophore section of the shell were measured in this study. All specimens were caught alive, which means that the last increment was formed during the year of collection. By counting backwards, each increment width could be assigned to a particular calendar year. Increments were analysed in chondrophore sections of the shell to produce both estimates of growth performance and to reconstruct time series of inter-annual growth variation. The flesh was removed from the shell and the right shell was cut in 2 through the umbo along the axis of maximum growth according to Sejr et al. (2002b). One half of the right shell was then embedded in epoxy (Epofix; Struers, Denmark) and polished and etched with acid as described by Sejr et al. (2002b). Increment widths were analyzed under a dissecting microscope (magnification 10 to 100×) and measurements were performed on digital images (Fig. 2) of the chondrophore using the software ImageJ ver. 1.33.

In order to test the reliability and precision of the reconstructed time series, we also analysed external summer increments visible on the outer surface of the shells collected at 2 sites in Disko Bay. Here, increment widths were measured to the nearest 0.1 mm with vernier callipers as in Tallqvist & Sundet (2000).

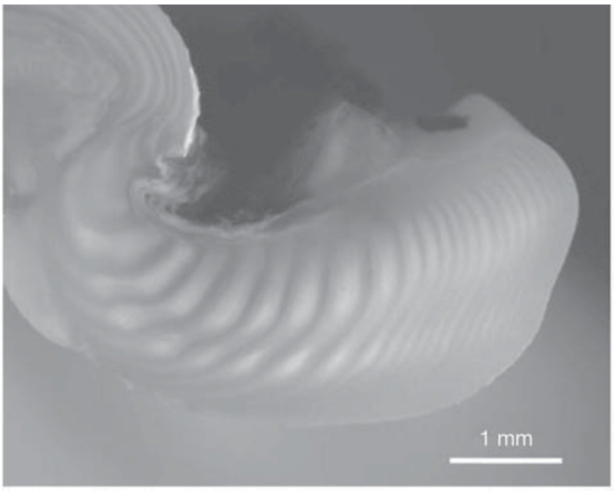

Fig. 2. *Clinocardium ciliatum.* Growth increments in the chondrophore section of the shell of the Arctic cockle

Spatial variation in growth. To compare growth between the different sites, we used the maximum increment of the chondrophore ($G_{\max}$), i.e. the widest average summer increment (see Fig. 5a) was used as an estimate of growth performance. Growth rates were also evaluated by comparing the von Bertalanffy growth equations (see below).

Reconstructed time series of bivalve growth. The annual shell growth in bivalves is highly age dependent, typically decreasing with age (e.g. Sejr et al. 2002b, this study). This trend must be removed to allow comparison of growth between age classes and construction of time series. The shell growth can be modelled by the generalised von Bertalanffy growth function:

$$L_t = L_\infty \times (1 - \mathrm{e}^{-K(t-t_0)})^D \quad (1)$$

where L_t is the shell length at age t; L_∞ is the asymptotic shell length; K is the annual growth coefficient; and D is the shape parameter determining if growth is more or less sigmoid. This growth model was fitted to summed increments-at-age data from each site in order to describe the 'mean' growth. To remove age-dependence, a growth index was constructed by dividing measured increment growth by the growth predicted from the fitted von Bertalanffy growth equation:

$$\mathrm{GI}_t = \frac{M_{(\mathrm{obs})t}}{M_{(\mathrm{pred})t}} \quad (2)$$

where GI_t is the summer growth index for a single individual at age t, $M_{(\mathrm{obs})t}$ is the observed increment width at age t, and $M_{(\mathrm{pred})t}$ is the predicted increment width from the fitted von Bertalanffy growth equation. This method of removing the age-related growth trend is known as detrending and was developed in studies of tree rings and subsequently adapted for the study of growth increments in bivalves (Schöne 2003, Witbaard et al. 2003). The year-by-year record of relative growth indices (GI_t) for each individual were then transformed into a standardised growth index (SGI) by subtracting the mean (GI_{mean}) across years for that individual and dividing by the standard deviation of the mean (GI_{SD}):

$$SGI = \frac{(GI_t - GI_{mean})}{GI_{SD}} \quad (3)$$

This ensures that results from each individuals are standardised to their own mean and standard deviation and allows particularly fast and slow individuals to be directly compared. Finally, we calculated the mean SGI for each calendar year by averaging across all individuals. Standardisation removes the correlation between mean and variance and allows SGIs of young and old specimens to be compared directly (Schöne 2003). The SGI index is therefore a year-by year record of whether growth, i.e. summer increment width, in a specific year was higher (SGI > 0) or lower (SGI < 0) compared with the mean of the entire period. As the SGI index is calculated back in time, it is based on decreasing number of (old) individuals. We only used SGI values based on 5 or more individuals. For all sites, the SGI index was calculated based on increments in the hinge region. In addition, for the Disko Bay sites, the SGI index was calculated based on increments visible directly on the shell surface. We thereby produced duplicate time series for each of the Disko Bay sites used in order to estimate the precision and reliability of the method. A total of 91 (Disko Bay A) and 87 (Disko Bay B) individuals were used to produce time series based on external increments. Time series of SGI were related to sea ice and climate indices using the Pearson correlation coefficient.

RESULTS

Sea ice

High correlation between local and regional sea ice data confirmed that representative data on local ice conditions could be extracted from a few pixels (data not shown). The average R^2 from correlations between local and regional ice data was 0.92. From the average seasonal change (1979 to 2003) in sea ice and daily daylight hours, we estimated the average productive open-water period (POWP) for each site (Fig. 3).

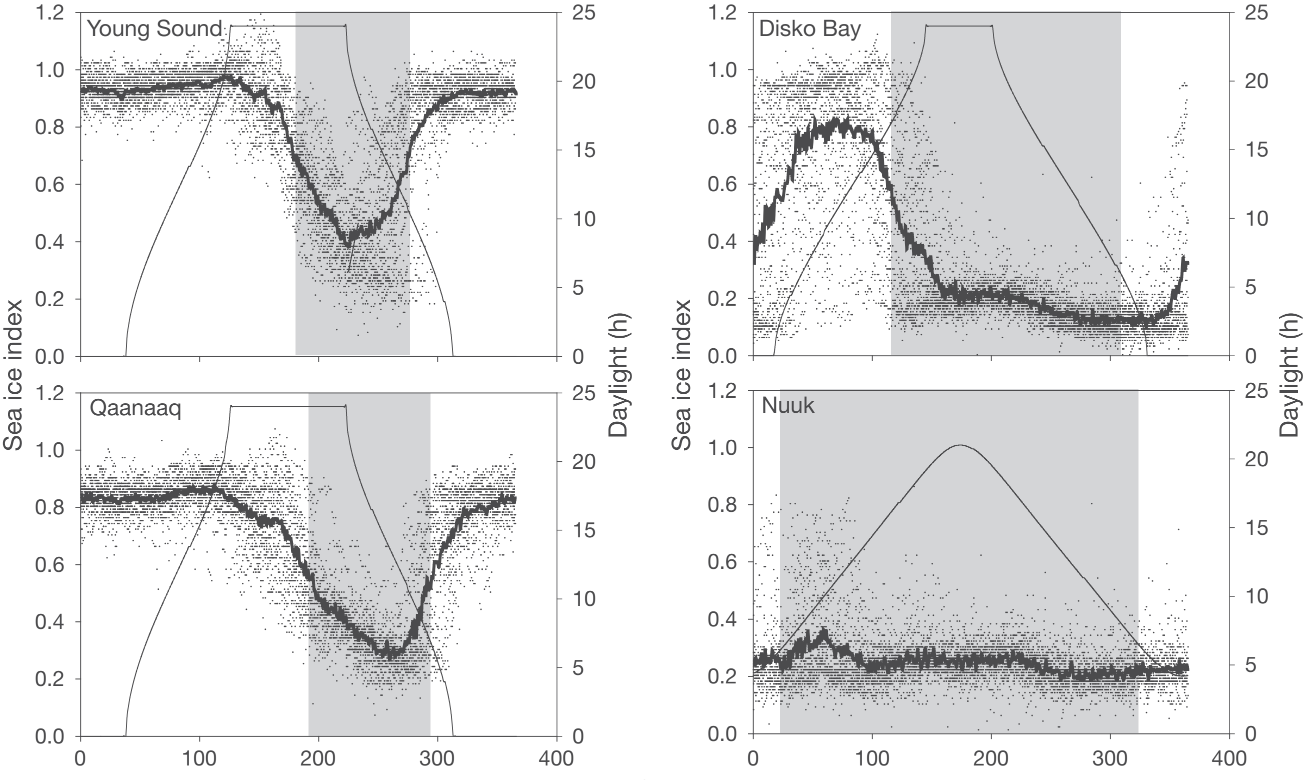

Fig. 3. Seasonal variation in daily sea ice index obtained from satellites: single-day observations (dots); average seasonal variation (thick line); daylight variation (thin line). Minimum index values correspond to ice-free water. Grey areas show average productive open-water period defined as days with average sea ice index <50 % of winter maximum, and minimum 6 h of daylight

Table 2. *Clinocardium ciliatum*. Von Bertalanffy growth equation parameters (defined in 'Materials and methods') fitted to data (see Fig. 5B), with ±95% CI values given in parenthesis

Location	L_∞ (mm)	K (yr^{-1})	t_0 (yr)	D	R^2
Qaanaaq	2.023 (0.042)	0.061 (0.006)	1.750 (0.148)	0.067 (0.050)	0.98
Young Sound	1.608 (0.034)	0.110 (0.018)	0.740 (0.494)	1.004 (0.220)	0.99
Disko Bay A	3.612 (0.038)	0.175 (0.012)	0.585 (0.328)	1.820 (0.360)	0.99
Disko Bay B	4.152 (0.063)	0.167 (0.010)	0.753 (0.304)	1.774 (0.226)	0.99
Nuuk	5.461 (0.052)	0.13 (0.008)	1.368 (0.164)	1.647 (0.202)	0.99

Qaanaaq and Young Sound were estimated to have 90 and 85 d, respectively, of open water during the productive season while Nuuk had 290 (Table 1). In Nuuk, the POWP was not constrained by sea ice. The sites can be divided into 2 categories: Arctic sites with a permanent ice cover in winter (Qaanaaq and Young Sound) where the POWP is highly restricted by sea ice, and sub-Arctic sites (Disko Bay and Nuuk) where ice cover is variable even during winter and where sea ice only plays a minor role for the productive period. For Young Sound, the estimated average POWP of 85 d was confirmed by annual on-site observations since 1950 (Rysgaard & Glud 2007). Inter-annual variation in summer sea ice index for Qaanaaq, Young Sound and Disko Bay (Fig. 4) show some degree of synchrony between sites but linear correlations were not significant. All 3 locations show a general decreasing trend from 1996 to 2003. At Nuuk, sea ice cover was too low in summer to calculate inter-annual variation.

Spatial variation in bivalve growth

The mean width of internal shell increments in the chondrophore (Fig. 5a) showed a typical bivalve growth pattern with strong effect of age on annual growth rate. The largest maximum increment width, ($G_{\max}$) was found at Nuuk. The $G_{\max}$ in specimens from Young Sound and Qaanaaq were only 35 and 43%, respectively, of that in specimens from the Nuuk site (Table 1). By adding up increment widths, the average individual growth at each of the locations was estimated (Fig. 5b), showing reduced growth in Young Sound and Qaanaaq and maximum growth in Nuuk. Parameters of the fitted von Bertalanffy growth equations are shown in Table 2. The growth parameter, K, is lower in Nuuk compared to the Disko Bay locations. This is mainly a result of the higher maximum age found at Nuuk. Furthermore, $G_{\max}$ showed a significant relationship (Fig. 6) with the POWP ($G_{\max} = 0.32 \times$ [POWP] + 14.3, $p < 0.01$, $R^2 = 0.95$). When $G_{\max}$ values for the sea urchin *Strongylocentrotus droebachiensis* were included (recalculated from Blicher et al. 2007)

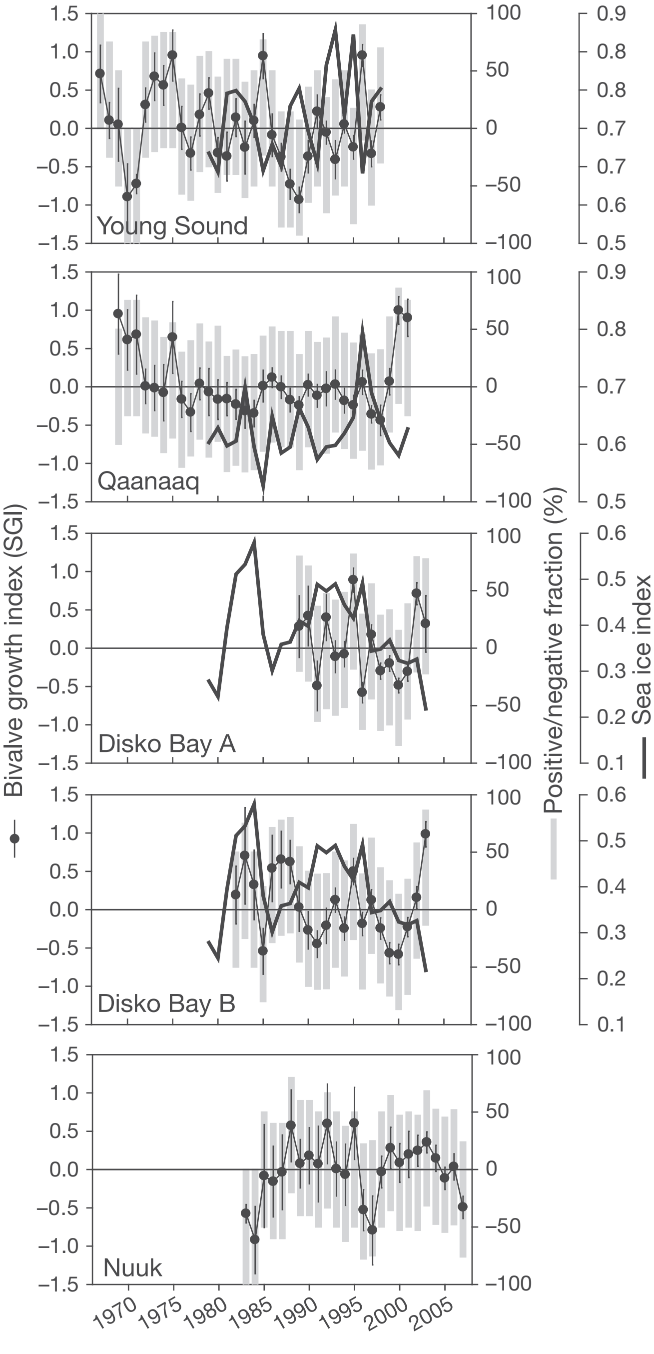

Fig. 4. *Clinocardium ciliatum*. Reconstructed time series of variation in annual shell growth (–●–) at 5 locations. Average (±1 SE) and percentage of the collected specimens with positive/negative index values (grey bars). Inter-annual variation in summer sea ice index (▬) at 3 locations in Greenland. Sea ice at Nuuk was too low in summer to calculate index values

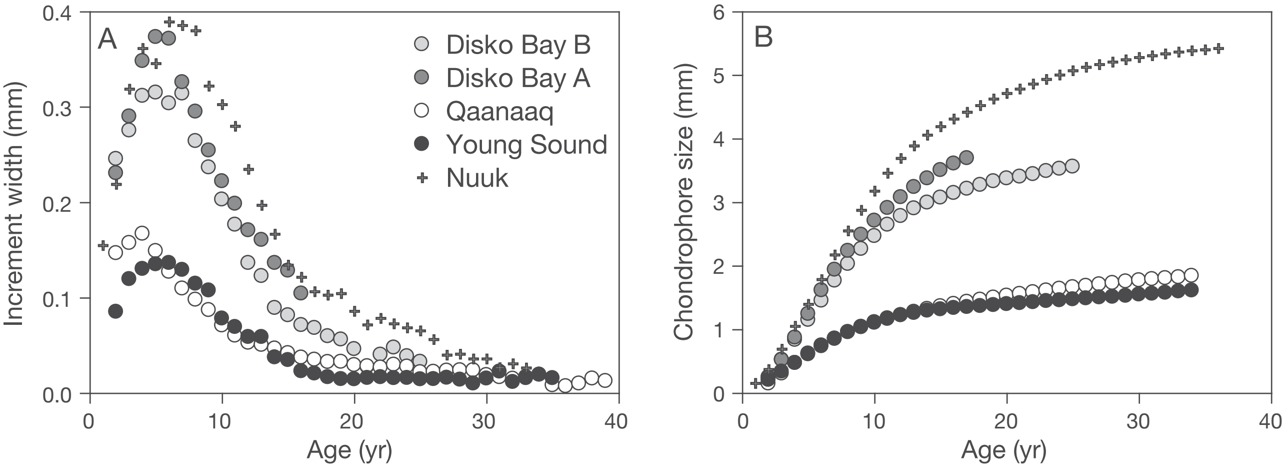

Fig. 5. *Clinocardium ciliatum*. For 5 sites in Greenland: (A) Average width of summer increment in the chondrophore section of the bivalve; (B) Average growth curves obtained by summing up individual increments shown in (A)

there was a clear tendency (Fig. 6, solid line) in sites with a long POWP showing (1) increased growth performance ($G_{max} = 0.24 \times [POWP] + 19.4$, $p < 0.01$, $R^2 = 0.78$), and (2) larger variation in G_{max} values.

Reconstructed time series of bivalve growth

Time series of SGI and the relative distribution of individuals with positive and negative SGI are presented in Fig. 4. The shorter life span of the individuals found in Disko Bay resulted in shorter time series. In general, the average SGI values reflect the population trend, i.e. a negative SGI for a given year is mostly a result of the majority of the individuals having a negative SGI and not due to a few individuals influencing the mean. Significant negative correlation between summer sea ice index and bivalve SGI was found for Young Sound ($p = 0.03$, $n = 20$, $R^2 = 0.26$) and Qaanaaq ($p = 0.01$, $n = 23$, $R^2 = 0.28$) (Table 3). No significant correlations between bivalve growth and climatic indices, AO or ACRI, were found (Table 3).

Several of the bivalve sites displayed synchronous patterns in SGI time series (Table 4). A high positive correlation was found between the 2 sites in Disko Bay but also between the 2 high-Arctic sites, Young Sound and Qaanaaq, situated in East and West Greenland. A significant negative correlation was found between

Table 3. *Clinocardium ciliatum*. Pearson correlation coefficients between time series of bivalve growth variation and measures of sea ice, climate indices (Arctic Oscillation, AO and Arctic Climate Regime Index, ACRI), number of summer days with windspeeds >10 m s^{-1}, and bottom water temperature (T) at Fyllas Band off SW Greenland. Significant correlations ($p < 0.05$) are given in **bold**. YS = Young Sound; Qa = Qaanaaq; DB A and B = Disko Bay A and B, respectively

	YS	Qa	DB A	DB B	Nuuk
Local ice index	**–0.51**	**–0.53**	–0.22	–0.24	0.18
AO					
Annual mean	–0.12	–0.03	0.32	–0.10	0.31
Ann. mean 1 yr lag	–0.02	–0.09	0.11	–0.21	0.24
2 yr running mean	–0.09	–0.07	0.26	–0.19	0.33
ACRI					
Annual mean	–0.03	0.12	0.05	0.08	–0.03
Ann. mean 1 yr lag	0.07	0.17	–0.46	0.03	–0.06
2 yr running mean	0.02	0.20	–0.26	0.07	–0.06
Wind days > 10 m s^{-1}	0.12	0.18	0.08	0.11	–0.26
T at Fylla Bank	–	–	–	–	0.30

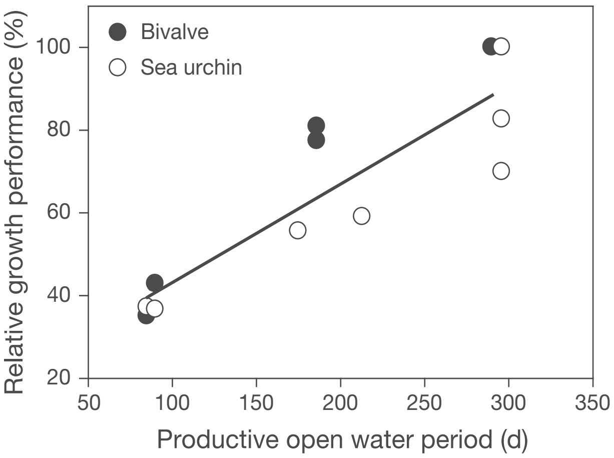

Fig. 6. Growth performance (G_{max}) of the bivalve *Clinocardium ciliatum* estimated as maximum annual shell growth plotted against the productive open-water period (POWP). Data for the sea urchin *Strongylocentrotus droebachiensis* recalculated from Blicher et al. (2007). Linear regression for the combined species data set: $G_{max} = 0.24 \times [POWP] + 19.4$, $p < 0.01$, $R^2 = 0.78$

Table 4. *Clinocardium ciliatum.* Pairwise Pearson correlations between time series of growth indices reconstructed from analysis of shell increments at different locations in Greenland. Significant correlations are in **bold** ($^{*}p < 0.05$, $^{**}p < 0.01$). N is given in parenthesis

	Qaanaaq	Young Sound	Disko A	Disko B
Qaanaaq				
Young Sound	**0.61**** (27)			
Disko Bay A	0.07 (13)	**−0.65*** (10)		
Disko Bay B	0.17 (17)	**−0.60*** (14)	**0.67**** (15)	
Nuuk	0.07 (24)	−0.30 (21)	0.46 (15)	0.42 (19)

Young Sound and the 2 sites in Disko Bay. The growth pattern for bivalves in Nuuk was positively correlated to the bivalve growth pattern at the 2 Disko Bay sites but not significantly so (p = 0.07 and p = 0.09).

The duplicate time series produced for each of the Disko Bay sites based on external increments on the shell generally showed a pattern very similar to the time series based on increments in the hinge region (Fig. 7). Linear correlation between the duplicate time series was highly significant ($p < 0.001$) and R^2 was 0.65 and 0.66 for locations A and B, respectively.

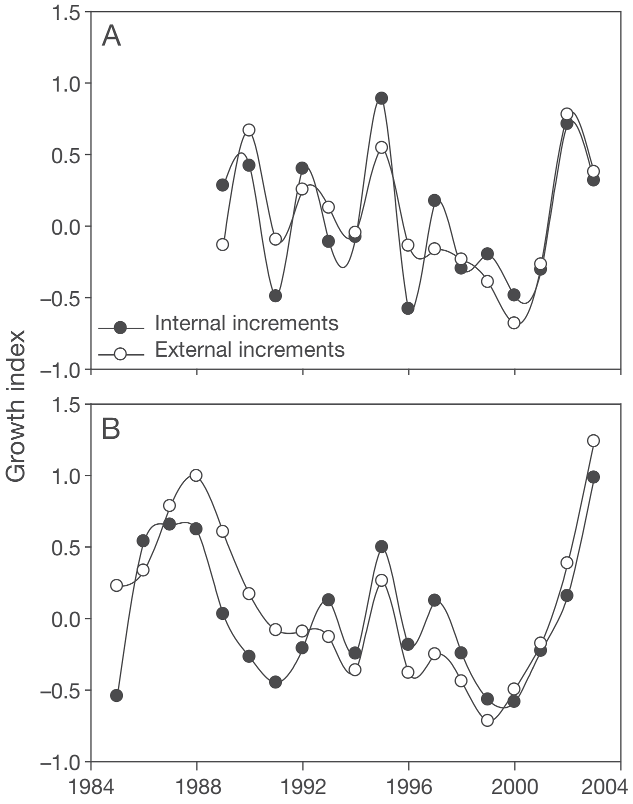

Fig. 7. *Clinocardium ciliatum.* Comparison of duplicate time series of growth indices (SGI) extracted from 2 separate areas of the shell at 2 sites (A and B) in Disko Bay, West Greenland

DISCUSSION

Spatial variation in growth

The clear differences in growth between collection sites are most likely the result of a multitude of environmental factors. Food availability is generally considered the primary constraint on growth in polar benthos (e.g. Blicher et al. 2007, Sejr & Christensen 2007). The significant relation between the average length of the POWP and bivalve growth indicates that sea ice cover can influence annual growth rates of benthic fauna. We suggest that it could do so by influencing the annual primary production through light limitation, as shown by Rysgaard et al. (1999) and Arrigo et al. (2008). The data available on annual primary production from the studied areas support the idea of sea ice-induced differences in primary productivity. In Young Sound, data from 2001 show that 49.5% of the annual incoming photosynthetically active radiation (PAR) occurred during the period of sea ice cover, compared with ~10 to 15% in Disko Bay (Sejr et al. 2007). Depending on snow cover, the light under sea ice is reduced to between 0 and 3% of surface PAR (Sakshaug 2004). Correspondingly, annual phytoplankton production has been estimated at only 10 gC m^{-2} in Young Sound (Rysgaard et al. 1999) compared with 92 gC m^{-2} in the Disko Bay (Andersen 1981) and 75 to 160 in Nuuk (Smidt 1979, Mikkelsen et al. 2008a,b). Although no data on annual phytoplankton production are available from Qaanaaq, ice conditions are very similar to those in Young Sound, and primary productivity is most likely comparable at the 2 high-Arctic sites.

In a study on geographical variation in growth rates of the sea urchin *Strongylocentrotus droebachiensis* (Blicher et al. 2007), maximum annual growth at Qaanaaq and Young Sound was reduced to ~40% compared with growth in Nuuk, which supports the hypothesis concerning the influence of sea ice on marine productivity. However, the present study is based on relatively limited data, which makes it necessary to examine alternative explanations. Food availability unrelated to sea ice cover could also be an important component. For example, the proportion of the pelagic production available to the benthos could differ between sites. This proportion is often related to bathymetry since benthos at depths from 15 to 35 m are able to feed directly on nutrition-rich subsurface plankton blooms, whereas at greater depths, both the quantity and quality of food reaching the sea floor will be lower due to prior grazing by the pelagic food chain (Wassmann et al. 2004). We attempted to sample at comparable depths to minimize this effect. Unfortunately, specimens in Nuuk were only found between 50 and 60 m. This greater depth is expected to influence the growth estimate from Nuuk negatively.

Different levels of competition for available food could also influence the observed growth patterns and cannot be ruled out since data on benthic density or biomass are not available from all sites. However, we do not have indications of increased competition in Young Sound and Qaanaaq compared with the other sites.

Temperature is known to be an important regulator of bivalve growth in temperate areas (e.g. Dekker & Beukema 1999, Witbaard et al. 1999). In Young Sound, the summer temperature at 25 m depth rarely exceeds –0.5°C (Rysgaard & Glud 2007). No data are available from Qaanaaq, but it is reasonable to assume a seasonal temperature regime similar to that of Young Sound. In Disko Bay, summer temperature may reach 4 to 4.5°C at 25 m (Nielsen & Hansen 1999). At the sampling site in Nuuk, temperatures at 50 m depth show distinct seasonal variation with maximum temperatures of about 4°C (M. Blicher unpubl. data). In a short-term study of a fast-growing Antarctic bivalve, Heilmayer et al. (2005) showed elevated shell growth rates in juveniles kept at 3°C compared to a control group kept at 0°C, which suggests that even small changes in temperature can affect growth.

Factors unrelated to food availability and temperature may also be involved. Parasites can potentially influence growth of bivalves. However, examination of 12 individuals from each of the sites in Disko Bay B and Qaanaaq showed no signs of infection, and parasites do not seem to be a likely explanation of the observed growth patterns.

In conclusion, we suggest that geographical differences in annual growth rate are linked to food availability, which is strongly influenced by the duration of the POWP determined by local sea ice conditions. However, based on this analysis alone, we cannot reject the possibility of temperature being a contributing factor to increased growth performance in bivalves at the sub-Arctic sites.

Inter-annual variation in growth

Significant correlation between sea ice cover and bivalve growth was found only at the 2 high-Arctic sites: Qaanaaq and Young Sound. Both sites are covered by fast ice every winter and have short periods of open water in summer (Fig. 3). We suggest that the significant correlation between sea ice cover and bivalve growth is a result of the controlling effect of sea ice on phytoplankton production and, hence, food availability for the bivalves. Only at sites with pronounced ice cover will sea ice be important for the inter-annual variation in primary productivity; hence, a significant correlation is found only in Young Sound and Qaanaaq. Insufficient data on annual primary productivity from Qaanaaq and Young Sound are available for testing whether inter-annual variability is related to ice cover. However, previous studies in Young Sound have shown that light availability is a strong regulating factor of benthic primary production due to the extensive sea ice cover in the area (Borum et al. 2002, Glud et al. 2002, Roberts et al. 2002). Based on satellite data, sea ice dynamics show similar variability at Qaanaaq and Young Sound, which makes it reasonable to assume that variation in sea ice cover will regulate annual primary production and thus bivalve growth equally at these 2 high-Arctic sites. In Disko Bay, the ice cover is far less pronounced and often breaks up during the winter (Fig. 3) and in Nuuk, ice cover is absent most of the year. At these 2 sites, the annual primary productivity is not strongly coupled to light availability but potentially to factors such as water column stability and nutrient availability (Nielsen & Hansen 1999). Such factors can also cause variation in annual primary production and affect bivalve growth. In Nuuk, the annual primary production at the same site was 75 and 104 g C m^{-2} yr^{-1} in 2006 and 2007 (Mikkelsen 2008b) and the inter-annual variation in bivalve growth is comparable to the more northern sites. Nutrient availability is generally determined by the concentration in the surface layer prior to the spring bloom (Sakshaug 2004). Secondary blooms can, however, develop later in the season following a period with strong winds causing upwelling of nutrient-rich water (Nielsen & Hansen 1999, Sakshaug 2004). We correlated bivalve growth to the number of summer days with wind speeds >10 m s^{-1}, extracted from Cappelen et al. (2000). Although wind data in single years are missing, no significant correlation was found for any of the bivalve sites (Table 4). To test for a complex effect of several features of climate, bivalve growth was correlated to the AO and the ACRI, but no significant correlation with growth was found in any of the bivalve sites.

Temperature might cause variation in growth rates as discussed previously; however, we found no significant correlation between our bivalve growth index in Nuuk and the temperature time series at the nearby Fyllas Bank. At sites further north, seasonal and inter-annual variability in temperature are smaller, suggesting that temperature is not important for the inter-annual variation in bivalve growth at these high latitudes.

The lack of correlation with physical factors suggests that biological interactions could be important for inter-annual variation in growth. In a study from the North Sea on the bivalve *Arctica islandica*, no direct link could be established between long-term growth data and phytoplankton biomass because food availability was modified by copepod abundance (Witbaard et al. 2003). Although the bivalves in this study were sampled at relatively shallow depths and thus graze directly on sub-surface plankton blooms, it is well-documented that copepods can control phytoplankton stocks through grazing (Rysgaard et al. 1999) and, thus, influence food availability for the benthos.

We are aware of 2 other studies that have attempted to establish a link between sea ice and bivalve growth in the Arctic. Using the same species, Tallqvist & Sundet (2000) sampled 3 sites in the Barents Sea without finding a significant correlation with ice cover. Two possible explanations are: (1) None of the sites sampled in the Barents Sea seem to be covered by seasonal fast ice to the extent found in Young Sound and Qaanaaq (satellite data extracted in this study; data not shown). Even at the very northern location ('Moffen' at 80° N in Svalbard) sea ice cover was much less pronounced compared to Qaanaaq and Young Sound. (2) Sampling depth was greater (80 to 130 m), which potentially weakens the pelagic benthic coupling. In another study from a Svalbard fjord with ice conditions comparable to those in Young Sound and Qaanaaq, inter-annual variation in growth of *Serripes groenlandicus* was partly related to large-scale sea ice data when excluding the last 4 yr of a 20 yr time-series (Ambrose et al. 2006).

Evaluation of time series

When attempting to reconstruct growth patterns from increment analysis and relate results to large-scale factors such as sea ice, at least 3 important aspects must be considered: (1) Are the increments formed annually? (2) Are the increment measurements and age determinations precise and reliable? (3) Do the collected specimens display a common synchronous signal that can meaningfully be correlated with climatic factors operating on a large scale? For this species, the annual formation of increments has not been tested experimentally; however, evidence from other Arctic species (Sejr et al. 2002b, Ambrose et al. 2006) suggests that the pronounced seasonal input of food makes annual increments a common feature in Arctic bivalves. Also, age determinations as well as growth equations give results comparable to those found in other Arctic bivalves, which makes it reasonable to assume that increments are formed annually (see also Tallqvist & Sundet 2000).

Testing whether a group of individuals exhibits a common synchronous growth signal is not straightforward. We have found it useful to analyse a sufficient number of individuals to calculate a robust average. It also allows the proportion of individuals displaying positive/negative values to be calculated. This makes it possible to check that average SGI values also correspond to a general pattern in the sample and is not a result of a few outliers. Finally, the fact that bivalves were sampled at 2 locations separated by a few kilometres (Disko Bay A and Disko Bay B) and the finding of a significant positive correlation between the constructed time series strongly suggest that large-scale factors do play an important role for the inter-annual variation in bivalve growth at least in these 2 locations. Hence, we believe there is sufficient evidence that the reconstructed time series are valid indicators of past growth conditions.

CONCLUSIONS

The combined results from the geographical and inter-annual variation in growth indicate that summer growth of the bivalve *Clinocardium ciliatum* is linked to sea-ice dynamics at sites with pronounced sea ice cover. We suggest that this link is created through bottom-up regulation of the annual phytoplankton production. At sites with prolonged sea ice cover, bivalve growth is primarily limited by food due to low primary production. At sites with moderate ice cover, bivalve growth will, to a larger extent, be influenced by a multitude of physical and biological factors affecting primary production and benthic food availability. Additional studies are necessary to improve our understanding of how the complex interactions between physical and biological parameters governing benthic productivity are linked to sea ice cover in the Arctic and to confirm whether sea ice does indeed directly influence growth rates of benthic macrofauna through bottom-up regulation of phytoplankton production.

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Paper III

SEASONAL GROWTH VARIATION IN CHLAMYS ISLANDICA (BIVALVIA) FROM SUB-ARCTIC GREENLAND IS LINKED TO FOOD AVAILABILITY AND TEMPERATURE

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Seasonal growth variation in *Chlamys islandica* (Bivalvia) from sub-Arctic Greenland is linked to food availability and temperature

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ABSTRACT: In order to assess the role of different environmental parameters in the population dynamics of marine invertebrates in the Arctic, we examined seasonal variation in individual biomass, shell growth, and mass production of somatic and reproductive tissues of immature and maturing scallops *Chlamys islandica* suspended in culture nets at 15 and 30 m depth in SW Greenland from May 2007 to October 2008. All 3 parameters varied both seasonally and between depths. Individual shell growth rate and biomass were poor proxies for the actual mass growth rate on a seasonal scale. Minimum and maximum mass growth rates were observed from November to February and in April–May, respectively. Simultaneous monitoring of biotic and abiotic parameters in the water column made it possible to establish a growth model relating variation in mass growth rate to variation in environmental conditions. The best-fit model ($R^2 = 0.71$) indicated that total mass growth rate depended on chlorophyll *a* concentration, carbon-to-nitrogen ratio of seston, and water temperature. While availability of high-quality food items affected growth positively, the growth model indicated a negative effect of increasing temperature on the mass growth rate of *C. islandica*. These results indicate that scallops in SW Greenland are resource-limited and that elevated temperature through its effect on metabolic costs reduces growth efficiency. Hence, it is most likely that the growth capacity of *C. islandica* in SW Greenland is either never realized or only attained for short periods of time (hours to days) under the present conditions.

KEY WORDS: Bivalve · Scallop · Temporal dynamics · Production · Food availability · Sub-Arctic · Pectinid · Temperature · Shell growth

INTRODUCTION

The strong seasonality in the Arctic is known to be a major component affecting the life cycles and survival strategies of animals at all trophic levels (e.g. Conover & Huntley 1991, Heide-Jorgensen et al. 2003, Rysgaard & Nielsen 2006). However, studies of temporal variation in the structure and function of the marine ecosystem in the Arctic are relatively few. Partly due to the logistical challenges in Greenland, long-term monitoring programs covering all seasons have not been initiated until recently (www.G-E-M.dk), resulting in little knowledge of the coupling between environmental variation and ecological characteristics in this region. Benthic macrofauna has been recognized as important for carbon cycling in the Arctic marine ecosystem (e.g. Grebmeier et al. 2006, Sejr & Christensen 2007). Still, very little is known about the relation between benthic population dynamics and the seasonality of their habitat.

Reduction of the seasonal sea ice cover (spatial extent, duration, and thickness) and increased freshwater input from land are direct consequences of the ongoing warming of the Arctic (Peterson et al. 2002, Johannessen et al. 2004, Hanna et al. 2008, Lindsay et al. 2009, McPhee et al. 2009). Both factors have the potential to directly or indirectly affect the magnitude and the seasonal dynamics of marine primary produc-

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tion (Rysgaard et al. 1999, 2003, Dagg et al. 2004, Wassmann et al. 2006, Arrigo et al. 2008), potentially leading to altered food conditions for secondary producers. Low temperature is considered an important component of high-latitude marine environments, affecting physiological rates of ectotherms at all trophic levels (Gillooly et al. 2001). Thus, it might be expected that future changes in ocean temperature and food availability in the Arctic will affect the productivity of secondary producers (Blicher et al. 2007). However, the combined effect may not be straightforward. Hence, it is still debated whether the apparent temperature-dependence of the basal metabolism of ectotherms is solely a consequence of thermodynamics, or if the processes involved in metabolism have been subject to evolutionary adaptation to maximize production in a given environment, i.e. maximizing the difference between energy intake and metabolic costs (e.g. Clarke & Johnston 1999, Gillooly et al. 2001, Clarke 2003). In any case, it seems likely that the effect of increasing temperature on organism growth is dependent on the ability of an organism to compensate for the elevated metabolic cost of maintenance through increased energy assimilation. This ability is likely to differ between taxa, functional groups, and life styles, but is ultimately dependent on resource availability (Clarke 2003, Clarke & Fraser 2004). This is in accordance with Harrington (1987), who suggested that a latitudinal cline in growth of the venerid bivalve genus *Protothaca* in the NE Pacific was related to the length of the period during which individuals could feed.

Feeding experiments have indicated that the filter-feeding bivalve *Hiatella arctica* from high-Arctic NE Greenland is resource-limited in its natural environment and is highly capable of increasing energy assimilation in response to increased phytoplankton concentrations despite temperatures <0°C (Sejr et al. 2004). In another study compiling all previously published estimates of pectinid metabolic rates across latitudes, a relation between mean ambient temperature (range: 0 to 25°C) and standard metabolic rate was established, demonstrating a Q_{10} of 2.97, thus indicating tight coupling to temperature. However, temperature did not explain variations in growth performance, suggesting decreased growth efficiency with increasing temperature (Heilmayer et al. 2004). Still, Heilmayer et al. (2005) argued that growth rates of juvenile Antarctic scallops *Adamussium colbecki* were positively affected by temperature; unfortunately, however, their study did not take into account the potential role of food.

Another filter-feeding bivalve, the scallop *Chlamys islandica*, is a circumpolar species occurring in coastal areas and fjords off the entire west coast of Greenland (Pedersen 1994). It is regarded as an ecologically important species (Blicher et al. 2009). Feeding experiments in northern Norway have indicated that seston composition can affect the absorption efficiency of *C. islandica*, and thus potentially influence the growth rate of this species (Vahl 1980). Moreover, oxygen consumption in actively feeding specimens did not relate to ambient temperature in a laboratory study (Vahl 1978), indicating that other factors, such as food availability, are potential key drivers of metabolic activity, as suggested for Antarctic sea urchins (Brockington & Clarke 2001). The objective of the present study was to describe the variation in individual production of *C. islandica* suspended in cages in the field, in relation to seasonal and spatial variation in temperature, salinity, and food availability in a sub-Arctic fjord. We hypothesized that, on a seasonal scale, bivalve growth was resource-limited. However, if bivalves were not limited by food availability the alternative hypothesis was that temperature, through its effect on physiological rates and filtering capacity, affected growth positively.

MATERIALS AND METHODS

Experimental setup. *Chlamys islandica* specimens were collected using a triangular dredge in the outer Kobbefjord, SW Greenland, at 50 to 60 m depth in May 2007 (Fig. 1). After collection, bivalves were immediately transferred to containers with aerated seawater. Scallops were then tagged individually with numbered shellfish tags (4 × 8 × 0.15 mm, Hallprint) on the upper shell (Ross et al. 2001). Tags were attached near the shell margin with a cyanoacrylate adhesive after dabbing the shell dry with a towel. Shell heights (SH) of all specimens were measured with digital callipers to the nearest 0.01 mm, and the scallops were divided into 2 initial size groups, representing: (1) immature ($15 \leq SH \leq 35$ mm), and (2) maturing bivalves ($35 < SH \leq 55$ mm) (Blicher et al. 2009), and transferred to lantern box nets (FUKUI type, Coastal Aquacultural Supply) with tiers of 0.2 m^2 each and 12 mm mesh size. We allowed scallops to cover no more than 25% of the tier area, i.e. a maximum of 10 and 20 individuals per tier for size groups 2 and 1, respectively, which was similar to the densities observed in the natural environment (Blicher et al. 2009). A total of 752 scallops, equally represented by the 2 size groups, were tagged. Lantern nets were deployed in the outer part of the Godthåbsfjord (Fig. 1) using anchors and buoys to keep the lanterns suspended 5 m above the sea floor (Narvarte 2003). Each of the 2 size groups was suspended at 2 different depths, 15 and 30 m, respectively. Thus, we analysed 4 separate groups, differing in size and/or deployment depth. Obviously, the sizes of the scallops changed during the experiment due to

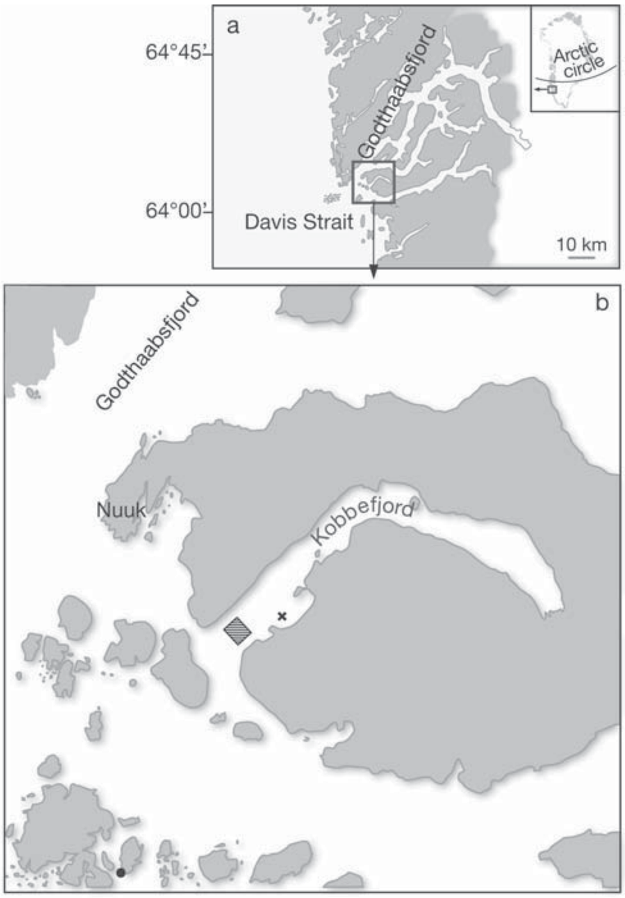

Fig. 1. (a) Location of the study site in Greenland. (b) Hatched area in the outer part of Kobbefjord indicates the site of collection of *Chlamys islandica*. The initial deployment site is indicated by ●; × is the location in Kobbefjord to which scallops were transferred after being suspended for 2.5 mo

growth, but in the text we use the terms Group 1 and Group 2 to refer to the initial SH size groups of the scallops. In the beginning of August 2007 we moved the lantern nets to Kobbefjord (Fig. 1) for reasons explained in 'Results — Environmental parameters'.

Sampling and calculations. After an initial recovery period of ~2.5 mo, we measured SH of each tagged scallop at approximately monthly intervals until the end of the experiment in October 2008. Scallops were carefully retrieved from the lantern nets and placed in aerated sea water at ambient temperature, after which SH was measured quickly using digital callipers before individuals were placed in the lantern nets again. Thus, for each individual we were able to calculate the average shell growth rate, G_s (mm d^{-1}), in any given monthly period:

$$G_s = \frac{SH_2 - SH_1}{\Delta t_{12}} \tag{1}$$

where SH_1 and SH_2 are individual SH (mm) at times 1 and 2, respectively, and Δt_{12} is the number of days between times 1 and 2. In order to establish a general shell growth function, size increment data (SID) for a complete seasonal cycle, from August 2007 to August 2008, were fitted to a modified specialized von Bertalanffy growth model (Brey 2001):

$$SH_2 = SH_1 + (SH_\infty - SH_1)(1 - \exp(-K\Delta t_{12})) \tag{2}$$

where SH_∞ is the asymptotic SH (mm), K is a growth coefficient (d^{-1}), and Δt_{12} is the number of days from August 2007 (t_1) to August 2008 (t_2). The first derivative of the specialized von Bertalanffy model is equal to the predicted daily shell growth rate, $\hat{G}_s$ (mm d^{-1}), at SH:

$$\hat{G}_s = K \times SH\left(\frac{SH_\infty}{SH} - 1\right) \tag{3}$$

The ratio between the observed individual shell growth rate, G_s, and the predicted shell growth rate, $\hat{G}_s$, in a given period during the year was regarded as an index of shell growth rate, GI_s:

$$GI_s = \frac{G_s}{\hat{G}_s} \tag{4}$$

At each sampling date we sub-sampled 10 specimens from each size group and depth for the analysis of biomass. Immediately after sampling, we carefully dissected the scallops into gonad and somatic tissue (adductor muscle, digestive gland, mantle, and gills). Dry mass (DM) was determined by drying at 60°C for 72 h. In order to obtain a general relation between SH and DM we fitted biomass-at-size data obtained from a total of 13 sampling dates through a period of 17 mo to the allometry equation:

$$\log_e(DM_{pred}) = a + b\log_e(SH) \tag{5}$$

Where DM_{pred} is the predicted DM, a is the intercept, and b is the slope. The general relations between (1) SH and gonad mass, DM_{gonad}, (2) SH and somatic mass, $DM_{somatic}$, and (3) SH and total tissue mass, DM_{total} were used to calculate individual index values for biomass, BMI:

$$BMI = \frac{DM_{obs}}{DM_{pred}} \tag{6}$$

where DM_{obs} is the observed individual DM, and DM_{pred} is the DM predicted from Eq. (5). Average BMI ($\overline{BMI}$) was calculated for each of 4 sub-samples (dependent on initial size and depth) at any given sampling date. This approach was based on the assumption of a common coefficient, b (Eq. 5) for all seasons. ANCOVA models containing the predictor variables SH (covariate) and sampling date (categorical), and the interaction term SH × sampling date, were used to test for seasonal variation in the relation between SH and BMI (somatic, gonad, and total). We estimated instantaneous individual mass growth rates, G_m (d^{-1}), in the period between sampling dates by combining $(\overline{\text{BMI}})$ values with changes in individual SH:

$$G_{\text{m},12} = \frac{\text{Ln}\left[\dfrac{\text{DM}_\text{pred} \times \overline{\text{BMI}}_{i(2)}}{\text{DM}_\text{pred} \times \overline{\text{BMI}}_{i(1)}}\right]}{\Delta t_{12}} \qquad (7)$$

Where $G_{\text{m},12}$ is the mass growth rate in the period between time 1 and time 2. DM_pred is estimated from the observed individual SH, and $(\overline{\text{BMI}}_{i(1)})$ and $(\overline{\text{BMI}}_{i(2)})$ are average BMI at times 1 and 2, respectively, and i refers to the 4 combinations of depth (15, 30 m) and size group (1 and 2).

We wanted to be able to study the effect of key environmental drivers on the seasonal growth variation of scallops independent of potential differences in individual SH and changes in SH (due to growth) during the study period. A general function describing the effect of SH on the instantaneous mass growth rate, including a more sophisticated approach to variance, made it possible to remove any size dependence of our estimates of seasonal growth variation. Thus, we prevented any bias of the results caused by differences in SH between groups or changes in SH within groups during the 17 mo study period. Overall, the procedure ensured that data could be compared across the relevant spatial and temporal scales. This normalization of our data is described below:

The combined G_m at SH data (somatic, gonad, and total, respectively) were fitted to an exponential model:

$$\hat{G}_\text{m} = a \times \exp(b \times \text{SH}) \qquad (8)$$

where $\hat{G}_\text{m}$ is the predicted mass growth rate at size SH, and a and b are coefficients in the model. An error term, ε, was considered, such that

$$G_\text{m} = \hat{G}_\text{m} + \varepsilon \qquad (9)$$

where G_m is the actual mass growth rate. ε is assumed to be normally distributed with zero mean and a power relationship between its variance and SH:

$$\varepsilon = N\{0, (q\text{SH}^z)^2\} \qquad (10)$$

where q and z define the variance. This is a flexible expression of variance, which implies potential heteroscedasticity. However, the expression contains, and can easily be collapsed to, the common simple forms, e.g. $z = 0$ gives homoscedastic errors, $z = 1$ gives standard deviation (SD) proportional to SH. Parameters were fitted by maximizing the joint likelihood of the ε values, ln(l) (e.g. Lebreton et al. 1992).

The size-dependent mass growth data were normalized to a mass growth index, GI_m, by dividing the observed deviation from the predicted mass growth rate with the modelled SD (Eq. 10), also known as a standard score (Larsen & Marx 2005):

$$\text{GI}_\text{m} = \frac{G_\text{m} - \hat{G}_\text{m}}{q\text{SH}^z} \qquad (11)$$

$\text{GI}_\text{m} = 0$ is equal to the predicted mass growth rate, while $\text{GI}_\text{m} = \pm 1$ means that the difference between the observed and the predicted mass growth rate equals ±1 SD. Average GI_m $(\overline{\text{GI}}_\text{m})$ was calculated for each of 4 groups (dependent on initial size and depth) for any given sampling period. The present study was specifically focused on producing comparable estimates of seasonal growth rates independent of size, which involved this rather complex process of normalization. However, values of GI_m could easily be back-calculated to the more commonly used absolute mass growth rates; a calculation that provides the opportunity to describe in detail how size affects the ability to maintain a positive energy balance in different seasons.

Environmental parameters. Temperature was registered every 6 h at each culturing depth throughout the experimental period using temperature loggers (HOBO U22 Water Temp Pro v2, Onset Computer Corporation) mounted on each of 2 lantern nets. Approximately every 2 wk we took water samples with a Niskin-type sampler (KC-Denmark) for the analysis of photosynthetic pigments, and particulate carbon and nitrogen at the specific site and depth. This was supplemented with CTD casts (SBE 19+, Sea-Bird Electronics) specifically to measure salinity and generally to get a better spatial understanding of water column properties at the site.

Seawater samples from 15 and 30 m depth were filtered (Whatman GF/C, <0.2 bar) for determination of chlorophyll *a* (chl *a*). The filters were extracted in 96% ethanol for 18 h in the dark. After extraction, the samples were analysed on a Turner Designs TD-700 fluorometer. Chl *a* in the samples was calculated in accordance with Parsons et al. (1984).

Total particulate carbon (TPC) and nitrogen (PON) were measured on water samples filtered onto Whatman GF/C filters. After filtration the samples were dried at 60°C for 24 h and stored separately until analysis on an elemental analyser (ANCA-GSL, SerCon).

Coupling of growth to environmental variation. The total $\overline{\text{GI}}_\text{m}$ data set was used to construct a growth model relating environmental parameters (chl *a*, TPC, C:N, temperature, salinity, chl *a*:TPC, and interaction terms) to mass growth rate. Environmental parameters were averaged by interpolating linearly between data points, as illustrated in Fig. 2a–e, and dividing the integrated area between each scallop sampling by the number of days in the given periods. In this way, the estimates of GI_m and environmental variables represented the same time intervals. The model selection process was based on minimizing the Akaike information criterion (AIC) using a forward selection method. The relative model probability was examined with Akaike weights (W_i) (Johnson & Omland 2004). Models were tested for autocorrelation structure (lag = 1). To examine the robustness of the results to the fact that data were sampled at 2 different depths, dummy variables for depth were added to the model. Data were analyzed using SAS statistical software (SAS Institute 2006).

RESULTS

Environmental parameters

During the initial study period from May to August 2007, it became clear that water column properties at 15 and 30 m depth at the deployment site did not differ as much as we expected. We concluded that the site was too exposed to give the intended variation in environmental parameters between depths, and as a consequence we relocated the lantern nets to a more protected site in Kobbefjord (Fig. 1), where a pycnocline had established during spring and summer.

Temperature. The annual temperature cycle at 15 and 30 m depth is illustrated in Fig. 2a, which shows an amplitude ranging from –1.5°C at both depths in February and March to a maximum of 4.5 to 6°C at 15 m depth and ~3°C at 30 m depth in late summer and early autumn. The time of the relocation of lantern nets from the exposed site to the more protected site in Kobbefjord is easily recognized; in August 2007 the temperature at the 2 depths was very similar indicating a well-mixed water column. The sudden decrease in temperature at 30 m marks the relocation to the Kobbefjord site where the water column was more stratified.

Salinity. Seasonal dynamics in the freshwater runoff from land caused differences in salinity between 15 and 30 m depth during summer. The lowest salinity was observed in summer 2007. During the entire study period, salinity ranged from 29.5 to 33.5 (Fig. 2b).

Chl *a*. A phytoplankton spring bloom was observed in May 2007 and May 2008, when chl *a* concentrations peaked at 2 to 3 µg l^{-1} followed by declining concentrations at both 15 and 30 m depth. A second bloom occurred in August–September at 15 m in both years, while chl *a* concentrations at 30 m declined continuously during the late summer to a minimum of ~0.01 µg l^{-1} during winter (Fig. 2c).

TPC. The concentration of TPC at 15 and 30 m depth in Kobbefjord ranged between ~0.06 and ~0.5 mg l^{-1} in winter and spring–summer, respectively. Distinct peaks were observed in spring at both depths in 2007 and 2008 (Fig. 2d).

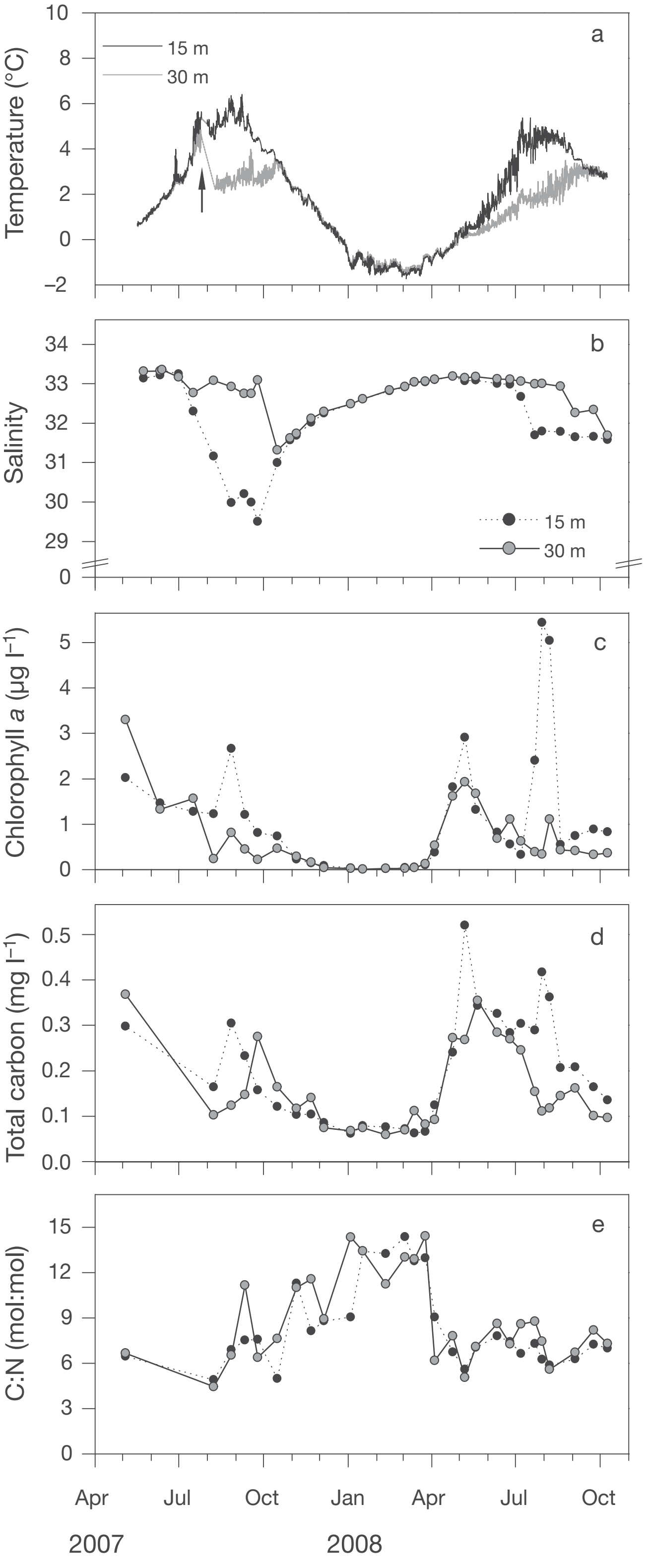

Fig. 2. Variation in environmental parameters at the study site at 15 and 30 m depth from May 2007 to October 2008. (a) Temperature (°C), (b) salinity (PSU), (c) chl *a* (µg l^{-1}), (d) total particulate carbon (TPC) (mg l^{-1}), (e) C:N ratio (mol:mol). Arrow in Fig. 3a marks the time of relocation of scallops

C:N. There was a clear seasonal cycle in the C:N ratio in Kobbefjord. From April to October, C:N values were relatively low, ranging from ~5 to ~8.5 at both depths. Values increased throughout autumn and winter to a maximum of ~14.5, until they steeply decreased again at the onset of the phytoplankton growing season (Fig. 2e).

Tag retention and mortality

The highest tag loss and mortality of scallops was, not unexpectedly, observed in the recovery period following collection and tagging. Of the 752 tagged scallops 6 (0.8 %) had lost their tags during the first ~2.5 mo after deployment. The number of dead specimens in the same period was 10 (1.3 %), after which both mortality and tag loss remained at a constantly low level until the end of the experiment. During the entire study period of 17 mo, 14 tags were lost and 19 individuals died.

Overall patterns in biomass and growth

The general relations between SH (mm) and tissue DM (g) are given below, and illustrated in Fig. 3a:

$$\log_e(DM_{\text{pred somatic}}) = -11.45 + 3.034\log_e(SH)$$
$$(n = 502,\ R^2 = 0.93,\ p < 0.001)$$

$$\log_e(DM_{\text{pred gonad}}) = -28.27 + 6.773\log_e(SH)$$
$$(n = 496,\ R^2 = 0.85,\ p < 0.001)$$

$$\log_e(DM_{\text{pred total}}) = -12.23 + 3.269\log_e(SH)$$
$$(n = 502,\ R^2 = 0.94,\ p < 0.001)$$

The specialized von Bertalanffy growth function established from SID from August 2007 to August 2008 was:

$$SH_{pred} = 94\{1-\exp(-5.9 \times 10^{-3}\ t)\}$$
$$(n = 259,\ R^2 = 0.96,\ p < 0.001)$$

According to this function, the asymptotic SH_∞ was 94 mm and the growth coefficient, K, was 5.9×10^{-3} d^{-1}. The first derivative, which describes shell growth rate, $\hat{G}_s$ (mm d^{-1}) as a function of SH (Fig. 3b), was:

$$\hat{G}_s = 5.9\times10^{-3}SH\left(\frac{94}{SH}-1\right)$$

Overall relations between SH and mass growth rate, G_m, were established by maximizing the joint likelihood. The resulting growth model parameters are listed in Table 1, and show decreasing growth rate with increasing size ($b < 0$). All 3 models gave heteroscedastic variation ($z \neq 0$). The gonad mass growth rate model showed increasing SD with SH ($z > 0$), while the somatic growth rate model showed decreasing SD with increasing SH ($z < 0$). In combination, this resulted in a slightly negative z value in the total mass growth rate model (Fig. 4).

These general models for biomass, shell growth rate, and mass growth rate as a function of SH provided a basis for describing the seasonal dynamics of these parameters.

Seasonal shell growth variation

Both size groups showed the same principal seasonal pattern in shell growth rate, with minimum values

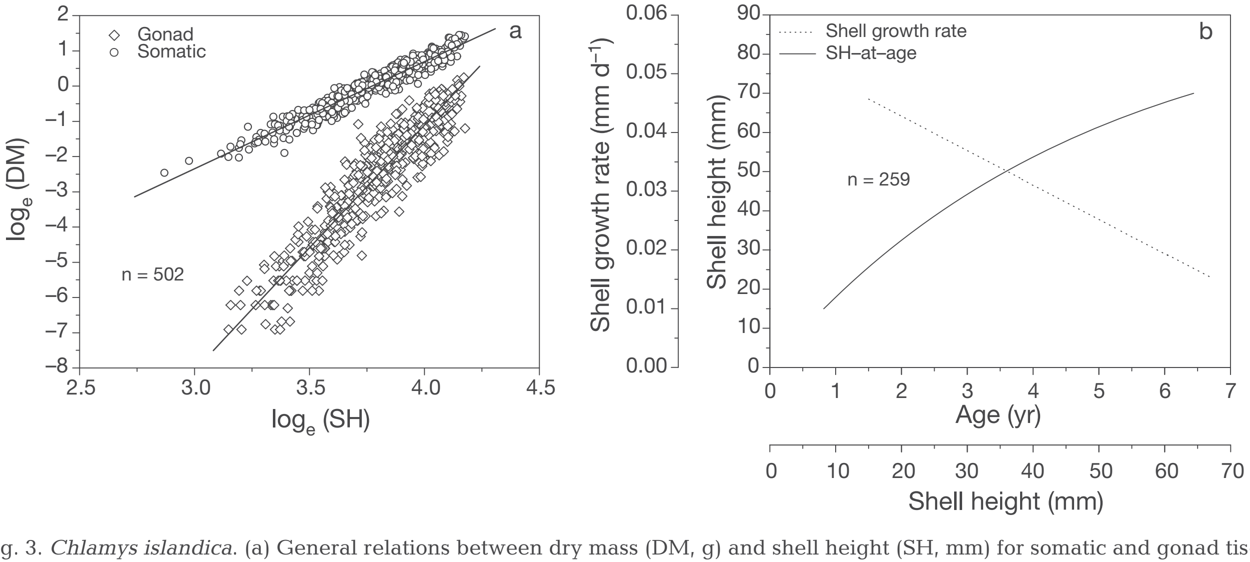

Fig. 3. *Chlamys islandica*. (a) General relations between dry mass (DM, g) and shell height (SH, mm) for somatic and gonad tissues. (b) von Bertalanffy growth function $SH_{pred} = 94\{1-\exp(-5.9 \times 10^{-3}\ t)\}$ estimated from size-increment-data (SID), and its first derivative, showing the average daily shell growth rate as a function of SH

Table 1. *Chlamys islandica.* Parameters of the regression of mass growth rate on shell height (SH) as described in Eqs. (8), (9) & (10). Parameters were obtained by maximizing joint likelihood. Illustrated in Fig. 4

Mass growth	Parameters				Statistics		
model	*a*	*b*	*q*	*z*	n	R^2	p
Somatic	0.0213	−0.0476	0.0124	−0.3440	5186	0.16	<0.0001
Gonad	0.0353	−0.0438	0.0023	0.3815	5186	0.08	<0.0001
Total	0.0197	−0.0443	0.0131	−0.3635	5186	0.16	<0.0001

from January to April and peaking in autumn from August to November (Fig. 5). However, scallops at 30 m depth had lower maximum shell growth rates than those at 15 m depth. This difference was most pronounced in 2007. For scallops in Group 2, the seasonal cycle in shell growth rate was interrupted by an abrupt decline in June–July 2008 concurrent with spawning (see 'Results — Seasonal variation in mass growth').

Seasonal variation in BMI

The ANCOVA tests did not reveal any statistically significant effects of SH or SH × sampling date on BMI ($p > 0.05$), indicating that season did not affect the slope, *b* in Eq. (5), and that BMI could be regarded as size-independent in all seasons. The annual cycle in the somatic biomass index, $\text{BMI}_{\text{somatic}}$, of *Chlamys islandica* was characterized by a fast increase during spring from April to July–August followed by a more stable period during autumn. Winter was characterized by a slower but steady decrease until early April (Fig. 6a,b). The variability of $\overline{\text{BMI}}_{\text{gonad}}$ values at the specific dates was higher than for $\overline{\text{BMI}}_{\text{somatic}}$, but it was still evident that BMI of gonad and somatic tissues did not follow the same seasonal pattern. $\overline{\text{BMI}}_{\text{gonad}}$ at 30 m depth was relatively constant throughout the study period, while at 15 m depth we observed an increase in $\overline{\text{BMI}}_{\text{gonad}}$ from January 2008 to July 2008, where it declined abruptly (Fig. 6c,d). This sudden decline was also reflected in $\overline{\text{BMI}}_{\text{total}}$, which, apart from that, followed a pattern very similar to $\overline{\text{BMI}}_{\text{somatic}}$ (Fig. 6e,f). $\overline{\text{BMI}}$s were generally at a slightly higher level at 15 m than at 30 m depth. This difference was most pronounced in autumn (October–November).

Seasonal variation in mass growth

We observed clear seasonal variation in GI_m of *Chlamys islandica*. Values generally peaked in April–June and were lowest from November to March (Fig. 7). Mass growth rates at 15 m and 30 m were similar during peak growth in spring, but differed in late summer and early autumn, with higher mass growth rates at 15 m than at 30 m depth. A single spawning event indicated by highly negative gonad GI_m values independent of size group and depth, was registered in June–July 2008. Thus, scallops, which were immature at the beginning at the experiment (Group 1) were apparently maturing at the end of the study period.

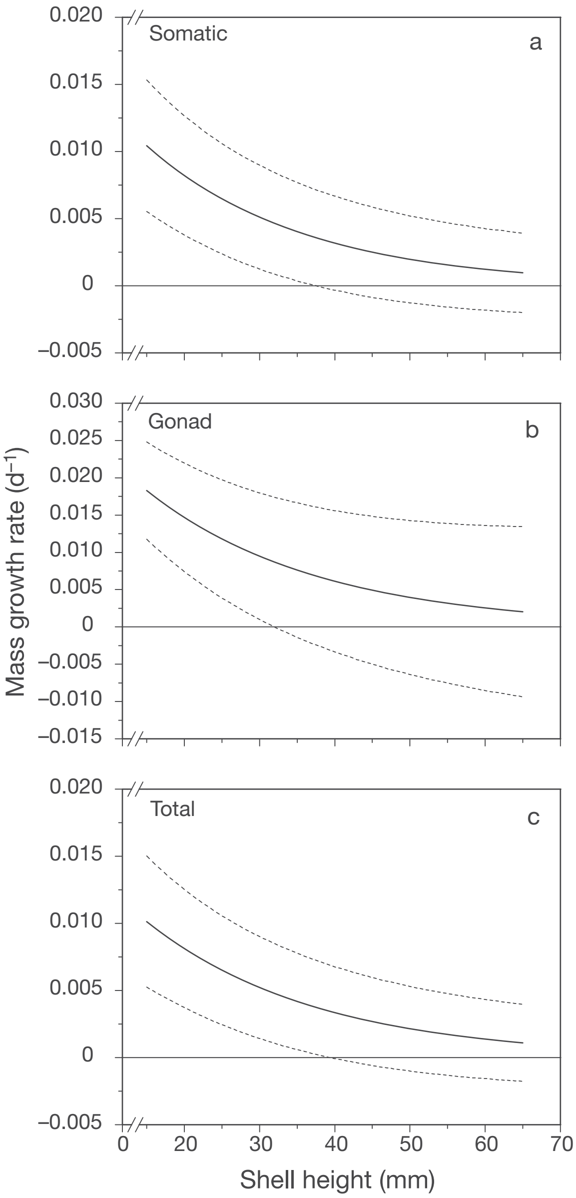

Fig. 4. *Chlamys islandica*. Overall relations between mass growth rate, $\hat{G}_\text{m}$ (somatic, gonad, and total) and shell height (SH). Dotted lines indicate standard deviation (SD). See Table 1 for parameters of the functions

Coupling of mass growth rate to seasonal environmental variation

We corrected for the considerable biomass loss resulting from spawning in early July 2008 by assuming BMI_{gonad} to have the same values as observed in the June sampling, thus removing the effect of spawning on the estimates of GI_m. We did this to exclude any loss of biomass not directly related to the balance between energy intake and metabolic costs. Though not optimal, this approach prevented any bias of data and allowed us to focus on the effects of key environmental drivers on the energy balance of scallops.

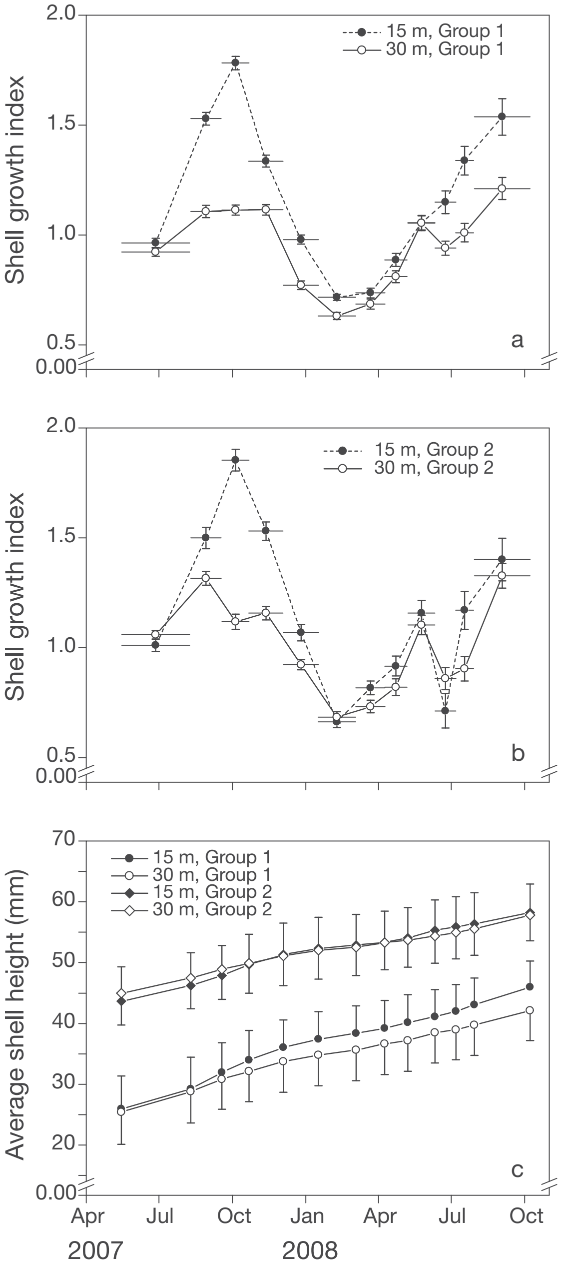

Fig. 5. *Chlamys islandica.* Seasonal variation in shell growth index, GI_s, at 15 and 30 m for the 2 size groups (a) Group 1 and (b) Group 2. Vertical error bars indicate SD. Horizontal bars specify the period for which the average GI_s values were estimated. (c) Average shell height (SH) (±SD) of the 4 separate groups throughout the study period

Chl *a* was found to have a strong and statistically significant ($p < 0.0001$) positive effect on total GI_m of *Chlamys islandica* (Model I, AIC = 80.4, $r^2 = 0.66$). However, this model indicated a statistically significant autocorrelation structure of the residuals ($p < 0.05$). Adding temperature as a second independent variable resulted in an increase in the model fit (Model II, AIC = 76.1, $R^2 = 0.69$), indicating a statistically significant negative effect of increasing temperature on the mass growth rate of scallops ($p < 0.001$). We obtained the best growth model fit by including C:N, which had a statistically significant negative effect ($p < 0.001$) on the mass growth rate (Model III, AIC = 72.1, $W_i = 0.55$, $R^2 = 0.71$). Neither TPC, chl *a*:TPC, nor salinity had any statistically significant effect ($p > 0.05$) and increased the AIC (models not shown). Likewise, no interaction terms increased model fit significantly. We found no significant autocorrelation in Models II and III ($p > 0.05$) and the non-significant autoregressive parameters were backward eliminated. Dummy variables for depth were added to Model III to test the robustness of the model. The effect of depth was not statistically significant ($p = 0.88$), and neither size nor the statistical significance of the coefficients was affected by adding dummies to the model (Model IV, AIC = 72.9, $W_i = 0.37$, $R^2 = 0.72$) (Table 2).

DISCUSSION

Mass growth rate in relation to environmental variation

The seasonal cycles of temperature and food availability (chl *a*, C:N, TPC) were partly decoupled in SW Greenland. The spring phytoplankton bloom went on at very low temperature (~0°C), followed by an increase in temperature and a late summer bloom at 15 m depth. This made it possible to distinguish between the effects of these factors on the growth rate of *Chlamys islandica*. Seasonal variation in the total mass growth rate of *C. islandica* correlated statistically significantly to food availability (chl *a* and C:N) and temperature. The forward selection procedure of regression models indicated that the concentration of chl *a* in the surrounding water column was the most important explanatory parameter for the variation in mass growth rate of *C. islandica* (Table 2). Together with the fact that the effect of seasonal variation in C:N

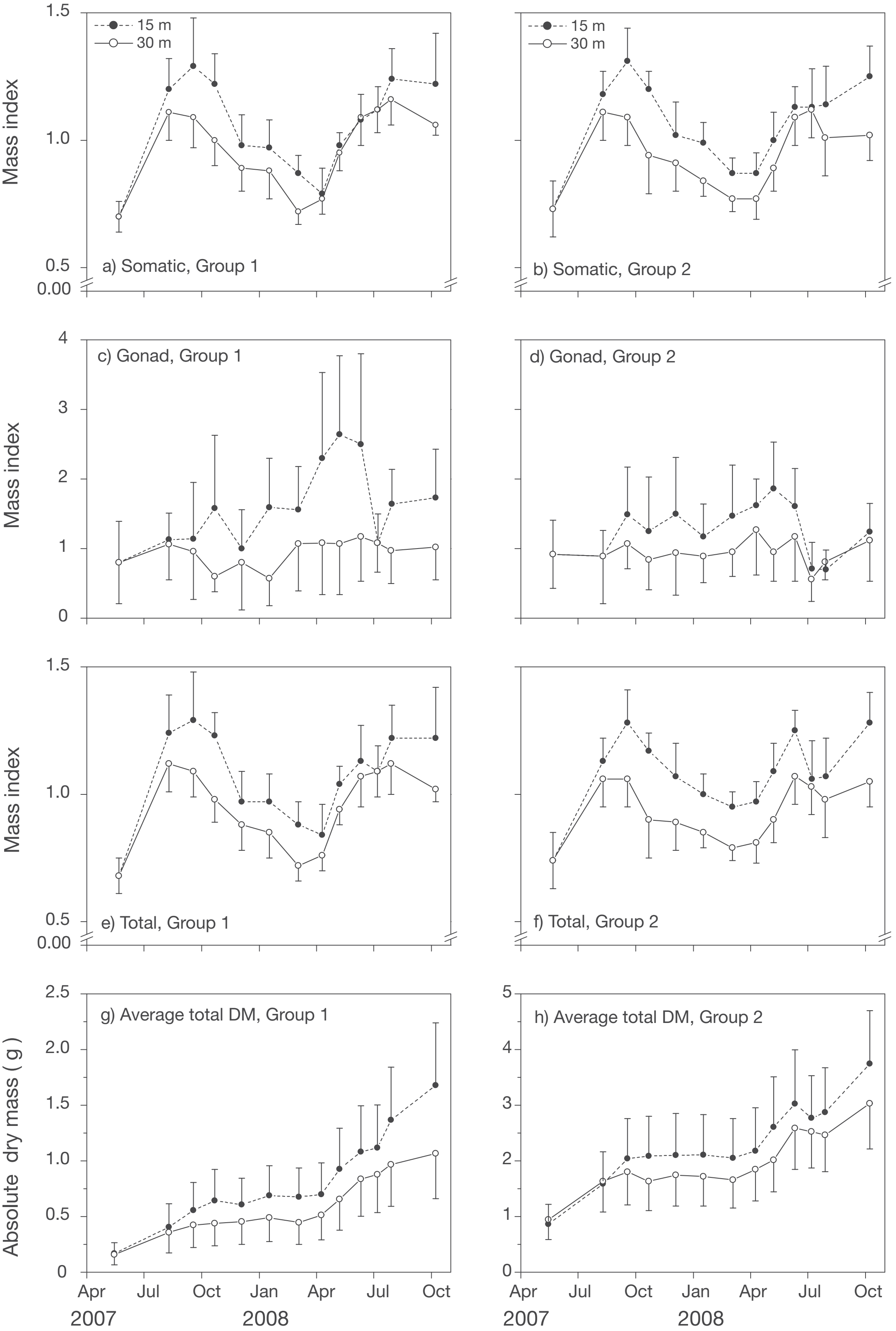

Fig. 6. *Chlamys islandica.* (a–f) Seasonal variation in average biomass index, $\overline{\text{BMI}}$ (somatic, gonad, and total) at 15 and 30 m for the 2 size groups (Group 1 and Group 2), respectively. (g,h) Temporal development in average individual biomass in absolute values for Groups 1 and 2 at 15 and 30 m, respectively, throughout the study period. Vertical error bars indicate SD

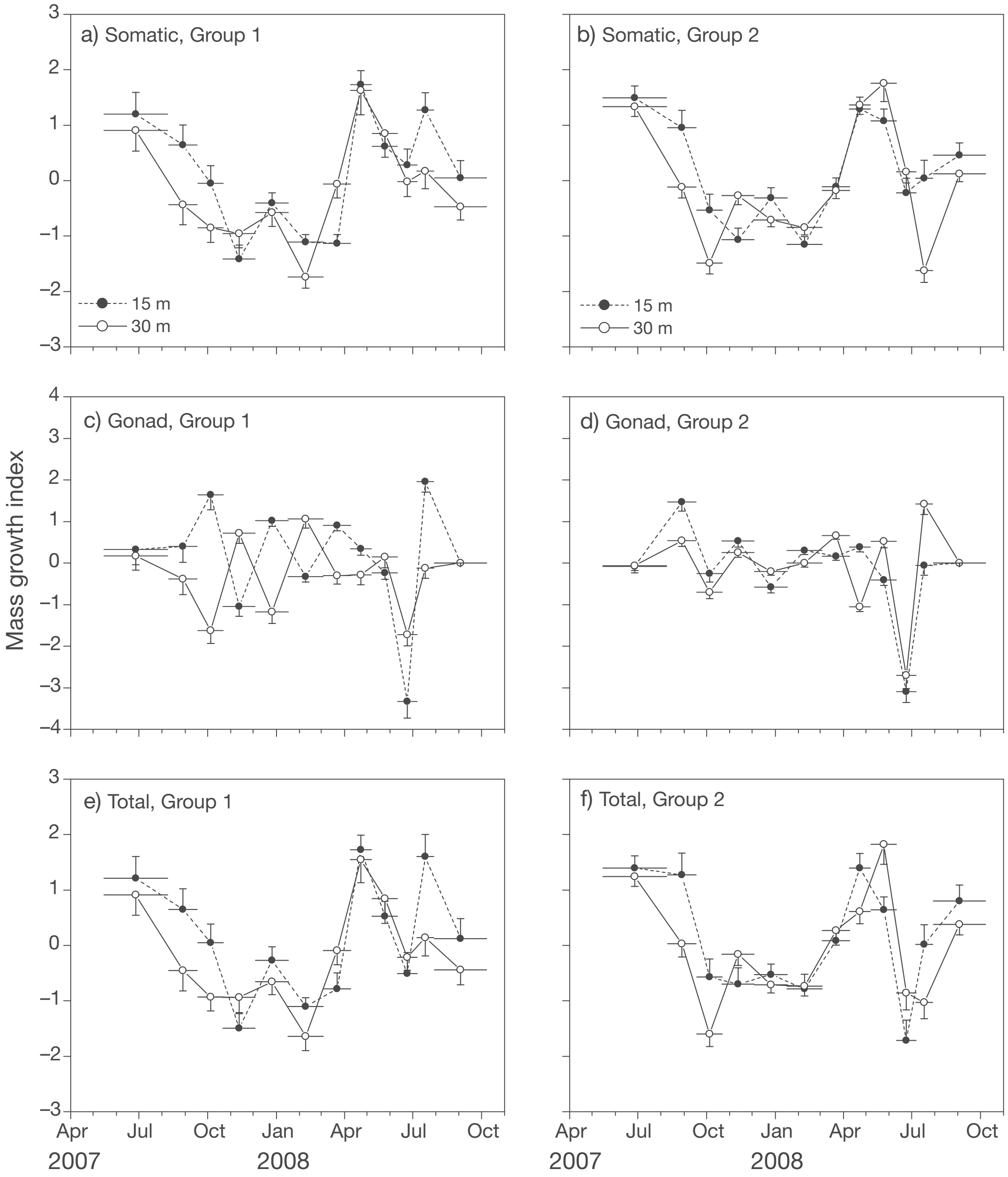

Fig. 7. *Chlamys islandica.* Seasonal variation in average mass growth index, GI_m (somatic, gonad, and total) at 15 and 30 m for the 2 size groups (Groups 1 and 2) respectively. Vertical error bars indicate the SD. Horizontal bars specify the period for which the average GI_m values have been estimated

ratio was statistically significant, and that TPC was not, this result indicated that the availability of high-quality food items such as phytoplankton is essential for the mass growth rate of scallops. Other potential sources of food, such as sedimentary, resuspended, or allochtonous matter being partly degenerated, were apparently not utilized efficiently and were therefore of secondary importance in the study area. However, from Fig. 2c it seems highly likely that chl *a* and TPC covary, and this potential co-variation might account for the lack of significant effects of TPC using the forward selection procedure. Actually TPC correlated significantly to GI_m ($p < 0.01$, $R^2 = 0.42$); however chl *a* was selected as the better predictor (Table 2), and in the following steps TPC came out insignificant. In any case, although TPC did not come out as statistically significant in the growth model, low-quality food items might be of crucial importance during starvation in the winter period in order to maintain or minimize the loss of biomass.

Table 2. Coefficients (±SE) and Akaike's information criterion (AIC) of the forward selected regression models for the effect of environmental parameters on mass growth (total GI_m, n = 48) of *Chlamys islandica*. W_i (AIC) = Akaike weight (model probability). Non-significant parameters (ns) were backward eliminated (except for control variables). $^*p < 0.05$, $^{**}p < 0.01$. Model III was the best-fit model with a model probability (W_i) of 55%. –: not included in model

	Model			
	I	II	III	IV
Intercept	-0.68^{**} (0.18)	-0.71^{**} (0.12)	ns	ns
Chl *a* ($\mu g\ l^{-1}$)	0.93^{**} (0.16)	1.25^{**} (0.13)	1.13^{**} (0.11)	1.14^{**} (0.12)
Temperature (°C)	–	-0.16^{**} (0.05)	-0.19^{**} (0.04)	-0.19^{**} (0.05)
C:N (mol:mol)	–	–	-0.06^{**} (0.01)	-0.06^{**} (0.01)
Autocorrelation				
Lag 1	0.37^{*} (0.15)	ns	ns	–
Control variables				
15 m	–	–	–	-0.02^{ns}
30 m	–	–	–	0.00
R^2	0.657	0.687	0.713	0.717
AIC	80.4	76.1	72.1	72.9
W_i (AIC)	0.009	0.074	0.549	0.368

Our results are in accordance with Thorarinsdóttir (1994) who suggested that the growth season for *Chlamys islandica* in Iceland coincided with the period of high phytoplankton levels. Likewise, Harrington (1987) suggested that large-scale variations in the growth of the venerid bivalve genus *Protothaca* in the NE Pacific were caused by differences in the length of the period during which organisms could feed. This also agrees with a laboratory study of a high-Arctic clam *Hiatella arctica* at sub-zero temperature concluding that energy assimilation increased with chl *a* concentrations until an optimum at 8 $\mu g\ l^{-1}$ chl *a*, which was never attained in its natural environment (Sejr et al. 2004). In comparison, maximum chl *a* concentrations found at our study site were 3 to 5 $\mu g\ l^{-1}$ during blooms. Another proxy for the nutritional value of seston, the ratio between inorganic and organic particles (PIM:POM), was suggested to affect the energy balance of *C. islandica* in northern Norway by reducing the absorption efficiency at high fractions of PIM (Vahl 1980, Wallace & Reinsnes 1985). This indicated that *C. islandica* might be susceptible to elevated inputs of inorganic particles from land, and to resuspension of bottom material, which has been suggested for other bivalve species (Riisgård 2001, Ellis et al. 2002, Safi et al. 2007). In temperate and tropical areas the seasonal and short-term variations in metabolism and clearance rate, shell growth, condition, or mass production of bivalves have been studied intensively. Effects of current speed and wave exposure, particle size, as well as salinity changes have been suggested in some studies (Kirby-Smith 1972, Roman et al. 1999, Sobral & Widdows 2000, Steffani & Branch 2003). However, a number of studies have indicated that spatial or temporal variation in food availability, expressed either as the amount of chlorophyll, the organic or energetic content of seston, or total seston, is a major factor regulating the production of scallops (Macdonald & Thompson 1985, Lodeiros et al. 1998, Pilditch & Grant 1999, Navarro et al. 2000, Hunauld et al. 2005). The importance of different proxies for the quality or quantity of food seems to vary depending on site and seston characteristics and on species. Other studies have reported either positive or negative effects of increasing temperature on the energy balance of bivalves within the normal range of habitat temperature (Witbaard et al. 1997, Han et al. 2008, Beukema et al. 2009). The growth rate of the bay scallop *Argopecten irradians* was independent of chl *a* concentrations (0.5 to 5.5 $\mu g\ l^{-1}$) at low temperatures for its natural habitat (10 to 16°C), but became increasingly correlated with chl *a* levels at higher temperatures (22 to 28°C) (Kirby-Smith & Barber 1974), reflecting the increased metabolic costs at higher temperatures. In combination, the available studies support the idea of interrelated effects of temperature and resource availability on the energy balance of bivalves and other ectotherms (e.g. Clarke 2003). It is well documented that elevated temperature increases the metabolic rate of ectotherms living within their thermal limits (Q_{10} = 2 to 4) (Gillooly et al. 2001), and pectinids are no exception (Heilmayer et al. 2004). Elevated physiological rates can be assumed to affect the filtering capacity of bivalves positively (e.g. Petersen et al. 2003), thus increasing the potential consumption of food and the capacity for growth. On the other hand, in a food-limited environment (absolute or temporal) elevated physiological rates might turn into an energetic disadvantage, because the increased energetic demands cannot be completely compensated for by higher energy intake (Pilditch & Grant 1999, Clarke 2003, Clarke & Fraser 2004). *C. islandica* in SW Greenland is well within the thermal limits of this species (Jonasson et al. 2004). Thus, the negative effect of increasing temperature on the mass growth rate of *C. islandica*, as suggested in the mass growth model in this study (Table 2), supports the indication of resource limitation at the study site in SW Greenland. Hence, within the existing range of resource quality and quantity and temperature, the capacity for consumption or growth of *C. islandica* is either never realized or only attained for short periods of time. Instead, low water temperature (~0°C) provides the basis for

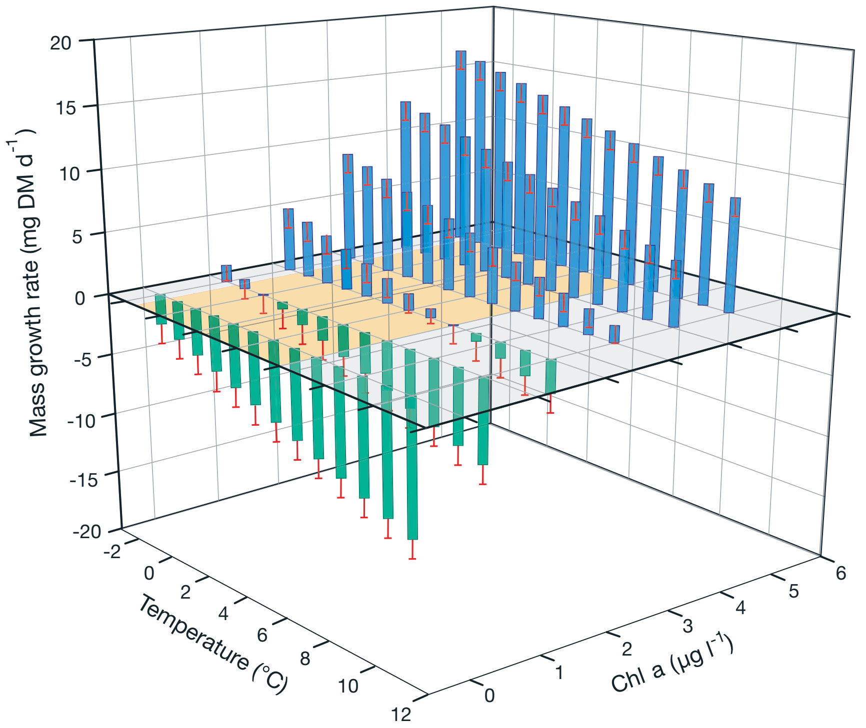

Fig. 8. *Chlamys islandica.* Absolute mass growth rate of an individual of 1 g dry mass (DM) (42 mm shell height, SH) plotted against temperature and chl *a* at C:N = 6.6 (Redfield ratio). Red bars indicate the negative effect of the C:N ratio increasing to 14. Yellow shaded area shows the range of environmental parameters in the study area during 2007 and 2008

low metabolic costs of *C. islandica* during the starvation period in winter and for maximizing the growth efficiency during the spring phytoplankton bloom. Therefore, potential phytoplankton blooms during the warmer summer period, as observed in 2008, cannot be converted into mass growth as efficiently as in spring as a consequence of higher basic metabolic costs. This is illustrated with absolute values of mass growth rate in Fig. 8, which describes visually how small changes in the seasonal dynamics of temperature and food conditions affect the energy budget of *C. islandica*. The yellow shaded area indicates the range of parameters given in the study area during 2007–2008. However, *C. islandica* is able to exist successfully under warmer conditions than the ones recorded in SW Greenland, e.g. in Norway and Iceland (Vahl 1978, Thorarinsdóttir 1994). For scallops there is no indication of an uncoupling of basal metabolism and temperature on a geographical scale (Heilmayer et al. 2004). Thus, increased metabolic costs in response to elevated temperature should be compensated for by higher energy assimilation, ultimately resulting in reduced growth efficiency at higher temperatures, which is implicit in our mass growth model and in agreement with a comparative analysis of scallop species living at different temperature regimes (Heilmayer et al. 2004). On an evolutionary time-scale marine ectotherms are probably not selected for their high growth efficiency as much as for their absolute rate of new tissue production (Clarke 1993, Pörtner et al. 2005). However, it is evident that high energy efficiency is an effective way of maximizing absolute growth in a resource-limited environment like our study site in SW Greenland.

In conclusion, it is reasonable to suggest that, within the ranges of environmental parameters given in this study, the growth capacity of *Chlamys islandica* is determined by temperature. However, this growth capacity cannot be realized due to food limitations, which makes food fluctuations the most important factor for scallop growth in sub-Arctic Greenland.

Still, it is important for us to stress that the present study solely considers the effect of seasonal variation in environmental parameters on the mass growth rate of *Chlamys islandica*, not geographical variation nor long-term changes. The extent to which our results can be considered representative of other spatial and temporal scales as well as of other macrobenthic species is still to be tested. We are convinced, however, that the changes in seasonal dynamics of physical as well as biological structures are the basis for potential long-term changes of ecosystems, which in itself emphasizes the perspective of the present study.

Comparison of wild and suspended scallops

The overall shell growth pattern of the cultured scallops, as expressed through the von Bertalanffy growth function, differed from the wild population from 50 to 60 m depth in Kobbefjord (Blicher et al. 2009). Scallops growing in culture at 15 and 30 m depth have a markedly faster average annual growth rate and were able to reach a SH of 60 mm within ~5 yr, while it takes more than 10 yr to reach the same size in the local wild population (Blicher et al. 2009), which is similar to Svalbard and other localities in west Greenland. Wild populations in northern Norway, Canada, and Iceland reached 60 mm SH in 6 to 7 yr (Pedersen 1994 and references therein). Markedly increased growth rates of *Chlamys islandica* in suspended cultures at shallow depth compared to a natural population have been observed previously in Iceland (Thorarinsdóttir 1994). Even though our mass growth model (Table 2) is based on data for suspended scallops, we believe that growth of scallops living under natural conditions on the seabed is affected by the same exogenous parameters as growth of scallops in a suspended culture. Based on the growth rate model we suggest that spatial differences in food availability and temperature are major causes of growth variation in scallops. In the present study, the suspended scallops were placed at depths near the subsurface peak in algal biomass observed during spring and autumn (Mikkelsen et al. 2008). In addition, wild scallops might episodically be faced with the challenge of resuspension of bottom material containing high amounts of inorganic material. However, in the natural environment in Greenland the abundance of *C. islandica* is low at depths <20 m (Pedersen 1994, Blicher et al. 2009), which indicates that other factors than the ones investigated in the present study prevent them from spreading to this seemingly favourable habitat. The distribution pattern may be affected by: (1) substrate-dependent settling indirectly related to depth; (2) depth-related differences in epi-growth (e.g. barnacles, macroalgae, sponges) with an effect on mortality on a longer time-scale than our study; (3) other types of inter-specific competition or predation. Firstly, it is well-established that certain substrates are more favourable for settling of *C. islandica* than others (Harvey et al. 1993, Arsenault & Himmelman 1996a). In the study area *C. islandica* seems to prefer settling on coarse substrates or shell gravel (Pedersen 1994, Blicher et al. 2009), and juveniles are often found attached to the inner side of old scallop shells (M. E. Blicher pers. obs., Arsenault & Himmelman 1996b). Therefore, depth-related changes in the sea bed structure might affect the distribution of *C. islandica*. Secondly, it has been suggested that epi-growth can be responsible for relatively high mortalities of scallops in otherwise favourable habitats (Lodeiros et al. 1998). In the wild population of *C. islandica* at 50 to 60 m depth in Kobbefjord we observed high epi-growth of primarily barnacles on the shells of some of the largest (>75 mm SH) and presumably oldest individuals, potentially affecting their fitness. However, the scallops suspended at 15 and 30 m depth were not affected by epi-growth to any large extent, and differences between depths were not clearly detectable, even though filamentous macroalgae were more abundant on the lantern nets at 15 m compared to 30 m depth (not quantified). A third possibility is that scallops are prevented from spreading to a more favourable habitat by shallow-living competitors. In a previous study in Kobbefjord it was found that the sea urchin *Strongylocentrotus droebachiensis* dominated the epibenthic community down to 20 m depth. Thus, sea urchins and scallops were to a large extent separated vertically (Blicher et al. 2009). *S. droebachiensis*, which is very common in Greenland (Blicher et al. 2007), can be an aggressive grazer on a variety of diets and produces barrens (Himmelman et al. 1983, Meidel & Scheibling 1999, Balch & Scheibling 2000, Gagnon et al. 2004), and might be a co-factor affecting the distribution of *C. islandica*. Also the crab *Hyas areneus*, which is common in the study area, can be an important predator on juvenile *C. islandica*, and field experiments have shown that the vulnerability of scallops to predators is highly affected by substrate and the possibility of finding refuge (e.g. crevices, dead shells) (Arsenault & Himmelman 1996b)

The factors controlling the depth distribution of scallops are still unresolved, however. Even though we may have left out some potentially important factors affecting the overall success of *Chlamys islandica* in the ecosystem, the coupling of growth to food availability and temperature is still valid and can be considered important within the ecological niche of this species. Our conclusions are strengthened by the fact that the experiment was carried out in the natural environment, thus increasing the relevance on a broader ecological scale.

The use of proxies for seasonal mass growth

The present study also provides the opportunity to evaluate the use of biomass indices and shell growth as proxies for seasonal variation in production. These and other parameters have been used in a number of studies as alternatives to measures of actual soft tissue production (e.g. Wallace & Reinsnes 1985). Though not always tested, the suitability of these proxies varies and is highly dependent on the experimental set-up, e.g. the temporal scale (Wo et al. 1999). Our study of *Chlamys islandica* indicates a mismatch between tissue production and shell growth ($R^2 = 0.01$, $p = 0.49$, $n = 48$), which has been observed in other polar ectotherms (Peck et al. 2000), potentially resulting in a decreasing biomass index (BMI) during a period with relatively constant individual biomass (Fig. 6e–h). We observed the highest tissue growth rates in May, while shell growth did not peak until October (Figs. 5 & 7), albeit showing similar tendencies with regard to differences between depths on an annual scale. This might be interpreted as a lag between tissue production and shell growth. However, a positive effect of temperature on the rate of elemental uptake into the shell of bivalves has been shown (Strasser et al. 2008). Seasonal variation in shell growth rate of *C. islandica* in this study was positively correlated to temperature ($R^2 = 0.63$, $p < 0.01$, $n = 48$). However, at present it is uncertain whether this was a result of a causal relationship. In any case, neither seasonal variation in shell growth nor that in biomass index of *C. islandica* would be reliable proxies for the actual soft tissue production.

CONCLUDING REMARKS

Different concepts have been proposed regarding the relative importance of temperature and food availability for the population dynamics of polar marine ectotherms (Krogh 1916, Clarke 2003, Pörtner et al. 2005). Based on ecosystem monitoring studies and laboratory experiments, food limitation has been suggested to be a general phenomenon for Arctic macrobenthos (Ambrose & Renaud 1995, Sejr et al. 2004, Grebmeier et al. 2006, Blicher et al. 2009). However, this apparent resource dependency has not been described in detail. In the present study, we observed a high degree of seasonal and spatial variation in the growth of *Chlamys islandica*, which was strongly linked to variation in food availability as well as temperature, confirming the initial hypothesis that this species is resource limited in SW Greenland, and that increased temperature through its effect on metabolic costs reduces growth efficiency. Thus, our study provides detailed information on the degree of seasonality and the processes controlling benthic production in the Arctic. The expected future shifts in annual temperature cycle, and changes in sea ice dynamics and in freshwater run-off potentially affecting the level of primary production in the Arctic area, are likely to affect the seasonal energetics of *C. islandica*, and consequences may be long-term. *C. islandica* might benefit from future climate changes in high-Arctic areas where reduced sea ice cover will increase primary production markedly, but water temperature will remain constantly low (~0°C). However, in warmer sub-Arctic areas the energetic outcome is expected to be more dependent on the timing between phytoplankton blooms and the seasonal temperature dynamics, which is difficult to predict at present. In conclusion, our results emphasize the importance of understanding ecological relationships on a short-term scale in order to be able to interpret long-term changes.

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Paper IV

SEASONAL AND SPATIAL VARIATIONS IN THE RNA:DNA RATIO AND ITS RELATION TO GROWTH IN SUB-ARCTIC SCALLOPS

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Seasonal and spatial variations in the RNA:DNA ratio and its relation to growth in sub-Arctic scallops

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ABSTRACT: We examined the RNA and DNA concentration of field-caught scallops *Chlamys islandica*, maintained in suspended cultures at 15 and 30 m depth, and scallops from a wild population at 50 to 60 m in Kobbefjord, southwest Greenland. General relations between RNA and DNA concentrations and individual shell height were established, and we found that the RNA:DNA ratio (RD) worked well as a standardisation of the RNA concentration independent of size and sex. During an experimental period of 14 mo, we observed a pronounced seasonal pattern in RD and mass growth, and differences between depths. Even though the period with high levels of RD reflected the growth season relatively well, RD was a poor predictor of individual mass growth rates of *C. islandica*. However, we found a non-linear response in RD to increased food concentrations resulting in RD being up- and down-regulated at the beginning and end of the productive summer season, respectively. These results indicate that short-term dynamics in the actual mass growth rate might be controlled through regulation of ribosome activity rather than ribosome number (RNA concentration). This adaption would allow scallops to up-regulate protein synthesis more rapidly, thereby ensuring efficient utilisation of the intense peaks in food availability in coastal areas in the Arctic. Therefore, we suggest that RD in *C. islandica* reflects the growth potential rather than the actual growth rate. Still, the amount of unexplained variance in RD is considerable and not independent over time, suggesting the existence of unresolved mechanisms or relationships.

KEY WORDS: Macrobenthos · Bivalve · Pectinid · *Chlamys islandica* · Greenland · Biomarker · Food availability

INTRODUCTION

Bivalves dominate shallow benthic communities in the Arctic and are considered to have a large functional importance in the marine ecosystem in coastal areas (Sejr et al. 2000, 2007, Blicher et al. 2009). Not only do they affect the physical and biochemical characteristics of the benthic habitat (Graf & Rosenberg 1997, Ragnarsson & Raffaelli 1999, Riisgård & Larsen 2005), but they are also important sources of food for several dominant predators, i.e. eider duck, long-tailed duck, walrus, bearded seal, cod, and wolf fish (Liao & Lucas 2000, Link & Garrison 2002, Born et al. 2003, Dehn et al. 2007, Merkel et al. 2007). Hence, the population dynamics of bivalves are expected to affect other trophic levels both directly and indirectly.

Individual production of bivalves in Greenland varies considerably on different temporal and spatial scales (seasonally, inter-annually, along depth gradients, and geographically; Sejr et al. 2009, Blicher et al. in press). However, traditional approaches to studying growth variation in bivalves (cohort analysis, tag-recapture, annual growth increments) are time-consuming and elaborate. This is further complicated by the logistical challenges in Greenland, which spans from 60 to 84° N in its geographical range (~2700 km)

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with a pronounced seasonal sea ice cover. Consequently, little is known about the spatial or the temporal dynamics in the marine environment off Greenland. This is in strong contrast to the need for knowledge about the ecological relationships in the marine environment in the Arctic (ACIA 2005). Therefore, the validation of an easily obtained proxy for the growth rate of Arctic marine fauna would be of great value in studies of population dynamics. It would provide the opportunity to study growth dynamics at a multitude of locations with contrasting habitat characteristics, potentially revealing causal relationships between environment and biota. The RNA:DNA ratio (RD) of animal tissue is a measure of the capacity for protein synthesis (Wright & Hetzel 1985, Dahlhoff 2004). RD has been widely used in studies of fish larvae, where it has been validated as a proxy for the mass growth rate or the physiological condition (Buckley 1984, Clemmesen & Doan 1996, Grønkjær et al. 1997, Caldarone et al. 2003, Buckley et al. 2008). In studies of invertebrate taxa, it has been suggested that variations in nucleic acid ratios (RD, RNA:protein, or total RNA concentration) relate to metabolic activity, physiological robustness, reproductive state, food availability, or temperature (Robbins et al. 1990, Lodeiros et al. 1996, Buckley & Szmant 2004, Dahlhoff 2004, Kim et al. 2005, Norkko et al. 2005a, 2006b, Fraser et al. 2007). Some studies have suggested that RD is affected by size and sex (Robbins et al. 1990, Lodeiros et al. 1996, Roddick et al. 1999, Chicharo et al. 2007). Even though it has often been assumed that RD can be regarded as an indirect measure of mass growth rate, only few studies have measured the actual growth rate of bivalves simultaneously with RD. However, Lodeiros et al. (1996) found that a highly significant positive correlation between growth rate and RD of juvenile scallops in Venezuela weakened in maturing individuals. Altogether, these results indicate that a number of parameters need to be taken into account when interpreting RD variations, and that its suitability as a proxy for the mass growth rate should be critically examined before implementation into research and monitoring programs. Still, it is likely that RD has a large potential in marine ecological studies in polar areas (Norkko et al. 2005a).

The scallop *Chlamys islandica* is common from temperate to high-Arctic areas at depths down to 130 m. It is widely distributed along the coast of Greenland (Pedersen 1994). Studies of growth variation of *C. islandica* in Kobbefjord, SW Greenland, showed that growth differed significantly between depths and seasons, and that these differences were caused primarily by variation in food availability. Thus, we have suggested that *C. islandica* is generally food limited in its natural habitat in SW Greenland (Blicher et al. 2009, in press). In parallel with studying the temporal and spatial growth variation, we took tissue samples for the analysis of RNA and DNA concentration in *C. islandica*.

Here our aim was to describe seasonal variations in RD in the tissue of *Chlamys islandica* at 3 different depths in Kobbefjord. We then compared these data to variations in mass growth rate in order to evaluate the potential of RD as a general proxy for the growth rate of this species. We hypothesised that mass growth rate and RD varied synchronously, revealing a causal relationship. In addition, we examined the possibility of a direct coupling to scallop condition and to variations in food availability and temperature in the surrounding water column.

MATERIALS AND METHODS

Experimental setup. ***Suspended scallops:*** *Chlamys islandica* were collected using a triangular dredge in May 2007 at 50 to 60 m depth in the outer Kobbefjord. To be able to estimate future individual growth rates, we measured the initial shell height (SH) of all scallops to the nearest 0.01 mm and tagged them individually with numbered shellfish tags (4 × 8 × 0.15 mm, Hallprint) on the upper shell. Scallops were divided into 2 different initial size groups, representing immature (15 to 35 mm SH: Group 1) and maturing bivalves (35 to 55 mm SH: Group 2; Pedersen 1994, Blicher et al. 2009), and transferred to lantern box nets (FUKUI type, Coastal Aquacultural Supply). Each of the 2 size groups was suspended in lantern nets at 2 different depths, 15 and 30 m, approximately 1 nautical mile from the site of collection in Kobbefjord. Thus, we analysed 4 separate groups, differing in size and/or deployment depth. Despite individual growth during the experiment, we will keep the separation of individuals into 'size groups 1 and 2' referring to the initial SH of the scallops. During a period of ~14 mo, we measured the shell growth of all individuals at approximately monthly intervals. On 11 occasions, ~10 individuals from each size group and depth were randomly sub-sampled (n = 436 in total).

Wild scallops: In addition to the suspended scallops, we collected wild scallops at 50 to 60 m depth in the outer part of Kobbefjord in the same intervals as the suspended scallops. Again, individuals were separated into size groups 1 and 2, with 10 individuals in each group (n = 216 in total).

Analysis of RNA and DNA concentration. Immediately after collection, we removed a tissue sample from the adductor muscle of each sub-sampled individual for analyses of RNA and DNA concentration. The tissue (10 to 100 mg wet mass) was transferred to a sterile Eppendorf tube and kept at –80°C. During the entire experiment we extracted tissue samples from a total of 652 individuals. During the period from sampling in Greenland until the analysis of RNA and DNA concentration in the laboratory at IFM-GEOMAR, Kiel, Germany, the tissue samples were continuously stored at a temperature below –60°C. They were transported from Greenland by ship (RV 'Dana') to Denmark stored in a –80°C freezer. During transport from Denmark to the laboratory in Kiel (~4 h), samples were kept on dry ice (–60°C). The concentration of nucleic acids in the tissue was analysed using a modification of the method of Clemmesen (1993) and Belchier et al. (2004). Adductor muscle tissue samples were freeze-dried in opened vials for 16 h, using a Christ Alpha 1-4 freeze-drier at –51°C and weighed to the nearest 0.1 µg (Sartorius microbalance SC2). From the total freeze-dried sample, a subsample with an approximate dry weight of 0.5 mg was cut out and transferred to a new vial. Three large (∅ 2 mm) and a spatula tip of small (∅ 0.2 mm) glass beads and 400 µl Tris-EDTA extraction buffer (Tris 0.05 M, NaCl 0.01M, EDTA 0.01M) containing a detergent (SDS 0.01 %) were added. Rehydration took place on ice for 30 min. Cells were disrupted by shaking in a cell mill (Mixer Mill MM2, Retsch) for 15 min. The homogenate was centrifuged for 8 min at 3829 × *g* (6800 rpm) and 0°C (Sigma Laboratories Centrifuges 3-18K). The supernatant (300 µl) was pipetted into a new 1.5 ml cap vial, diluted according to the dry weight of the sample, and vortexed, and 130 µl were pipetted into a black 96 well microtitre plate. For each measurement, calibration curves for RNA and DNA were determined ($r^2 > 0.98$), and a control homogenate was added. The fluorometric assay was performed on a Labsystems Fluoroscan Ascent using integrated dispensers for both the nucleic acids stain (ethidium bromide) and buffer (Tris-EDTA), with an excitation wavelength of 355 nm and measuring at an emission wavelength of 590 nm. Autofluorescence was measured first, before the fluorophore ethidium bromide was added. Subsequently, total nucleic acid fluorescence was measured, and RNase (Serva, Ribonuclease A, 34388) was added to degrade the RNA. After the enzyme treatment (30 min at 37°C), the remaining (DNA) fluorescence was measured. RNA fluorescence was calculated by subtracting DNA fluorescence from the total nucleic acid fluorescence. RNA was calculated based on the standard curve using 16S, 23S ribosomal RNA (Boehringer Mannheim, order no. 10206938001). The DNA concentrations were calculated using the relationship between RNA and DNA fluorescence described by Le Pecq & Paoletti (1966) using a slope ratio of 2.2 for DNA to RNA.

Scallop mass growth rate and condition. Scallops sampled for the analyses of nucleic acids and biomass were dissected into gonad and somatic tissues. The sex was determined by the colour of the gonads. We measured the wet mass and determined dry mass (DM) by drying at 60°C for 72 h or until they reached a constant weight. In the following text we refer to condition and mass growth in terms of total tissue mass.

Blicher et al. (2010) obtained a general relation between SH (mm) and individual DM (g) of *Chlamys islandica*:

$$\mathrm{DM_{pred}} = 4.86 \times 10^{-6}\ \mathrm{SH}^{3.269} \quad (n = 502,\ R^2 = 0.94,\ p < 0.001) \tag{1}$$

from which we calculated a biomass index (BMI) for each individual collected:

$$\mathrm{BMI} = \mathrm{DM_{obs}}/\mathrm{DM_{pred}} \tag{2}$$

For the suspended (and tagged) scallops, a combination of individual shell growth rates and changes in BMI were used to estimate the individual instantaneous mass growth rate, G_m (d^{-1}) of scallops between 2 sampling dates:

$$G_{\mathrm{m}(1,2)} = \frac{\mathrm{Ln}\left[\dfrac{\mathrm{DM_{obs(2)}}}{\mathrm{DM_{pred(1)}} \times \overline{\mathrm{BMI}}_{i(1)}}\right] \times 1000}{\Delta t_{(1,2)}} \tag{3}$$

where $\mathrm{DM_{pred}}$ is estimated from the general model, Eq. (1). $\overline{\mathrm{BMI}}_{i(1)}$ is the average biomass index at time 1, and the subscript *i* refers to the 4 combinations of depth (15, 30 m) and size group (1, 2). $\mathrm{DM_{obs(2)}}$ is the observed dry mass for an individual collected at time 2.

We also estimated an index of condition similar to what has been termed a 'gravimetric index of condition', CI, by Norkko et al. (2005b), which is the tissue dry mass to wet mass ratio (CI = DM:WM). Contrary to other biomass indices relating tissue DW to shell weight or height, CI is independent of a potential asynchrony in the growth of tissue and shell. The index is suggested to reflect tissue gain or loss within days to months (Norkko et al. 2005b). The mass of the muscle tissue used for RNA and DNA analysis was included in the calculation of CI and mass growth rate.

Environmental parameters. Temperature was registered every 6 h at 15 and 30 m depth throughout the experimental period using temperature loggers attached to the lantern nets (HOBO U22 Water Temp Pro v2, Onset Computer Corporation). At 55 m depth, temperature was registered with a CTD (SBE 19+, Sea-Bird Electronics). Approximately every second week, and always on the days of scallop sampling, we took water samples with a Niskin-type sampler (KC-Denmark, Silkeborg) for the analysis of photosynthetic pigments and particulate carbon at the specific sites and depths.

Seawater samples from 15, 30 and 55 m depth were filtered (Whatman GF/C, <0.2 bar) for determination of chlorophyll *a* (chl *a*). The filters were extracted in 96 %

ethanol for 18 h in the dark. After extraction, the samples were analysed on a Turner Designs TD-700 fluorometer. Chl *a* in the samples was calculated according to Parsons et al. (1984).

Total particulate carbon (TPC) was measured on water samples filtered onto Whatman GF/C filters. After filtration, the samples were dried at 60°C for 24 h and stored separately until analysis on an elemental analyser (ANCA-GSL, SerCon).

Statistical analyses. We examined the reliability of RD as a general proxy for the mass growth rate, G_m, by linear regression using data from all individuals collected. However, the instantaneous mass growth rate was assumed to be size dependent. Also, results from studies of fish larvae indicate that temperature can affect the relation between growth and RD due to the effect of temperature on the turnover of RNA (e.g. Buckley et al. 2008). To test this, the relation between G_m and the independent variables RD, SH and water temperature on the day of scallop sampling was examined by multiple linear regression analysis. Residuals were tested for autocorrelation structure (Lag = 1). We used R-square and the Akaike Information Criterion (AIC) to compare the fit of the models.

The relations between the average RD and environmental parameters, TPC, chl *a*, and temperature, respectively (measured on the day of scallop sampling), were examined by non-linear regression using a maximum likelihood estimation method taking heteroscedasticity into account (Blicher et al. 2007). We used either a logistic function or the Gompertz function, depending on which gave the best fit of data:

$$\text{Logistic:} \qquad f(x) = \frac{A_1 - A_2}{1 + (x/x_0)^p} + A_2 \qquad (4)$$

$$\text{Gompertz:} \qquad f(x) = A\mathrm{e}^{-\exp(-K(x-x^*))} \qquad (5)$$

In the logistic function, A_1 is the initial value, A_2 is the asymptotic value, x_0 is the centre and p is the power. In the Gompertz function, A is the amplitude, x^* is the centre and k is a coefficient. Residuals from the best fit model were examined for any trends.

RESULTS

RNA and DNA concentration in relation to size and sex

RNA and DNA concentration in *Chlamys islandica* was size dependent, decreasing with increasing SH. This was fitted with power functions ($RD = a\text{SH}^b$) revealing identical effects of SH (mm) on RNA and DNA concentration (µg mg DM^{-1}), respectively ($b \sim -0.5$; Fig. 1a,b):

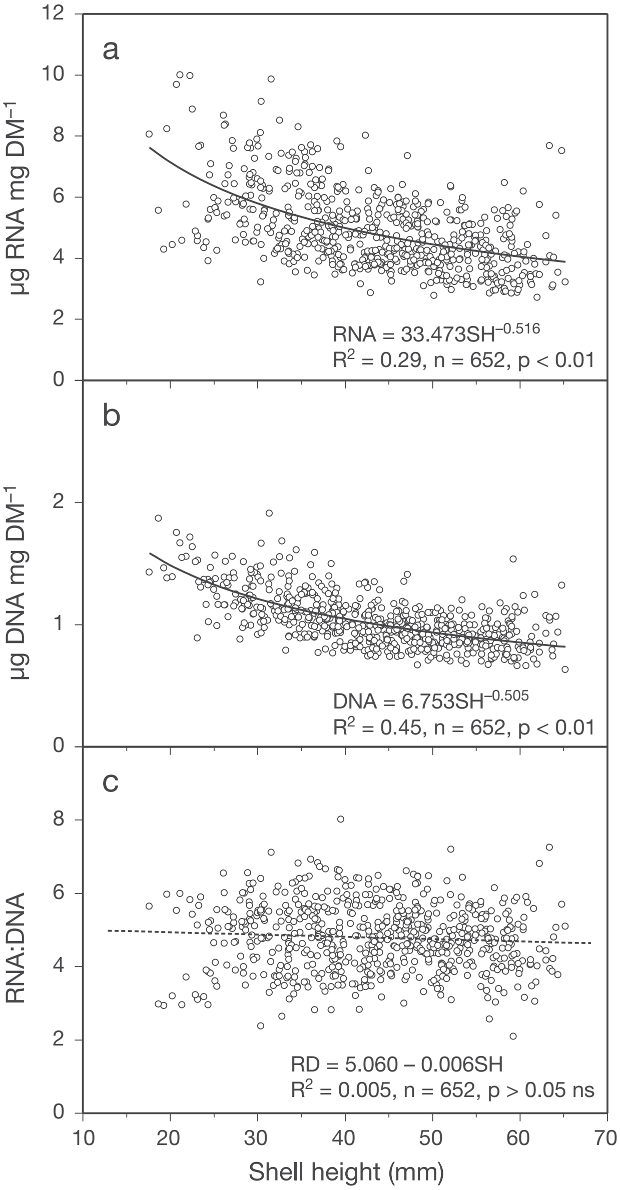

Fig. 1. *Chlamys islandica*. Plots of the effect of shell height on (a) RNA concentration, (b) DNA concentration and (c) RNA:DNA ratio (RD) in the adductor muscle. Plots include data from suspended cultures at 15 and 30 m depth, and from scallops from a wild population in Kobbefjord collected at 50 to 60 m depth. DM: dry mass; SH: shell height

$$\text{RNA} = 33.473\,\text{SH}^{-0.516} \qquad (R^2 = 0.29,\ n = 652,\ p < 0.01)$$

$$\text{DNA} = 6.753\,\text{SH}^{-0.505} \qquad (R^2 = 0.45,\ n = 652,\ p < 0.01)$$

The RNA concentrations ranged from 3 to 10 µg RNA mg DM^{-1}, with a general decrease from ~8 µg RNA mg DM^{-1} in the smallest individuals to ~4 µg RNA mg DM^{-1} in the largest scallops examined. The DNA concentrations ranged from 0.6 to 2 with an average of ~1.6 and ~0.8 in small and large scallops, respectively. However, there was no trend in RD plotted against individual SH (p > 0.05), and the average RD was ~5, ranging from a maximum of ~8 to a minimum of ~2 (Fig. 1c). Sex had no significant effect on individual RD (1-way analysis of variance [ANOVA], $F_{1,507}$ = 1.08, p = 0.29).

Seasonal and spatial variation in RD

We observed a clear seasonal pattern in the level of RD at all 3 depths (Figs. 2 & 3). This pattern was characterised by a high level during summer (May to September/October), decreasing through autumn and reaching a minimum in the winter months (January to April) followed by an abrupt increase in spring (April to May). The pattern was evident for both size groups. On the spatial level, the variation was almost identical at 15 and 30 m depth. No consistent differences between these 2 depths were observed until the last sampling date (Fig. 3). However, RD values in scallops collected from the wild population at 50 to 60 m depth were con-

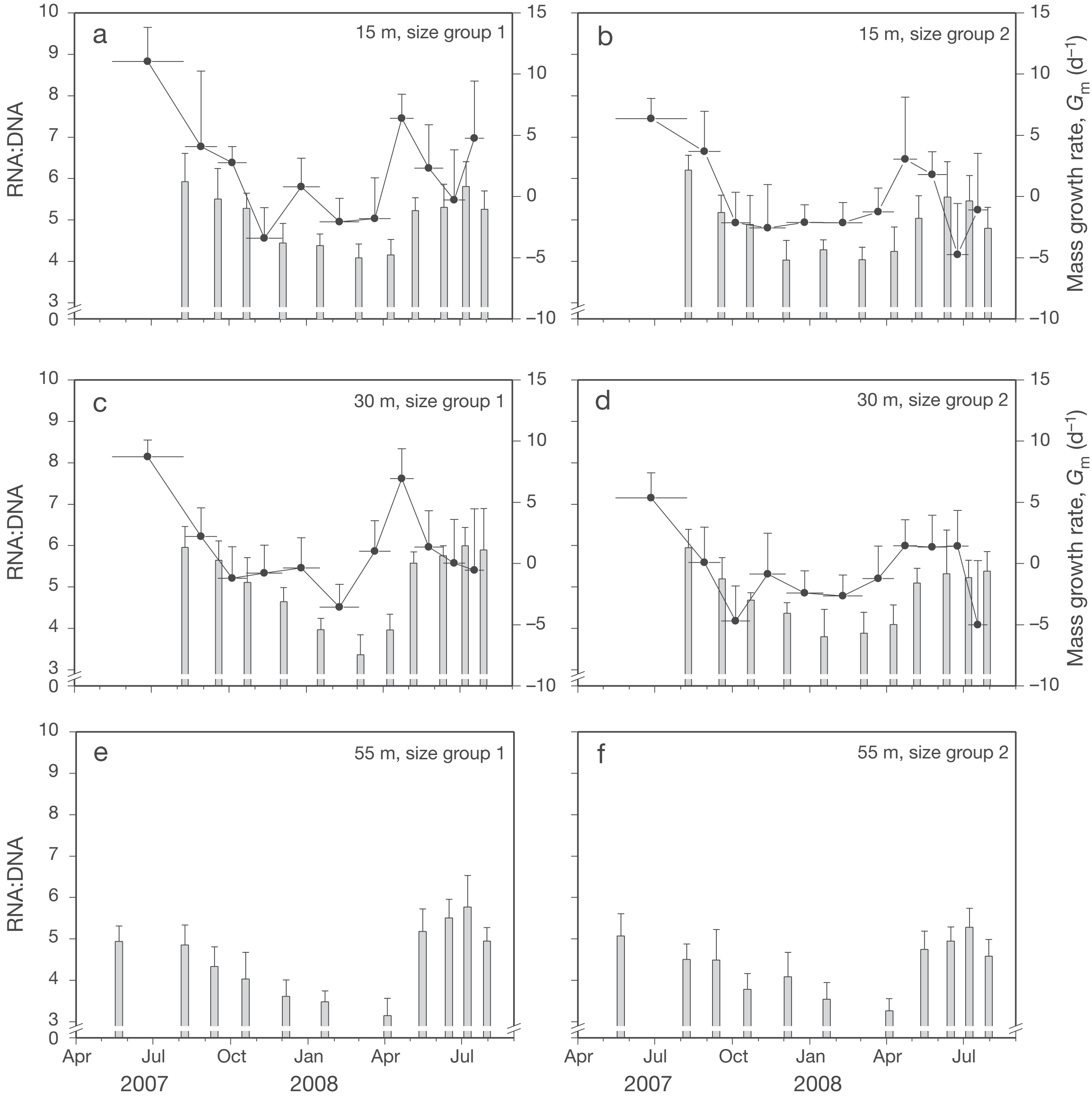

Fig. 2. *Chlamys islandica*. Seasonal variation in the average RNA:DNA ratio (bars) and the instantaneous mass growth rate, G_m (-●-), during 2007 and 2008 at (a,b) 15 m, (c,d) 30 m and (e,f) 50 to 60 m in Kobbefjord. Vertical error bars indicate the standard deviation (n = 10). Horizontal error bars for G_m indicate the period for which the average values were estimated

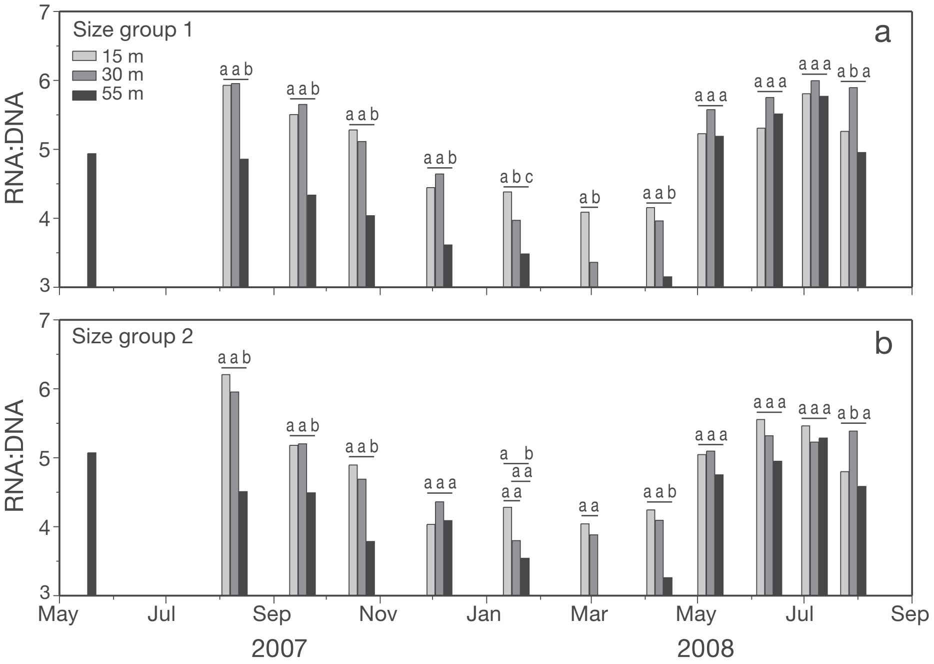

Fig. 3. *Chlamys islandica*. Comparison of the seasonal variation in average RNA:DNA ratio (RD; n = 10) at 15, 30 and 55 m depth in size groups 1 and 2, respectively. Different letters indicate significant differences in RD (1-way ANOVA, $p < 0.05$) between depths on the given sampling dates

sistently lower than in the suspended scallops from the beginning of the experiment until April 2008. During spring 2008, the RD level increased abruptly, reaching a level similar to that at the 2 shallower depths. This lasted throughout the period from May to the end of July, when the experiment was terminated (Fig. 3).

Coupling of RD to mass growth rate

As in the case of RD, we found a clear seasonal signal in the instantaneous mass growth rate of scallops in the suspended cultures at 15 and 30 m depth. We observed peak growth in spring and early summer, and zero growth or slightly negative growth rates during winter (Fig. 2a–d). A simple linear regression between individual G_m and RD gave a significant positive correlation ($R^2 = 0.19$, $p < 0.01$, $n = 436$; Fig. 4a, Table 1). Although significant, the correlation between CI and RD was even poorer ($R^2 = 0.11$, $p < 0.01$, $n = 652$; Fig. 4b), and therefore we only report results on G_m in the further presentation of data. Adding SH as a second independent variable resulted in an increase in the model fit (Table 1, Model II, AIC = 2452.4, $R^2 = 0.26$, $n = 436$), indicating a significant negative effect of increasing SH on the instantaneous mass growth rate of scallops ($p > 0.01$), which can be regarded as a correction for size dependence in G_m. Neither temperature nor the interaction term RD × Temp had any significant effect ($p > 0.05$) and increased the AIC (models not shown). However, to examine the robustness of the results to the fact that data were sampled at different depths,

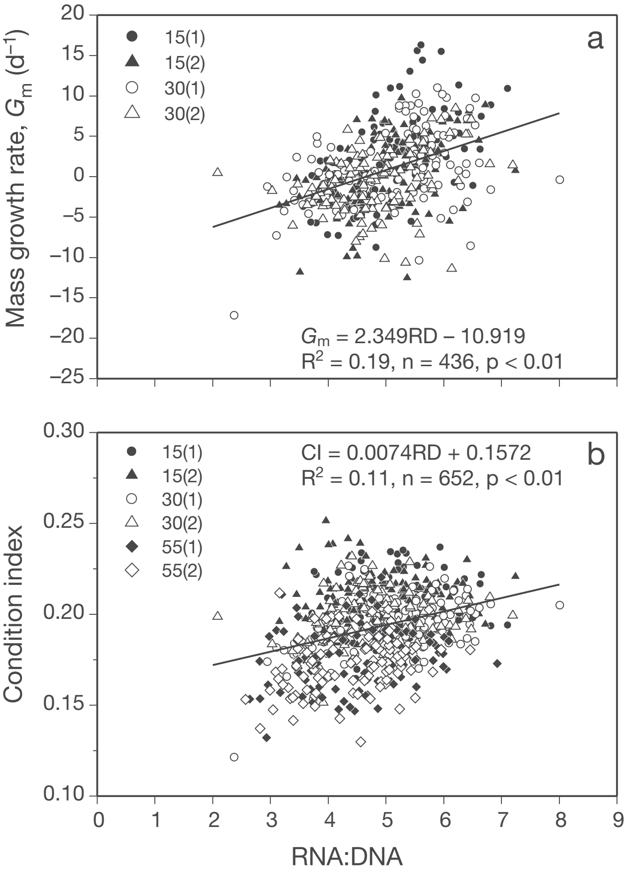

Fig. 4. *Chlamys islandica*. Simple linear regressions of the effect of individual RNA:DNA ratio (RD) on (a) mass growth rate, G_m, and (b) condition index, CI. Different depths (15, 30 and 55 m) and size groups (1 and 2) are illustrated by different symbols

Table 1. *Chlamys islandica*. Coefficients (±SE) and Akaike information criterion (AIC) of the regression models for the effect of RNA:DNA ratio (RD) and shell height on the instantaneous mass growth rate (G_m) (n = 436). To examine the robustness of the results, dummy variables for depth were added to the model, and we tested for autocorrelation structure of the residuals. Non-significant parameters (ns, p > 0.05) were backward eliminated (Temperature and RD × Temp). *p < 0.05, **p < 0.01

	Model			
	I	II	III	IV
Intercept	−10.919** (1.172)	−4.120** (1.540)	−4.409** (1.537)	−4.409** (1.537)
RNA:DNA	2.349** (0.232)	2.114** (0.225)	2.106** (0.224)	2.106** (0.224)
Shell height (mm)	–	−0.127** (0.012)	−0.129** (0.020)	−0.129** (0.020)
Control variables				
15 m	–	–	0.865* (0.383)	0.865* (0.383)
30 m	–	–	0.000	0.000
Auto correlation				
Lag 1	–	–	–	−0.403** (0.045)
R^2	0.191	0.262	0.270	0.385
AIC	2490.3	2452.4	2443.2	2372.6

dummy variables for depth were added to the model. Even though the model fit was only slightly improved, the result indicated significant spatial differences (p = 0.024) in the relation between G_m and RD (Table 1, Model III, AIC = 2443.2, R^2 = 0.27, n = 436). Moreover, there was a significant autocorrelation structure of the residuals of this model (Lag 1, p < 0.01) as shown in Model IV (AIC = 2372.6, R^2 = 0.385, n = 436).

Given the observed decline in the actual RNA concentration with increasing size (Fig. 1a), we found it intuitive to test whether the actual RNA concentration was a better predictor of the mass growth rate compared to the standardised (size-independent) parameter, RD. Therefore, we repeated the analytical approach with RNA concentration as the explanatory parameter. Although the RNA concentration correlated positively to G_m, it gave a slightly poorer fit (R^2 = 0.17, p < 0.01, n = 436). The model was not improved by adding other predictors, and also in this model, we found a significant autocorrelation structure of the residuals.

Coupling of RD to environmental parameters

The annual temperature cycle shows an amplitude ranging from −1 to −1.5°C in February and March, with similar temperatures at all depths, to 4.5 to 6°C at 15 m depth and 3 to 4°C at 30 and 55 m in late summer and early autumn, respectively. The concentration of TPC in Kobbefjord ranged between ~0.06 and ~0.5 mg l^{-1} in winter and spring/summer, respectively, within the depth range studied. Peaks were observed in the spring of both 2007 and 2008. Overall, a seasonal cycle could be separated into 2 distinct periods; a period from mid-April to October with relatively high levels of TPC (0.10 to 0.5 mg l^{-1}), and a period from November to April during which TPC was stable in the range 0.06 and 0.10 mg l^{-1} at all 3 depths. However, in the spring/summer season there was a depth gradient in TPC showing decreasing values of TPC with increasing depth, generally amounting to a factor of 2 in difference in the depth range studied. A similar pattern was observed for chl *a*, although concentrations were more variable throughout the spring and summer period. A phytoplankton spring bloom was observed in May 2007 and 2008, where chl *a* concentrations peaked at 1.5 to 3 µg l^{-1} followed by declining concentrations at all 3 depths. An intense late summer bloom occurred at the end of August 2007 and in late July 2008 at 15 m (chl *a* up to 5 µg l^{-1}), while chl *a* concentrations at 30 and 55 m declined continuously during late summer to a minimum of ~0.01 µg l^{-1} during winter.

When analysing the relationship of RD to TPC, chl *a* and temperature, TPC was the better predictor of RD following a sigmoid response curve (logistic function):

$$\mathrm{RD} = \frac{-5.709}{1+(\mathrm{TPC}/0.050)^{2.952}} + 5.368$$

$$(R^2 = 0.62,\ n = 66,\ p < 0.01)$$

corresponding to $A_1 = -0.341$, $A_2 = 5.368$, $x_0 = 0.050$ and $p = 2.958$ in Eq. (4). RD seemed to respond rapidly to small increases in food level until reaching a maximum at ~0.15 mg TPC l^{-1}, after which RD reached an upper level where it was independent of food concentrations (Fig. 5a). Using chl *a* as an explanatory parameter revealed a similar pattern, which was best fitted with a Gompertz function (Eq. 5):

$$\mathrm{RD} = 5.143e^{-\exp(-11.174(\mathrm{CHL}+0.996))}$$

$$(R^2 = 0.41,\ n = 66,\ p < 0.01)$$

However, this equation explained less of the variance in RD than TPC (Fig. 5b). RD displayed a weak but significant correlation to temperature when fitted with a Gompertz function (Fig. 5c):

$$\mathrm{RD} = 5.498e^{-\exp(0.359(\mathrm{TEMP}+4.105))}$$

$$(R^2 = 0.34,\ n = 66,\ p < 0.01)$$

The residuals from the best fit model (TPC as the explanatory parameter, R^2 = 0.62) were examined for any

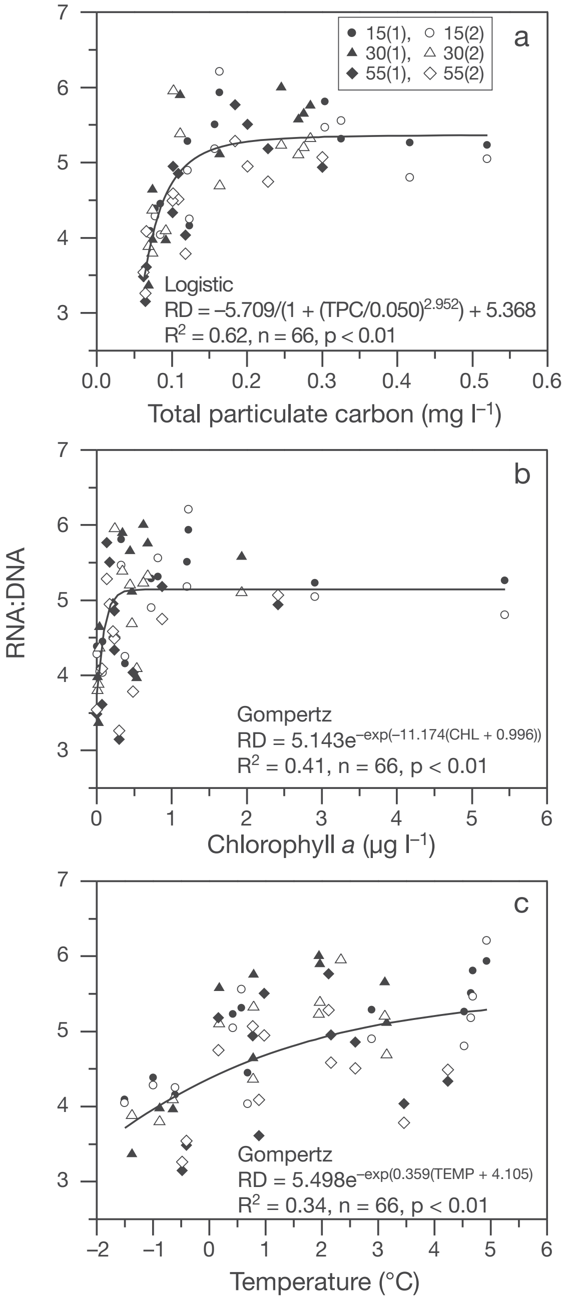

Fig. 5. *Chlamys islandica.* Plots of environmental parameters (a) total particulate carbon (TPC), (b) chlorophyll *a* and (c) temperature against the average RNA:DNA (RD) ratio. Depths (15, 30 and 55 m) and size groups (1 and 2) are illustrated by different symbols. Data are fitted with non-linear models

trends, but we found no significant correlation of the residuals to either chl *a* or temperature ($p > 0.05$). Nevertheless, a plot of the residuals against time indicates that the residuals of the model were not independent over time, and that the model could not explain all of the observed spatial differences in RD (Fig. 6).

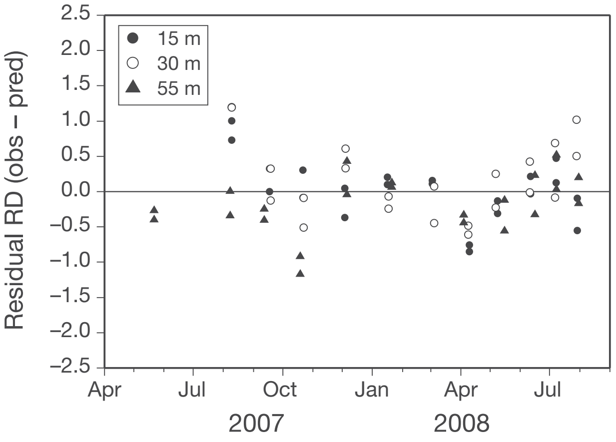

Fig. 6. Residuals ($RD_{observed} - RD_{predicted}$, where RD is the RNA:DNA ratio) of the best fit model (total particulate carbon as the explanatory parameter, Fig. 5a) plotted against time. Depths are indicated by different symbols

DISCUSSION

Effects of size on RNA and DNA concentration

RNA and DNA concentration in *Chlamys islandica* was size dependent, decreasing with increasing SH (Fig. 1a,b). Size dependence of RNA concentration has been observed in other studies (Norkko et al. 2005a, Norkko & Thrush 2006). Norkko & Thrush (2006) proposed that the RNA concentration would reach an asymptotic value in the largest size classes of the cockle *Austrovenus stutchburyi*, and suggested that this value represents the basic metabolism required for vital protein synthesis. In the present study, we focused on size classes with significant somatic growth potential, i.e. young specimens much smaller than the maximum SH of *C. islandica* (80 to 110 mm) (Pedersen 1994, Blicher et al. 2009). Thus, we could not completely validate the existence of a baseline value of RNA concentration for this species. However, our data seem to approach a minimum value of ~3 µg RNA mg DM^{-1} with increasing SH. It has been argued that the RNA concentration in polar organisms is high compared to warmer areas as a compensation for generally lower translation efficiencies at cold temperatures, or due to slower RNA turnover (Fraser et al. 2002, Caldarone et al. 2003, Norkko et al. 2005a, Storch et al. 2005, Clarke 2008). However, this is difficult to evaluate due to species-specific variations and differences in the analytical procedure between studies.

The RNA concentration in itself has been used as a biomarker in some studies due to inconsistent patterns in DNA concentration, which prevented its use for standardising RNA concentration using RNA/DNA ratios (e.g. Norkko et al. 2005a). It is evident from our results and the results of others that the use of RNA concentration as a biomarker should include a test for size dependence, or studies should concentrate on individuals within a very narrow size range in order to prevent any bias of the data.

In this study, we successfully standardised RNA data using DNA concentration. The RD ratio was independent of size, which is in contrast to findings in other bivalve studies of a negative relationship between RD and size (e.g. Lodeiros et al. 1996, Roddick et al. 1999), but consistent with studies of *Crassostrea virginica* and *Mya arenaria* (Pease 1976, Mayrand et al. 1994). RD was also unaffected by the sex of *Chlamys islandica*, unlike what was found for 3 marine species collected off Portugal (Chicharo et al. 2007). Thus, we conclude that RD data of *C. islandica* in SW Greenland can be compared directly independently of size and sex. However, this does not necessarily exclude potential differences in the RD dynamics of scallops at different stages of maturity.

Seasonal and spatial variation in RD

There was a clear seasonal trend in scallop RD, which also varied significantly between depths. The seasonal signal in RD was consistent between size groups. First of all, in combination with the overall seasonal pattern found at the 3 depths, with relatively high values during summer and decreasing RD during autumn and winter until a sharp increase in the spring, these results indicated that the RNA and DNA concentration in scallop muscular tissue could be measured accurately enough to reveal potential differences between habitats and seasons. Therefore, it also seemed reasonable to conclude that this high-resolution dataset qualified to test the potential of RD as a proxy for the mass growth rate, or alternatively, to examine the causal relationships behind the seasonal and spatial variation in the RD of *Chlamys islandica*.

RD and mass growth rate

RD was only weakly correlated to temporal and spatial variations in scallop mass growth rate. Even though we found a pattern of RD variation very similar to what was expected according to our hypothesis, with high ratios during the productive summer, minimum values during winter, and lower RD at deeper compared to shallow depths, our data indicated that RD did not reflect the variation in mass growth rate very accurately, neither on a temporal nor on a spatial scale (Table 1, Models III and IV). First of all, the difference in mass growth rate between scallops at 15 and 30 m depth, respectively, which was most pronounced during late summer, was not reflected in the RD data. Also, during the summer of 2008, the RD of wild scallops at 50 to 60 m was not significantly different from that of cultured scallops, which was unexpected because size-at-age data for scallops collected at the site have indicated relatively slow growth compared to suspended scallops (Blicher et al. 2009, 2010). Moreover, the peaks in mass growth rate during spring and summer could not be identified in the RD, which did not show any large fluctuations from May to August, but rather appeared to have a stable and high level during this period. By including scallop SH, the model fit was improved (Table 1, Model II), indicating that G_m decreases with increasing individual size. This was expected (Blicher et al. 2010), and the inclusion of SH in Model II (Table 1) can be regarded as a simple correction for this size dependence. However, the large fraction of unexplained variation and the significant autocorrelation of the residuals seemed to indicate that RD explained the seasonal cycle in the mass growth rate of *Chlamys islandica* poorly. This is in contrast to the results in studies of fish larvae growth, where RD has been validated as a proxy for the mass growth rate within a period of 2 to 7 d before RD analysis (meta-analysis in Buckley et al. 2008). Also, these studies have suggested that temperature has an effect on the relation between RD and growth, which we did not find. RD and actual growth rates have only been compared directly in marine invertebrates in a few studies. The majority of studies have either assumed that RD or RNA concentration reflects growth or used RD as an indirect measure of condition, nutritional status or metabolic activity (Dahlhoff & Menge 1996, Dahlhoff et al. 2001, Buckley & Szmant 2004, Norkko et al. 2005a). However, Frantzis et al. (1992) also found RD to be inefficient in predicting growth rates of field-collected sea urchins *Paracentrotus lividus*. Lodeiros et al. (1996) concluded that RD provided a good indicator of short-term growth of juvenile scallops *Euvola ziczac*, while being more difficult to interpret in maturing and mature scallops.

There can be several reasons why RD appears to be a poor predictor of the mass growth rate of *Chlamys islandica*: (1) RNA synthesis might be related to metabolic processes other than growth, i.e. mobilisation of muscular energy in support of gametogenesis (Lodeiros et al. 1996). However, the RD variation of immature scallops did not differ from that of maturing scallops in this study. Moreover, variation in RD did not correlate significantly to the overall seasonal variation in a gonad mass index (linear regression, $R^2 = 0.001$, $n = 617$, $p = 0.43$). (2) RD might reflect the general health status rather than growth (e.g. Chicharo & Chicharo 1995); however, our study did not include other known physiological indicators of stress in order to test this (Dahlhoff et al. 2001, Dahlhoff 2004, Moore et al. 2006). (3) RD and mass growth rate might have been measured on different time scales, which is an important aspect in interpretation of data (Norkko et al. 2006a). G_m is a monthly average, while RD is expected to vary on a scale of days (Dahlhoff 2004). RD also correlated weakly to the condition index, CI (Fig. 4b), which is suggested to reflect gains or losses in weight within days to months (Norkko et al. 2005b). Still, at this stage we cannot reject that differences in the time-scale of our estimates might have had an effect on the results of this analysis. (4) It is also possible that the RNA concentration does not reflect the actual growth rate of *C. islandica* if short-term changes in growth rate are regulated through adjustments in the ribosome activity rather than the quantity. This has been observed to be an important mechanism for adjusting protein synthesis in other animals (Henshaw et al. 1971, Smith et al. 2000). RD would then reflect the potential for growth rather than the actual growth rate.

Despite the possibility that our measurements of RD and mass growth integrate processes occurring on different time scales, our data suggest that RD is a poor predictor of the growth rate of this species and in the given habitat. Still, given the significant seasonal and spatial variation in RD, the questions of what controls the protein synthetic capacity in *Chlamys islandica*, and what it reflects, remain important to our ecological understanding.

Effects of food level on RD

RD correlated significantly to food level (TPC and chl *a*) measured on the day of scallop sampling following a non-linear pattern (Fig. 5a,b). This result indicated that the RNA level in the cells is up-regulated in response to the onset of the phytoplankton growth season, i.e. the shift from winter to spring/summer conditions, but within intermediate to high levels of food concentrations (TPC > 0.15 mg l^{-1}), RD is not affected by changing food levels. This is in accordance with a conceptual model of the dynamics of the RNA response of bivalves to added food, which followed a sigmoid pattern with a species-specific lower and upper level of RNA suggesting that food is the key driver of RD dynamics, often overriding potential negative effects of e.g. hypoxia and increased terrigenous sedimentation (Norkko et al. 2006a,b). Dahlhoff & Menge (1996) and Dahlhoff et al. (2001) also suggested that differences in food conditions are responsible for seasonal and spatial differences in the RD dynamics of molluscs in intertidal systems. However, the residuals of the best fit model in our study (TPC as the explanatory parameter, Fig. 5a) appeared not to be independent through time (Fig. 6), indicating that the fraction of unexplained variation in RD could be due to some forcing or mechanism not monitored in this study. A mechanism allowing faster up-regulation of RNA in response to favourable conditions compared to the down-regulation in response to stressful conditions as suggested by Norkko et al. (2006b) might lead to the observation of higher RD than expected during periods with decreasing food levels. Also, the general individual health status can affect the ability to respond to changing conditions (Norkko & Thrush 2006). Therefore, the response to a key environmental driver is likely to be affected by complex interactions on several ecological levels (individual, habitat, population, community and ecosystem). In any case, it is important to realise that the challenge of discovering causal relationships in ecological field studies is very sensitive to the risk of comparing measurements that integrate processes occurring on different temporal and spatial scales, which might add to the fraction of unexplained variation in the dependent parameters.

What do the dynamics in RD reflect?

The up-regulation of RD in *Chlamys islandica* during spring and summer followed by a down-regulation to winter conditions was a general feature, which matched the growth season with relatively high food levels well. However, from the given experimental setup, it is difficult to evaluate the relative importance of an underlying endogenous rhythm in RD compared to a direct response to environmental drivers. Still, based on the observed pattern, we suggest that the RD ratio primarily reflects the potential for growth in *C. islandica*. The actual growth rate would then vary through changes in RNA activity within the range set by ribosome quantity (RNA concentration). Two general mechanisms could operate to alter the protein-synthesising activity of the ribosomes, one controlling the fraction of ribosomes associated with mRNA (polyribosomes), the other regulating the synthesising activity of polyribosomes. Generally, the ribosomes are able to respond to changes in nutritional condition within hours by changing their activity, while the ribosome quantity is expected to be able to change within days (Henshaw et al. 1971, Millward et al. 1973, 1976, Houlihan et al. 1988, Fraser et al. 2002, Dahlhoff 2004). This would explain the large range of mass growth rates obtained at similar levels of RD as observed for *C. islandica* during spring and summer, as well as the fact that higher growth rates were obtained at 15 m depth compared to 30 m depth at identical RD levels. A high and stable level of RD throughout the spring/

summer would ensure a high capacity for growth in this period. The adaptation might have evolved to ensure an efficient utilisation of the short and intense, but somewhat sporadically occurring summer phytoplankton blooms in the Arctic and in coastal areas in general. Likewise, the winter minimum in RD might reflect a down-regulation of the growth potential in order to minimise metabolic costs in a period of continuously low food availability. This strategy has been observed in other marine invertebrates in polar areas (e.g. Brockington 2001, Brockington et al. 2001).

CONCLUSIONS AND IMPLICATIONS FOR FUTURE RESEARCH

We successfully analysed the RNA and DNA concentration in the tissue of *Chlamys islandica*, and our results revealed clear seasonal and spatial trends in the RNA:DNA ratio (RD), which worked well as a standardisation of the RNA concentration independent of size and sex. Even though the period with high levels of RD reflected the growth season relatively well, the quantity of RNA in the tissue of *C. islandica* was not a reliable proxy for the seasonal variation in mass growth rate of this species. A simple coupling between RD and mass growth rate was presumably obstructed by mechanisms that allowed fast regulation of ribosome activity instead of ribosome number (RNA concentration). Still, our data indicate that RD dynamics depend primarily on the same environmental parameter as the mass growth rate itself, namely food concentration. RD was sensitive to changing food levels from low to intermediate concentrations, resulting in RD being up- and down-regulated in response to the beginning and end of the productive summer season. Based on this relationship, we suggest that *C. islandica* has a higher potential for growth than obtained under the present conditions in SW Greenland, and that the inherent high capacity for growth during spring and summer is an adaptation that makes it possible to upregulate protein synthesis and thus rapidly ensure efficient utilisation of intense peaks in food availability. The pattern of the unexplained variation in RD indicates the existence of unresolved mechanisms or relationships, and future research should especially concern the temporal scale over which measurements of nucleic acids integrate, and the possible existence of an underlying seasonal endogenous rhythm in order to improve our understanding of the causal relationships.

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Paper V

EVIDENCE FOR STRONG TROPHIC COUPLING BETWEEN MACROZOO-BENTHOS AND EIDERS (*SOMATERIA* SPP.) IN A KEY WINTERING HABITAT IN SW GREENLAND

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EVIDENCE FOR STRONG TROPHIC COUPLING BETWEEN MACROZOOBENTHOS AND EIDERS (*SOMATERIA* SPP.) IN A KEY WINTERING HABITAT IN SW GREENLAND

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Running head: Trophic coupling between eiders and macrobenthos in Greenland

ABSTRACT

The Southwest Greenland Open Water Area is an internationally important wintering area for eiders (*Somateria* spp.) (Merkel et al. 2002). We monitored the number of eiders during the winters of 2008-10 in a shallow inlet, Nipisat Sound; a key wintering habitat in SW Greenland. In addition, macrobenthic species abundance and biomass were studied, and annual production was estimated by an empirical model including environmental characteristics, fauna composition and individual biomass. In spring 2008, average macrozoobenthic abundance and biomass were 6912 ind. m^{-2} and 28.4 g ash free dry mass (AFDM) m^{-2}, respectively. Annual production was estimated at 13.9 g AFDM m^{-2} yr^{-1}. Converted to energy this corresponded to a biomass of 647 KJ m^{-2} and a production of 317 KJ m^{-2} yr^{-1}, respectively. We observed a distinct wintering season for eiders lasting from late October through May. Eider abundance peaked at 12-15000 individuals in mid-winter with an average of *c.* 7800 individuals throughout the winter in the study area covering 17 km^2. In combination with estimates of the energetic requirements of eiders we estimated that wintering eiders consumed 17 to 33 % of the expected autumn biomass and 58 to 90 % of the total annual production of macrobenthos. Thus, eiders have a strong impact on the macrobenthic community structure, and our data indicate that they are capable of depleting their preferred prey species. Hence, it is likely that eiders wintering in Nipisat Sound to some extent must rely on non-preferred prey species to be able to cover their cost of living, and that they will have to build up body reserves for the breeding season elsewhere.

INTRODUCTION

During the 20th century the number of breeding northern common eider (*Somateria mollissima borealis*) in West Greenland declined by *c.* 80 %, presumably because of human activities (i.e. hunting, gillnet fishing) (Merkel 2004a). This observation is supported by Gilliland et al. (2009) who calculated that the high harvest levels reported in Greenland during 1993-2000 could alone explain the quickly declining numbers of wintering common eider in Greenland. However, the role of naturally occurring variations in weather conditions, food availability or diseases of the common eiders wintering in this sub-Arctic environment is poorly studied. The Godthaabsfjord system, including the coastal margins, is an important wintering site for eiders arriving to SW Greenland from their breeding areas in north-western Greenland and the eastern Canadian Arctic (Goudie et al. 2000). The total number of wintering common eider in the area was estimated at 57000 in March 1999 based on aerial surveys (Merkel et al. 2002). Nipisat Sound, a shallow inlet at the entrance to the Godthaabsfjord, is regarded as a key habitat for wintering eiders in the Godthaabsfjord system (Boertmann et al. 2004, Merkel et al. 2006). However, the actual number and the seasonal dynamics of wintering eiders in Nipisat Sound have not been studied before. Common eiders generally forage at shallow depths and have a strong preference for benthic invertebrates. A study of the oesophageal content of common eider wintering in Nipisat Sound and in the Godthaabsfjord showed that their diet primarily consisted of clams and polychaetes (Merkel et al. 2007b). Still, the macrobenthic community structure is largely unknown in the foraging areas in SW Greenland. Thus, it is uncertain whether their diet reflects the macrobenthic species abundance directly, and to which degree they are likely to experience limitations in food availability during their wintering. However, eiders wintering in the study area in SW Greenland between 2000 and 2002 were able to maintain constant body weights and lipid stores throughout the winter indicating that they did not experience any dramatic nutritional shortfalls (Jamieson et al. 2006).

Results from Kobbefjord, a nearby fjord branch in the Godthaabsfjord system, have shown a relatively high macrobenthic production compared to other Arctic areas, and the combined data indicate that the level of macrobenthic carbon requirements in the Arctic often reflects primary production of an area (Blicher et al. 2009). Thus, it might be expected that the macrobenthic fauna in Nipisat Sound follows this pattern, resulting in a highly productive macrobenthic community situated at depths within reach of foraging eiders. However, even though eiders can feed on a variety of different macrobenthic species (Merkel et al. 2007b), characteristics such as species composition, abundance, and size structure are known to potentially affect the actual amount of prey harvestable by bottom foraging birds (Zwarts & Wanink 1993, Richman & Lovvorn 2003, Merkel et al. 2007b, Lovvorn et al. 2009, Richman & Lovvorn 2009). Thus, increased knowledge about the general structure as well as the temporal and spatial dynamics of the macrobenthic communities in the wintering areas in SW Greenland, seems to be essential not only to fully assess the potential vulnerability of wintering eiders in the area, but also to get a better basic understanding of the marine ecosystem in this poorly studied region.

Here we describe the macrozoobenthic species composition and estimate biomass and annual somatic production in Nipisat Sound, SW Greenland. Through observations of the seasonal variation in the number of eiders, combined with estimates of their energetic cost of living, and with reference to previous studies of the diet of eiders in the area, the objective was to assess the functional coupling between these two trophic levels.

MATERIALS & METHODS

Study area

The study area, Nipisat Sound, is situated at the entrance to the Godthaabsfjord system. The area is basically a large, shallow and protected inlet with depths <15 m Mean Lower Low Water (MLLW) (Fig. 1), whereas the fjords to the east are characterized by steep slopes. The total area of the inlet, including the shallow areas outside its entrance (<30 m MLLW), is 20 km^2, of which *c.* 3 km^2 are inter-tidal areas. The average air temperature in Nuuk in the period from October through April is approximately -5.5°C (Cappelen et al. 2001), while sea surface temperature normally varies within a range of -1 to 2°C in the same period (Juul-Pedersen et al. 2009).

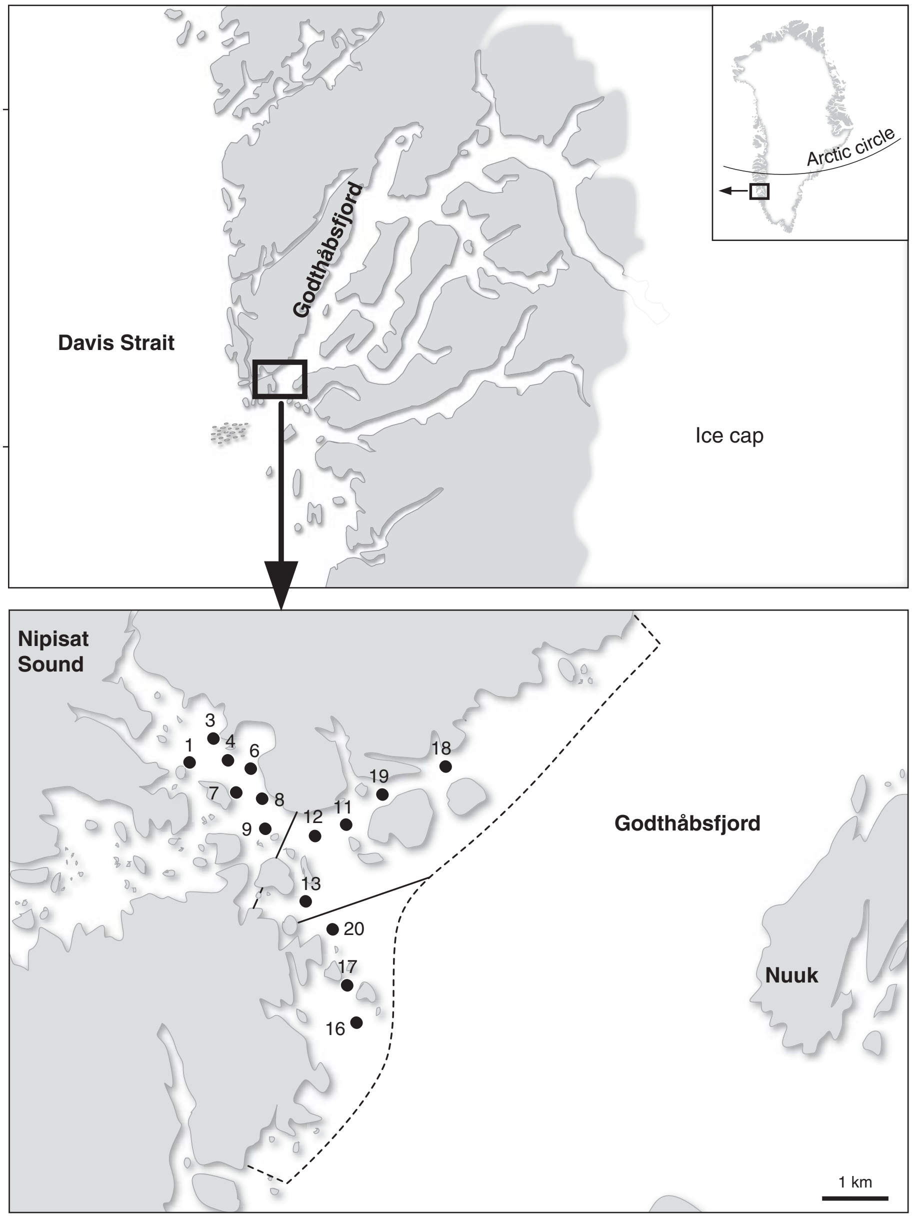

Fig. 1. Location of the study area, Nipisat Sound in SW Greenland. The dashed line approximately follows the 30-m depth stratum and bounds the core area for wintering eiders. Points (●) and numbers refer to sites of benthic sampling. Solid lines show the limits of the different regions defined on the basis of macrobenthic species composition (see Results section).

Macrobenthos

A total of 15 stations were visited in Nipisat Sound in April 2007 ranging in depth from 2 to 10 m MLLW (Fig. 1, Table 1). Three replicate van Veen grab samples (0.1 m^2) were collected at each station for the analysis of macrobenthos. The samples were sieved through a 1-mm sieve and the remaining material was fixed in approximately 4% borax-buffered formalin. Prior to fauna analysis the samples were transferred to 70% ethanol. Macrobenthos were identified and sorted to the lowest possible taxonomic level and counted. Dry mass (DM) and ash-free dry mass (AFDM) were determined by drying at 60°C for at least 24 h until constant weight, followed by ignition at 550°C in a muffle furnace for 12 h. AFDM was converted to KJ by the conversion factor 22.804 KJ g AFDM^{-1} (Brey 2001).

Multivariate analysis was used to explore the spatial patterns in species distribution. Abundances for individual samples were 4th root transformed and Bray-Curtis similarities between grab samples were depicted through ordination by non-metric multidimensional scaling (nMDS) using the PRIMER software v. 5.1.

Table 1. Depth (Mean Lower Low Water), grain size composition, ash-free dry mass (AFDM) and chlorophyll a (chl a) content of the sediment at sampling stations in Nipisat Sound, SW Greenland. Values are averages of three replicates per station.

Station no.	MLLW (m)	Sediment type	<63 µm (%)	63-125 µm (%)	125-250 µm (%)	250-500 µm (%)	>500 µm (%)	AFDW (% of DW)	Chl a (µg g dw^{-1})
1	2.4	Mud	77.8	18.1	1.4	0.8	1.9	1.15	5.00
3	2.1	Mud	79.0	18.7	0.7	0.4	1.1	1.24	5.57
4	3.2	Clay	82.7	14.3	1.6	0.4	1.0	2.60	19.60
6	4.7	Mud	42.2	27.8	22.6	3.8	3.7	1.29	7.98
7	5	Mud	25.2	24.5	39.6	8.7	2.2	1.74	12.12
8	6.4	Mud, sand	31.3	13.5	14.2	27.6	13.3	1.46	9.29
9	5.5	Mud, sand	22.1	27.1	32.3	13.7	4.8	1.61	8.52
11	7.7	Sand	9.2	22.5	55.6	11.2	1.5	0.80	6.49
12	6.8	Sand	11.1	15.9	34.7	28.3	10.0	0.80	9.86
13	6.6	Sand	9.4	22.0	37.8	23.9	6.8	0.87	13.44
16	10.5	Sand, gravel	1.4	0.7	2.1	66.5	29.4	0.72	7.46
17	9.8	Sand, gravel	2.3	3.1	14.9	51.1	28.6	0.36	19.32
18	6.7	Sand, gravel	10.7	33.7	17.2	16.1	22.3	1.78	7.71
19	10.5	Sand	5.5	19.0	64.8	8.8	1.9	1.02	6.94
20	6.1	Sand, gravel	3.7	9.6	16.5	44.4	25.8	0.67	15.17

An annual somatic production-to-biomass ratio (P:B) was estimated using an empirical model developed by Brey (1999) and later modified in Brey (2001). The model (version 4-04) is based on data from 1102 studies from different parts of the world, and is given by the equation (1):

$$\mathrm{Log}P/B = 7.947 - 2.294\log M - 2409.856(1/T+273) + 0.168(1/D) + 0.194D_{\mathrm{subt}} + 0.180D_{\mathrm{inf}} + 0.277D_{\mathrm{moti}} + 0.174D_{\mathrm{ann/crust}} - 0.188D_{\mathrm{echi}} - 562.851\mathrm{Log}M\,(1/T+273),$$

where M is average body mass (KJ), T is bottom water temperature (°C) and D is depth (m MLLW). Dummy variables are set at 0 (no) or 1 (yes) for the categories, 1) subtidal species (D_{subt}), 2) infauna (D_{inf}), 3) motile epifauna (D_{moti}), 4) Annelida or Crustacea ($D_{\mathrm{ann/crust}}$) and 5) Echinodermata (D_{echi}). Dummies for *Insecta* and *Lake* in the original model were left out. T was set at 1.8°C, which was the annual average in the top 15 m of the water column at the entrance to the Godthaabsfjord, 3 nm from Nipisat Sound, in the period 2005-08 (MarineBasic Nuuk Monitoring Programme; www.g-e-m.dk). Annual production was calculated for each separate sorting group by multiplying the P:B-ratio with the biomass for the respective group (KJ). Thus, estimates of density, biomass and annual somatic production of macrobenthos were obtained for each replicate van Veen grab sample.

Sediment

From each van Veen grab sample we took out three subsamples for the analysis of sediment characteristics: sediment chlorophyll *a* content (chl *a*), grain size composition and AFDM. Sediment was collected through the sampling ports of the closed van Veen grab using a 100-ml plastic cut-off syringe (diameter 30 mm). For chl *a* the upper 3 cm of the sediment was collected, another sample was taken of the upper 10 cm for grain size analysis, and for the analysis of AFDM a sample of the upper 5 cm was taken. The total surface area of the sediment samples was subtracted from the area collected by the van Veen grab (0.1 m^2) in the calculations of macrofauna density and biomass. Chl *a* content was determined fluorometrically. Pigments were extracted in the freezer (-18°) in the dark for 48 h, during which tubes were shaken periodically. Sediment was then centrifuged (4000 rpm for 10 min at 0°C) and the supernatant was analyzed (Turner Designs model 10-AU) before and after acidification with 20 % HCl. For grain size analysis sediment was wet sieved through a set of sieves (63, 125, 250 and 500 µm). AFDM was determined by drying sediment at 105°C until constant weight, followed by ignition at 550°C in a muffle furnace for 12 h.

Eiders

A small, slowly moving motorboat (3-5 knots) was used as an observation platform when counting wintering eiders. Depending on the wind direction we followed the same track at every count, either from south to north along the coast and into the sound, or vice versa, well covering the core area of the eider concentration (Merkel et al. 2006). We preferred to move with the wind because the eiders tended to take flight against the wind, passing the boat on approach, thus, avoiding pushing them in front of the boat. The counting of birds was done by two observers, both using handheld binoculars with 10x magnification and positioned outside in the front-end of the boat to gain a 270° free view.

When undisturbed, eiders avoid feeding during high tide, and most birds will roost in flocks (Merkel et al. 2009) making them easier to count. Counting dates were therefore planned to combine maximum high tide and the time within the first two hours of sunrise in order to minimize the risk of prior human disturbances that would affect distribution of the birds. Counts were made only when visibility was at least 5 km and wind speed below 5 m/sec. We made the first count of eiders in April 2008 prior to the macrobenthos sampling. Hereafter, counting dates were distributed from September 2008 through June 2009, and again from October 2009 to April 2010, preferably with no more than a month between two counts to ensure that any arrival or departure of staging birds causing significant change in bird numbers would be detected.

In coastal areas wintering king eiders, *Somateria spectabilis*, occur sympatrically with common eiders and they often stay in mixed flocks (Merkel et al. 2007a), however, it was generally not possible to distinguish the fraction of king eiders in the field, since females and juveniles of the two species are very similar in plumage, and larger flocks generally have a flight distance of more than 500 m of an approaching boat. For our calculations, the fraction of king eiders was assumed to be 10 % based on local hunting statistics and surveys of the local market in Nuuk (Merkel 2004b). The total number of bird days during the winter of 2008-09 was calculated by integrating the data plots of the number of observed eiders in Nipisat Sound against time (Julian day).

Two approaches were used to assess the individual energy intake by eiders; firstly, an estimate based on the assumption of a relation between individual basal metabolic rate, *BMR* (KJ d^{-1}), and consumption, *C* (Meire et al. 1994, Scheiffarth & Nehls 1997):

$$C = 3 \times BMR \times 1/Q \qquad (2)$$

where the assimilation efficiency of the food, Q, is set at 0.8. Secondly, we obtained an estimate based on the physiological energy requirement of different activities in combination with the observed behavioural pattern of eiders in the area; i.e. the amount of energy needed to balance the costs of living. Merkel & Mosbech (2008) monitored the behaviour of common eiders in the Nipisat area during the winter of 2002 (January-April). Eider activities were classified into three categories: feeding (diving and inter-dive pauses), locomotion (swimming or flying) and other activities (resting, comfort and social behaviour). Eiders in Nipisat spent almost the entire night on "other activities", while the period prior to sunrise until sunset was divided into *c.* 30 % feeding and *c.* 25 % locomotion, of which 5 % was flying (F.R. Merkel *unpubl.*). 45 % of the time during day was spent on other activities. Estimates of the energy costs (W kg^{-1}) of non-swimming activities on water were estimated from the equation: $E_{rest} = 5.48 - 0.9T_w$ (Jenssen et al. 1989), where T_w is sea surface temperature (°C). For surface swimming (E_{swim}) we used the value of 12.2 W kg^{-1} measured for common eider swimming at 1 m/s (Hawkins et al. 2000). The cost of flying was set at 93 W kg^{-1} (Lovvorn et al. 2009). For feeding we used an estimate of oxygen consumption during a whole dive cycle to 1.7 m depth (a dive and the interval after it) of 49.0 ml O_2 kg^{-1} min^{-1} (Hawkins et al. 2000). Using a conversion factor of 20.1 J ml O_2^{-1} (Brey 2001), this amounted to 59.1 KJ h^{-1} kg^{-1}. The body mass of common eiders was set at 1.942 kg, which represents an average of different age classes, sex and different periods during the winters of 2000-01 and 2001-02 (early winter, mid-winter, late winter and spring (Jamieson et al. 2006). The behavioural pattern and the metabolic costs of living were assumed to be similar for King Eiders. However, the absolute demand for energy is likely to differ due to differences in body mass. Thus, we made a separate estimate for King Eiders based on an average body mass of 1.661 kg (Oppel & Powell 2009). Based on these relations and the given activity pattern, we estimated the metabolic costs of common eiders and king eiders at 1241 and 1061 KJ d^{-1} ind^{-1}, respectively. With an assimilation efficiency of 0.8 the daily individual energy intake should be 1551 and 1327 KJ for common eiders and king eiders, respectively, to balance their cost of living. This estimate was somewhat different from the estimate obtained from the empirical relation between *BMR* and consumption, *C* (Eq. 1). Assuming a *BMR* equal to energy costs (W kg^{-1}) during rest on land, $E_{land} = 3.46 - 0.07T_{air}$, where T_{air} is air temperature (°C) (Jenssen et al. 1989), the individual consumption of common eider and king eider was estimated at 2419 and 2029 KJ d^{-1}, respectively. Hence, these two estimates of individual food consumption of common eider and king eider, respectively, represent a range within which we expect the actual food consumption to lie.

RESULTS

Sediment characteristics

We successfully collected triplicate van Veen grab samples at 15 stations in Nipisat Sound. The occurrence of macroalgae, gravel or stones at some other sites did prevent us from collecting grab samples of sufficient quality. However, the seabed in Nipisat Sound generally consisted of soft sediments and there was a clear gradient in grain size composition from the inner to the outer part of Nipisat Sound. At the inner stations (no. 1 to 9) the sediment was characterized as mud and the <63 µm fraction was dominant. At stations 11, 12, 13, 18 and 19 the sediment was coarser and dominated by grains in the size intervals 63-125 and 125-250 µm, with very small fractions of the smallest size fraction (<63 µm). The outermost stations 16, 17 and 20 had the coarsest sediment with highest fractions of grains >250 µm (Table 1). The AFDM was in the range of 0.36 % (station 17) to 2.6 % (station 4) with a tendency towards decreasing AFDM from the inner to the outer part of the inlet (Table 1). There was no clear geographical pattern in chl *a*; the concentrations varied from a minimum of 5.0 µg g DW^{-1} (station 1) to a maximum of 19.6 µg g DW^{-1} (station 4) (Table 1).

Macrobenthic abundance, biomass and production

We registered a total of 120 different species in Nipisat Sound, consisting of 13 bivalve species, 38 polychaete, 41 crustacea, 10 echinoderm and 9 gastropod species, and 9 species belonging to other taxonomic groups. The multivariate analysis of species abundance revealed differences between stations. In the nMDS plot (Fig. 2) samples with similar species composition are placed close together. One isolated cluster of stations was stations 16, 17 and 20, which corresponded to the outermost part of the Nipisat Sound. Other groupings were not uniquely identifiable. However, the addition of the <63 µm grain size fraction to the plot suggested a fur-

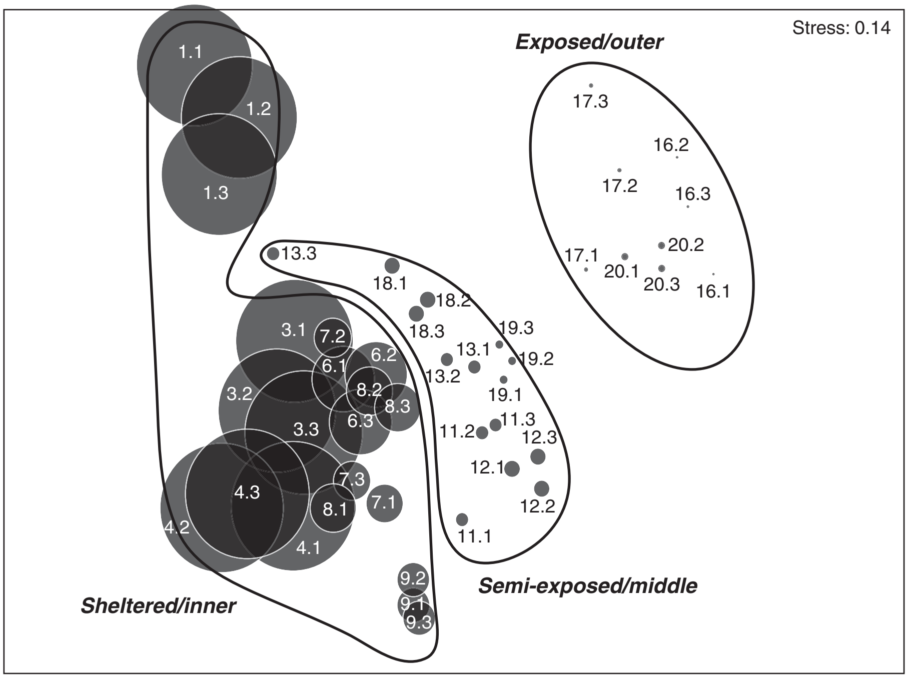

Fig. 2. Non-metric multidimensional scaling (nMDS) ordination for macrobenthic species abundance data. The size of the hatched circles refers to the contribution of the <63 µm-fraction in the sediment. Numbers refer to station number (Fig.1) followed by replicate number.

ther separation into two groups consisting of stations 1 to 9, and 11,12, 13, 18 and 19 (Fig. 2). These three groups seemed to represent the macrobenthic communities at sheltered, semi-exposed and exposed locations, respectively, corresponding to an inner, mid an outer region of the inlet; hereafter referred to as region 1, 2 and 3, respectively. The area of the regions, as they are defined in Fig. 1, was 6.5, 6.4 and 4.1 km^2, respectively.

Abundance, biomass and production data were summarized based on this grouping of stations (Fig. 3, Table 2). In terms of total abundance the averages for the three regions were quite similar, with 6261, 7715 and 6691 ind. m^{-2} in region 1, 2 and 3, respectively (area-weighted average 6912 ind. m^{-2}). However, the contribution by the different taxonomic groups varied substantially. In regions 1 and 2 polychaetes made up 75 and 67 %, respectively, of total abundance, while this fraction was only 20 % for region 3. In terms of bivalve abundance the opposite picture appeared with 7, 19 and 58 % of total abundance in regions 1, 2 and 3, respectively (Fig. 3a). The most abun-

Fig. 3. Contributions of different taxonomic groups to A) abundance, B) biomass, and C) annual production of the macrobenthic community in Nipisat Sound, SW Greenland, a key wintering habitat for eiders.

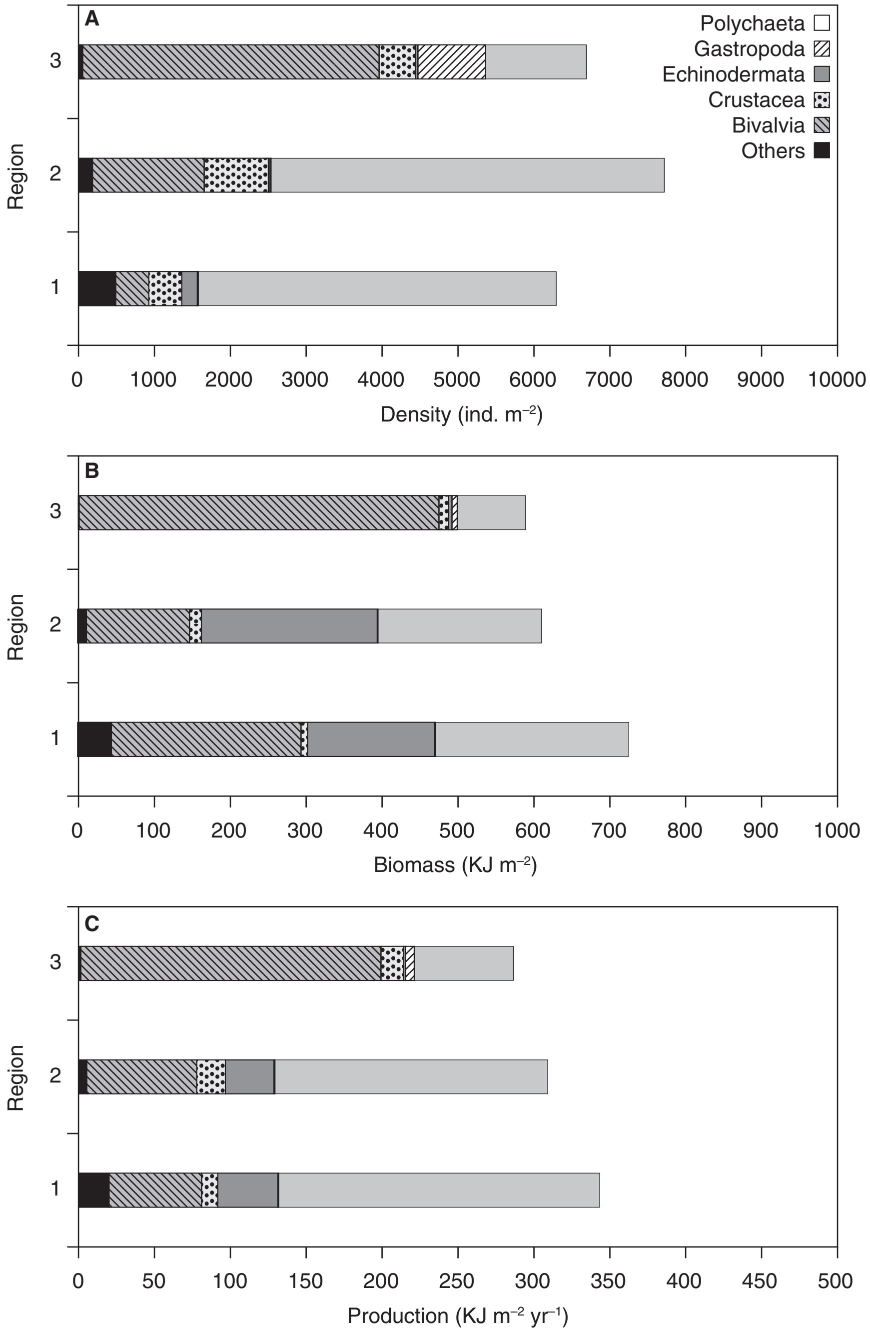

Table 2. Average abundance (ind. m^{-2}) and biomass (KJ m^{-2}) in parenthesis of the ten most abundant species shown for each of the three assemblages (sheltered, semi-exposed and exposed) in Nipisat Sound, SW Greenland. Abundance is given in bold when a species is among the ten most abundant. For each assemblage the relative contribution of the listed species to total abundance is given. *P* polychaeta, *C* crustacea, *B* bivalvia, *G* gastropoda, *A* anthozoa.

	Sheltered 84% **(7 stations)**		**Semi-exposed 82%** **(5 stations)**		**Exposed 86%** **(3 stations)**	
Cistenides granulata **(P)**	**1283.8**	**(18.2)**	**1180.7**	**(35.7)**	**344.4**	**(20.0)**
Pholoe sp. **(P)**	**1073.8**	**(22.5)**	**1148.7**	**(32.9)**	**260.0**	**(6.4)**
Euchone sp. **(P)**	**1049.0**	**(71.0)**	**256.0**	**(2.9)**	115.6	(5.6)
Polydora sp. **(P)**	**359.5**	**(16.5)**	**791.3**	**(14.7)**	63.3	(0.4)
Ampharete acutifrons **(P)**	**292.9**	**(9.0)**	154.0	(4.7)	3.3	(0.04)
Protomedeia sp. **(C)**	**250.5**	**(2.3)**	**381.3**	**(2.2)**	21.1	(0.3)
Athenaria spp. **(A)**	**373.3**	**(19.5)**	129.3	(8.1)	17.2	(0.5)
Macoma calcarea **(B)**	**181.9**	**(17.9)**	**630.0**	**(30.8)**	**661.1**	**(61.8)**
Amphitrite cirrata **(P)**	**165.7**	**(24.8)**	78.7	(10.5)	1.1	(0.05)
Spio sp. **(P)**	**110.0**	**(1.0)**	**186.0**	**(1.6)**	54.4	(0.9)
Mya neoovata **(B)**	101.4	(33.1)	**595.3**	**(80.9)**	**654.4**	**(116.8)**
Serripes groenlandicus **(B)**	24.3	(191.7)	90.0	(18.2)	**230.0**	**(1.2)**
Pygospio elegans **(P)**	11.4	(0.1)	**233.3**	**(2.5)**	17.8	(0.2)
Owenia fusiformis **(P)**	1.9	(0.1)	**514.7**	**(16.6)**	**304.4**	**(3.9)**
Thracia myopsis **(B)**	1.0	(0.1)	2.7	(0.3)	**194.4**	**(74.6)**
Crenella decussata **(B)**			0.7	(0.02)	**1841.1**	**(45.3)**
cf. *Rissoella* sp. **(G)**					**832.2**	**(3.1)**
Mysella sp. **(B)**					**144.4**	**(0.2)**

dant species were *Cistenides* (*Pectinaria*) sp., *Pholoe* sp., *Euchone* sp., *Polydora* sp., *Ampharete* sp.) for polychaetes, and *Mya* sp., *Macoma* sp., *Serripes* sp., *Crenella* sp. for bivalves. Only a few species not belonging to bivalves or polychaetes were among the ten most abundant in one or two of the regions, namely *Protomedeia* sp. (Crustacea), *Athenaria* spp. (Anthozoa) and cf. *Rissoella* sp. (Gastropoda) (Table 2). Thus, the major patterns in species composition and abundance could be summarized to a change in dominance from polychaetes in the sheltered inner part with very fine grained sediment to bivalves towards the more exposed areas with coarser sediment.

As regards total biomass, the averages for regions 1, 2, and 3 were 725, 611 and 580 KJ m^{-2} (31.8, 26.8 and 25.9 g AFDM m^{-2}), respectively. The area-weighted average biomass was 647 KJ m^{-2}. Bivalves made up as much as 80 % of the total biomass in region 3, while contributions by polychaetes, bivalves and echinoderms were quite similar (22 to 37 %) in the two other regions (Fig. 3b). The relatively large biomass of echinoderms compared to their abundance was primarily due to the presence of sea urchins, *Strongylocentrotus droebachiensis*. Of other major contributors to total biomass, not mentioned in Table 2, were the polychaetes, *Anaitides groenlandica* and *Nephtys* sp., and the echinoderm, *Chiridota laevis*. However, the latter was only found in region 1.

The annual somatic production (95 % confidence interval) was estimated at 343 (293-389), 309 (269-355) and 287 (249-327) KJ m^{-2} (15.1, 13.6 and 12.6 g AFDM m^{-2}) in region 1, 2 and 3, respectively (area-weighted average 317 KJ m^{-2} yr^{-1}). This corresponded to average P:B ratios of 0.47, 0.51 and 0.49 yr^{-1} in the three regions. However, examination of P:B ratios of the different taxonomic groups separately revealed rather large differences. The highest turn-over rate was estimated for crustaceans with an average P:B of 1.20 yr^{-1} in the Nipisat Sound as a whole, while the lowest ratio was for echinoderms at 0.22 yr^{-1}. Average P:B ratios for bivalves, gastropods and polychaetes were 0.40, 0.68 and 0.80 yr^{-1}, respectively. In all three regions bivalves and polychaetes were accountable for 80 % or more of the total production of the community. Thus, polychaetes contributed 62, 58 and 23 % of the total estimated production in region 1, 2 and 3, respectively, while these figures were 18, 23 and 69 % for bivalves (Fig. 3c).

Seasonal variation in eider abundance

At the first observation date in early April 2008, at the same time as the macrobenthic sampling, we registered 4450 eiders. The regular monitoring in the winter of 2008-09 revealed a clear seasonal cycle in the number of eiders in Nipisat Sound. From a level of up to *c.*1000 individuals in September and October the number of eiders increased rapidly to a rather constant level of 12-15000 in the period from November through February. Hereafter, we registered a steady decline to approximately the same level as observed in autumn, namely *c.* 1000 individuals in mid June (Fig. 4). An almost identical cycle was observed the following winter until the final count in late April. For the winter of 2008-09, for which we covered the eider wintering season from start to finish, the integrated number of bird days was estimated at 2.04 millions, corresponding to an average number of eiders *c.*7800 individuals in the period from September to June. Of these, 90 % and 10 %, were assumed to be common eider and king eider respectively (Merkel 2004b). Based on these numbers, and the high and low estimates of individual food consumption (see Materials & Methods), the total amount of energy needed by wintering eiders was estimated to lie in the range of 3.11×10^9 to 4.85×10^9 KJ. This corresponds to an average of 183 to 285 KJ m^{-2} in the sub-tidal areas of Nipisat Sound (17 km^2).

During the monitoring of eiders we also registered other bird species in the area; in relatively small numbers, however. The most abundant of these was the long-tailed duck (*Clangula hyemalis*) which had an intense peak in abundance in late autumn at 500 to 2000 individuals. A number of other species occurred more or less sporadically, among them mallard (*Anas platyrhynchos*), thick-billed murre (*Uria lomvia*), little auk (*Alle alle*), black guillemot (*Cepphus grille*) and great cormorant (*Phalacrocorax carbo*) (data not shown). Thus, eiders were the dominant genus representing >90 % of all registered birds in Nipisat Sound.

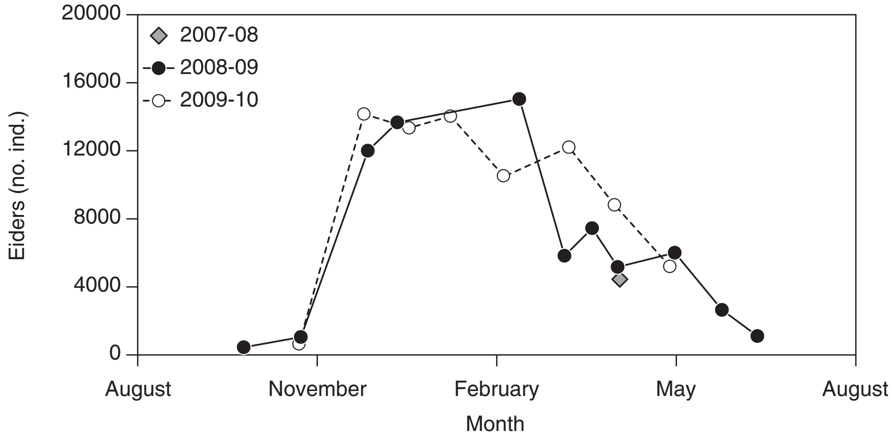

Fig. 4. Seasonal development in the number of wintering eiders (*Somateria* spp.) in Nipisat Sound, SW Greenland, in the period 2008-10.

DISCUSSION

Macrozoobenthic biomass and production

The macrobenthic species composition in Nipisat Sound reflected the physical structure of the habitat and was dominated by infauna species, such as polychaetes and clams. This was in contrast to the nearby Kobbefjord, where epifaunal sea urchins, *Strongylocentrotus droebachiensis* and scallops, *Chlamys islandica*, dominated the macrobenthic community <60 m depth on substrates of gravel, stones and rock (Blicher et al. 2009). Effects of sediment characteristics on macrobenthic community structure are well-described (e.g. Sejr et al. 2010), and were also found within the range of variations in Nipisat Sound. Differences in grain size composition from the inner, sheltered areas to the outer, exposed part of the sound seemed to explain variations in macrobenthic species abundance well (Fig. 2). The estimates of abundance of macrobenthos in Nipisat Sound were comparable to the deepest part of the Godthaabsfjord (357 to 626 m depth), as well as to the Fylla Bank, the shelf and shelf slope (47 to 956 m depth) outside the Godthaabsfjord (Sejr et al. 2010). Still, the total biomass in Nipisat Sound was generally several factors higher than in the deeper areas of the Godthaabsfjord and its margins (wet weights compared, data not shown). Estimates of abundance and total biomass were similar to results from shallow stations (6 to 58 m) in Disko Fjord in West Greenland (Schmid & Piepenburg 1993). The average estimate of total macrobenthic biomass of 647 KJ m^{-2} (28.4 g AFDM m^{-2}) for Nipisat Sound in the spring 2008 was also comparable to the result from another high-latitude fjord, Sørfjord in North Norway, reaching 441 KJ m^{-2} on average in a depth range from 18 to 128 m (Nilsen et al. 2006). However, the estimate was in the lower end compared to areas with a similar functional role as important foraging sites for migrating birds, namely the large intertidal Wadden Sea (26 to 65 g AFDM m^{-2}) stretching along the South-eastern shore of the North Sea (Nehls 1989, Scheiffarth & Nehls 1997) and the Oosterschelde Estuary (49 to 99 g AFDM m^{-2}) in SW Netherlands (Meire et al. 1994). Some regions of the Chukchi and Bering Seas also have very high infaunal biomasses of up to >100 g AFDM m^{-2}; generally lying in the range of 20 to 60 g AFDM m^{-2}, however, (assuming a conversion factor of 1.85 from g carbon to g AFDM, (Brey 2001)) (Grebmeier et al. 2006).

Annual production was estimated using an empirical model (Eq. 1). Although the model is based on a very high amount of data, an approach such as this always involves a degree of uncertainty of the estimates as indicated with 95 % confidence intervals. Also, the model output does not include production of reproductive tissue, which in some species can be of major importance for the total production, especially in populations dominated by old/mature individuals (Blicher et al. 2007, Blicher et al. 2009). Thus, our estimate might be regarded as a minimum estimate of total annual macrobenthic production. Compared to other high-latitude localities, the estimate of total somatic production (317 KJ m^{-2} yr^{-1} or 13.9 g AFDM m^{-2} yr^{-1}) of macrobenthos in Nipisat Sound is relatively high. Somatic production of the macrobenthic community in Sørfjord North Norway was estimated at 185 KJ m^{-2} yr^{-1} (Nilsen et al. (2006). Similar studies in North Bering and Chukchi Seas have suggested large regional variations in annual production, which ranged from 2 to 25 g AFDM m^{-2} yr^{-1} (assuming a production-to-consumption ratio of 0.27; (Brey 2001)) and was highly dependent on the productivity of the overlying water column (Grebmeier et al. 1989). Annual somatic production of macrobenthos in the high-Arctic Young Sound in NE Greenland was estimated at 2.7 g AFDM m^{-2} at depths from 0 to 40 m (Sejr & Christensen 2007). Even though the macrobenthic species composition in Nipisat Sound differed strongly from the nearby Kobbefjord in the Godthaabsfjord system, estimates of biomass were quite similar at 28.8 g AFDM m^{-2} of the dominant macrobenthic species at 0 to 60 m depth. However, the turnover in Kobbefjord was somewhat slower compared to the estimate for Nipisat Sound as indicated by a lower annual production (8.0 g AFDM m^{-2} yr^{-1}, including reproductive tissue) (Blicher et al. 2009). Several of the dominant genera in Nipisat Sound, such as *Mya*, *Macoma*, *Cistenides* (*Pectinaria*), *Euchone*, *Pholoe*, *Polydora*, *Spio* and *Pygospio*, were reported as being dominant at shallow sites (6 to 14 m) in Disko Fjord, West Greenland (Schmid & Piepenburg 1993). However, its rareness might lie in the physical properties of the area, namely several km^2 with shallow depth and soft sediments in a region generally characterized by steep slopes, and gravelly or rocky bottom habitats (Blicher et al. 2009, M. Blicher pers. obs.), causing the macrobenthic community in Nipisat Sound to contain relatively large numbers of polychaetes and clams within reach of bottom foraging birds.

Total eider consumption

The periods of arrival and departure of the wintering eiders in Nipisat Sound, as well as the number of birds, were very similar in the period 2008-10. Common eiders in Nipisat Sound show high site fidelity during their wintering (Merkel et al. 2006), and are therefore assumed to feed exclusively in the study area. Thus, the eiders were estimated to consume 183 to 285 KJ m^{-2} in Nipisat Sound during their wintering. With reference to the two methods for calculating food consumption, we regarded these two estimates as representing: 1) minimum food requirements to keep constant body condition and 2) food consumption in a situation with excess food and potential build up of body reserves. Thus, the actual food consumption would depend on food availability.

Based on our observations of the wintering season of eiders lasting from November to May/June, and knowledge about the growth season of macrobenthos in the region (Blicher et al. in press), the season with major eider predation and the period with high macrobenthic productivity were assumed not to overlap. Thus, the macrobenthic community would undergo two contrasting developments throughout the year: a winter period with a decrease in biomass followed by a period where the remaining macrobenthic community builds up biomass due to production, the early spring being the turning point. Thus, we would expect an increase in macrobenthic biomass from spring through late summer corresponding approximately to the estimated average annual production of 317 KJ m^{-2} and end up in the range of 867 to 1068 KJ m^{-2} depending on region (average 964 KJ m^{-2}) in the autumn. Our results indicate a balance between the expected winter consumption by eiders and the total production of macrobenthos during the productive summer season. Hence, the energy requirements of wintering eiders in Nipisat Sound only corresponded to 17 to 33 % of the expected macrobenthic biomass in autumn, which is similar to studies of total bird predation on macrobenthos in the Wadden Sea and SW Netherlands (13 to 25 %) (Meire et al. 1994, Scheiffarth & Nehls 1997). The estimated eider food consumption in Nipisat Sound was in the range of 58 to 90 % of the estimated total annual macrobenthic production. The actual amount of food consumed by eiders would depend on prey abundance, accessibility, detectability, ingestibility, digestibility and profitability of the available prey items (Guillemette et al. 1992, Richman & Lovvorn 2003, Lovvorn et al. 2009, Richman & Lovvorn 2009). In any case, given the fact that the estimated food consumption of the eiders corresponds to such a large fraction of the total annual macrobenthic production, a strong preference for a certain prey type or species is likely to affect the macrobenthic community structure in Nipisat Sound.

Prey selection and prey availability

Common eiders are known to feed on a variety of different organisms. However, mussels and clams are generally regarded as preferred prey items, while crabs (e.g. *Hyas* sp.) and sea urchins (*Strongylocentrotus* sp.) can be alternatives, although often non-preferred (Nehls 1989, Guillemette et al. 1992, Merkel et al. 2007b). Merkel et al. (2007b) reported that 57 % of the oesophageal content of common eiders in the Nuuk area consisted of polychaetes, *Cistenides* sp. and clams, *Mya* sp., in the winters between 1999 and 2002. Even though these two species occurred at very high densities in Nipisat Sound in April 2008 (Table 2), *Cistenides* sp. and *Mya* sp. only represented *c.*15 % of the total macrobenthic biomass (*c.*100 KJ m^{-2}). Assuming that 57 % of the eider energy costs during winter have been covered by these two species, this would correspond to 105 to 162 KJ m^{-2}. To balance this equation, the biomass of *Cistenides* sp. and *Mya* sp. would have to be at least two to three times higher at the beginning of the wintering period, compared to our observations in the early spring. This equals a reduction in biomass of *c.* 50 % or more during winter, which would be difficult to recover from during one productive summer considering the average P:B ratios of polychaetes and bivalves in Nipisat of 0.8 and 0.4 yr^{-1}, respectively. Given the number of eiders in Nipisat Sound, it therefore seems likely that they are capable of depleting their preferred prey species in the area. In April 2008 the average individual biomass of *Mya* sp. was only 0.175 KJ corresponding to a shell height of *c.* 9 mm. The maximum shell height of this species is 60 mm (Sejr & Christensen 2007). A strongly left-skewed size structure could result from severe predation on the larger, more profitable clams. Depletion of mussel beds by common eiders has been observed at some sites in Canada (Guillemette et al. 1995, Hamilton 2000). However, at some point in the process of prey depletion, eiders might have to explore alternative food sources, and/or leave the area in search of alternative feeding sites, due to foraging becoming unprofitable. For comparison Richman & Lovvorn (2009) calculated the foraging profitability for White-winged Scoter (*Melanitta fusca*, 950 to 1800 g body mass) foraging on clams of different sizes, densities and burial depths, and showed that for clams of a biomass of 0.380 KJ ind^{-1} scoters needed densities of at least 100 to 150 clams m^{-2} to be able to cover the energetic expenses of the dive itself. This threshold density would be even higher at a lower energy content of prey items as observed for clams in Nipisat Sound. Blue mussels, *Mytilus* sp. are known to be a preferred prey species for eiders (e.g. Guillemette et al. 1992, Hamilton 2000) and could be an alternative to clams. However, the number of *Mytilus* sp. was low in our samples from Nipisat Sound. This could be a result of the fact that *Mytilus* sp. often inhabit gravelly or rocky sites, and often in or near the intertidal zone, which are not effectively sampled with a van Veen grab. Thus, *Mytilus* sp. and other species preferring such substrates were likely to be underrepresented in our samples due to the fact that we did register sites with stony or gravelly substrate. However, Merkel et al. (2007b) reported that only 6 % of the diet of common eiders in Nipisat Sound from 1999 to 2002 consisted of *Mytilus*, which seems to indicate that they do not play a major role in the macrobenthic community in the area. Still, the abundance of *Mytilus* sp. might differ between years as a result of variability in recruitment success, and we cannot draw any certain conclusions as to the role of *Mytilus* sp. in the study period. Also, the role of two other common species inhabiting more gravelly and rocky sites, sea urchins, *Strongylocentrotus droebachiensis*, and crabs, *Hyas araneus*, is uncertain for Nipisat Sound. Results from 1999-2002 indicate that sea urchins make up a minor part of the diet of common eiders in Nipisat Sound; an important component in the diet of king eiders, however, which tend to forage at greater depths (Merkel et al. 2007a, Merkel et al. 2007b). Still, sea urchins, which can be very abundant at sites with hard substrates (Blicher et al. 2009), might be relevant as an alternative food source for common eiders in periods with shortage of the preferred prey species (Guillemette et al. 1992). Yet other profitable food sources might provide a significant energetic input during short periods of the season due to variations in accessibility. Swarming of the large polychaete, *Nephtys* sp. has been observed in November in Nipisat Sound (M. Blicher pers. obs.) providing a potentially profitable prey unlike when buried in the sediment. Similarly, the eggs of the lumpsucker (*Cyclopterus lumpus*) could be an important food source seasonally (Bustnes & Erikstad 1988). Nipisat Sound is locally known as a spawning area for lumpsucker, which start to migrate to coastal areas during late winter or early spring to spawn large amounts of eggs in batches at shallow depths (1-5 m). Merkel et al. (2007b) did not register any significant amount of fish eggs in the eider diet. However, this might be related to the fact that their sampling did not coincide with the peak spawning period for the lumpsucker in SW Greenland from early March through May (Ministry of Fisheries, Hunting and Agriculture, Greenland; *unpublished data*).

Also, the role of the Arctic intertidal areas is uncertain. Eiders are known to forage on tidal flats at high tide (e.g. Nehls 1989). However, the flats in Nipisat Sound are ice-covered or frozen, at least periodically, during winter. Since our counts were carried out at high tide and eiders were not observed foraging in these areas, we do not consider the tidal flats to be of significant importance for eiders in the area.

A strategy for the eiders might also be to turn to a higher degree of generalist feeding. In any case, our results suggest that a change in feeding strategy and diet, compared to the results from 1999-2002 (Merkel et al. 2007b), could be necessary for the eiders in Nipisat Sound to be able to cover their energy expenses. That said, it is clear that macrobenthic data from different seasons and years, concurrent with diet investigations of eiders, are necessary to provide more details on the specific effects of eider foraging on the macrobenthic community structure and vice versa. If eiders are forced to rely on non-preferred prey items we might also expect their energy yield to be sub-optimal. A situation in which eiders are prevented from accumulating energy, implies that the actual food consumption in Nipisat Sound would approach our low estimate of 183 KJ m^{-2} yr^{-1}, corresponding to a balance between the costs of living and food consumption. This would agree with Jamieson et al. (2006) who did not observe any build-up of body reserves in wintering common eiders in the area. In fact, it was found that adult eiders shot during spring migration at Cape Dorset in the Hudson Strait (assumed to have crossed the Davis Strait) had consistently higher lipid content than birds collected in Greenland during spring (2000-2002) (Jamieson 2003). This suggests that Canadian breeders accumulate energy for breeding upon arrival on the Canadian side and not while wintering in Southwest Greenland. By means of satellite tracking Mosbech et al. (2006) showed that migration speed for common eiders within or between Greenland and Canada was significantly slower during spring migration (on average *c.* 60 km day^{-1}), compared to moult migration (142 km day^{-1}) and autumn migration (190 km day^{-1}), which supports the suggestion that they feed while travelling to breed.

Inter-annual variation and predictability of the habitat

In Nipisat Sound the removal of macrobenthos by eiders is almost entirely restricted to the winter period, where macrobenthos is assumed to be unproductive (Blicher et al. 2010). Thus, summer provides the opportunity for the macrobenthic community to recover from the considerable winter predation through recruitment and growth. For the eiders, it is not only of fundamental importance that the macrobenthic community is able to recover from one winter to the next in terms of total biomass; it is also crucial that this new production is harvestable and profitable. However, macrobenthic recruitment is likely to vary to some extent between years and the frequency of successful recruitments might differ between species, leading to inter-annual variation in the amount of energy harvestable and profitable for eiders (e.g. Zwarts & Wanink 1993). Unfortunately, a description of the inter-annual variation in the macrobenthic community structure was not within the scope of this study. But given the relatively high turnover ratio of *c.* 0.5 yr^{-1}, we might expect the macrobenthic community structure to be susceptible to species-dependent and inter-annual variation in recruitment and production. Thus, it is likely that food conditions for eiders in Nipisat Sound vary between winters, and sub-optimal food conditions may occur sooner or later during the winter. It is expected, though, that eiders will migrate to other areas before the onset of severe nutritional stress. Therefore, eiders in Nipisat Sound, as observed in the period from 2008 to 2010, were probably able to cover their energy expenses to a large extent during their wintering. However, we speculate that the eiders are likely to switch between different feeding strategies or prey items, either during a wintering period and/or from one year to the next as an adaptation to variations in the macrobenthic community structure, in order to be able to cover their costs of living. On the other hand, the almost identical seasonal patterns and number of bird days in the period from 2008 to 2010 indicate a certain degree of predictability of Nipisat Sound as a wintering habitat. In that respect, the reliability of a certain level of harvestable and profitable food resources on arrival just before midwinter might be essential for the eiders. Another important feature of Nipisat Sound as a wintering area for eiders might be that it provides a relatively predictable habitat with respect to foraging accessibility (ice conditions) and the presence/absence of potential predators (white-tailed eagle) compared to the inner fjord areas (Merkel et al. 2006). Merkel (2008) found that eiders in the inner fjord were feeding only during twilight and at night and argued that this was due to predation risk. Here, the eiders can only feed very close to land, due to the lack of shallow waters elsewhere and thus become easy targets for white-tailed eagles. In contrast, the coastal habitats, and especially Nipisat Sound, support larger areas of shallow waters, at which eiders can feed at safe distances from land during daytime (Merkel 2008). Thus, even if Nipisat Sound becomes less optimal as feeding grounds for eiders, it may continue to be so in terms of predation risk. Furthermore, if eiders are limited to feeding nocturnally in the fjords, these habitats become increasingly less attractive as the season progresses and nights shorten. This also supports the suggested scenario that eiders wintering in the Nipisat Sound will have to build up body reserves for the breeding season elsewhere, closer to their breeding grounds.

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Paper VI

BENTHIC O_2 EXCHANGE RATES ACROSS HARD-BOTTOM SUBSTRATES QUANTIFIED BY EDDY CORRELATION IN A SUB-ARCTIC FJORD SYSTEM

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Running head: Benthic O_2 exchange across hard-bottom substrates.

Keywords: Benthic photosynthesis, remineralization, in situ technology, microsensors, *Psolus fabricii* , *Strongylocentrotrus droebachiensis*.

ABSTRACT

Oxygen exchange across seabeds is a key measure for quantifying benthic carbon turn-over. However, technical limitations have restricted such measurements to sedimentary areas and few assessments on hard-bottom substrates exist. Yet, such biotopes are frequent along many coastlines. In spring 2009 we used the non-invasive eddy correlation technique to quantify the in situ O_2 exchange rate across 3 typical substrates in West Greenland: (1) In soft sediments, the O_2 exchange in darkness averaged to 2.0 ± 0.2 mmol m^{-2} h^{-1} (SE, n = 61). This rate encompassed megafauna activity and a large footprint of natural variability. The rate exceeded the O_2 exchange quantified from core incubations and microprofile measurements by 24 % and 80 %, respectively. (2) Measurements across consolidated sand and stones revealed a high activity with average O_2 exchange rates that compared with that of sedimentary areas. Despite being net heterotrophic, the benthic primary production on average amounted to 27 ± 4 mmol O_2 m^{-2} d^{-1}, which per area compares with the pelagic production of the central fjord. Carbon fixed by benthic diatoms and coralline red-algae was efficiently recycled by microbes or grazed by abundant epifauna. (3) A vertical cliff covered with sea-cucumbers also reflected high O_2 consumption rates (1.2 ± 0.2 mmol m^{-2} h^{-1} (± SE, n = 42)). The O_2 exchange derived from the eddy correlation approach exhibited pronounced short term variability reflecting the interplay of several dynamic controls, most importantly short term variations of local hydrodynamics. All together, measurements across hard bottom substrates revealed an active benthic community that efficiently mediate high carbon turn-over rates.

INTRODUCTION

Aquatic sediments play a key role for the mineralization of organic material and nutrient regeneration in coastal environments (Middelburg et al 2008). However, less focus has been given to the fact that sediments also can host high phototrophic biomass that contribute significantly to the sustenance of coastal food webs (Jahnke et al. 2000, Glud et al 2009). Most quantitative assessments on benthic production or degradation of organic material have relied on laboratory or in situ determinations of benthic O_2 exchange rates (Glud 2008). These have either been determined using sediment enclosures or microprofile measurements, which generally are constrained to soft sediments. Only a few chamber or microelectrode investigations have successfully been carried out in natural sandy environments and in these cases they have been confined to relatively well-sorted sand (de Beer et al 2005, Huettel et al 2007, Cook et al 2007, Glud et al 2008). The difficulties of core sampling, chamber emplacement or sensor application to hard bottom heterogeneous benthic substrates have left such environments practically unstudied in the context of organic carbon turn-over. Yet such benthic substrates are frequent in coastal habitats in many areas. Rocks, high currents, wave action, ice erosion, coarse glacial deposits, down slope transport of coarse unsorted erosion material and high densities of large-sized epifauna are characteristic and dominant features of many Arctic and sub-Arctic coastlines (Hop et al 2002, Boertmann et al 2009).

The introduction of the aquatic eddy correlation approach (Berg et al 2003, Kuwae et al. 2006, Berg and Huettel 2008, McGinnis et al. 2008) has made it feasible to quantify the benthic O_2 exchange of such areas. The eddy correlation approach derives the benthic O_2 exchange rate at true in situ conditions by simultaneous recordings of the vertical flow velocity and the O_2 concentration at a given point within the benthic boundary layer and works equally well over soft and hard bottom substrates (Berg and Huettel 2008). The approach imposes a minimum of disturbance to the ambient light field, the benthic substratum and the local hydrodynamics. Further, it integrates the activity of a larger area (i.e. 10-50 m^2; Berg et al 2007) than traditional measurement and can resolve fluxes down to at least ~1 mmol O_2 m^{-2} d^{-1} (Berg et al 2009). At present, the current database on benthic exchange rates from marine environments derived from the eddy correlation only consists of 4 studies (Berg et al 2003, 2009, Berg and Huttel 2008, Kuwae et al. 2006), none of which include complex hard-bottom substrates.

The present study quantifies benthic O_2 exchange rates of different shallow-water and hard bottom substrates in a sub-Arctic fjord system using the eddy correlation technique. Applicability of the approach to such environments is evaluated and the auto- and the heterotrophic activity at each of the five measuring sites are discussed in the context of regional carbon cycling.

MATERIALS AND METHODS

Study site

The study was conducted in May 2009 within the Godthaabsfjord system in SW Greenland (Fig 1). We measured across 5 different substrates (8 deployments) at depths less than 20 m, each representing common benthic environments of the Godthaabsfjord system and of the sub-Arctic and Arctic in general (Fig 1). These sites included; St 1) a cohesive silty-sand substrate, St 2) a mixed, consolidated coarse sand overlain by small stones covered with coralline red algae, St 3) a mixed, fine sand-shell substrate with high densities of the sea urchin *Strongylocentrotus droebachiensis*, St 4) similar to station 3 but with higher densities of coralline red-algae, St 5) a vertical rock wall at a depth of about 17 m with high densities of the sea cucumber *Psolus fabricii* (Fig 2). Basic station characteristics are given in Table 1. Variations of O_2, temperature and salinity do not reflect analytical precision but variations are related to tidal currents and light that regulated biological activity during the 6-22 h of sampling.

Fauna densities and photo-documentation of the sea-bed

At each station the seabed was photographed (n=10-20) (Fig 2) using a submersible digital camera (Nikon D80 within a titanium casing, Ocean Imaging Systems) mounted on a metal frame. At Stations 1 to 4 the frame was lowered from the boat and as tension of a lead-weight connected to the releaser eased on bottom contact, the shutter was activated. At Station

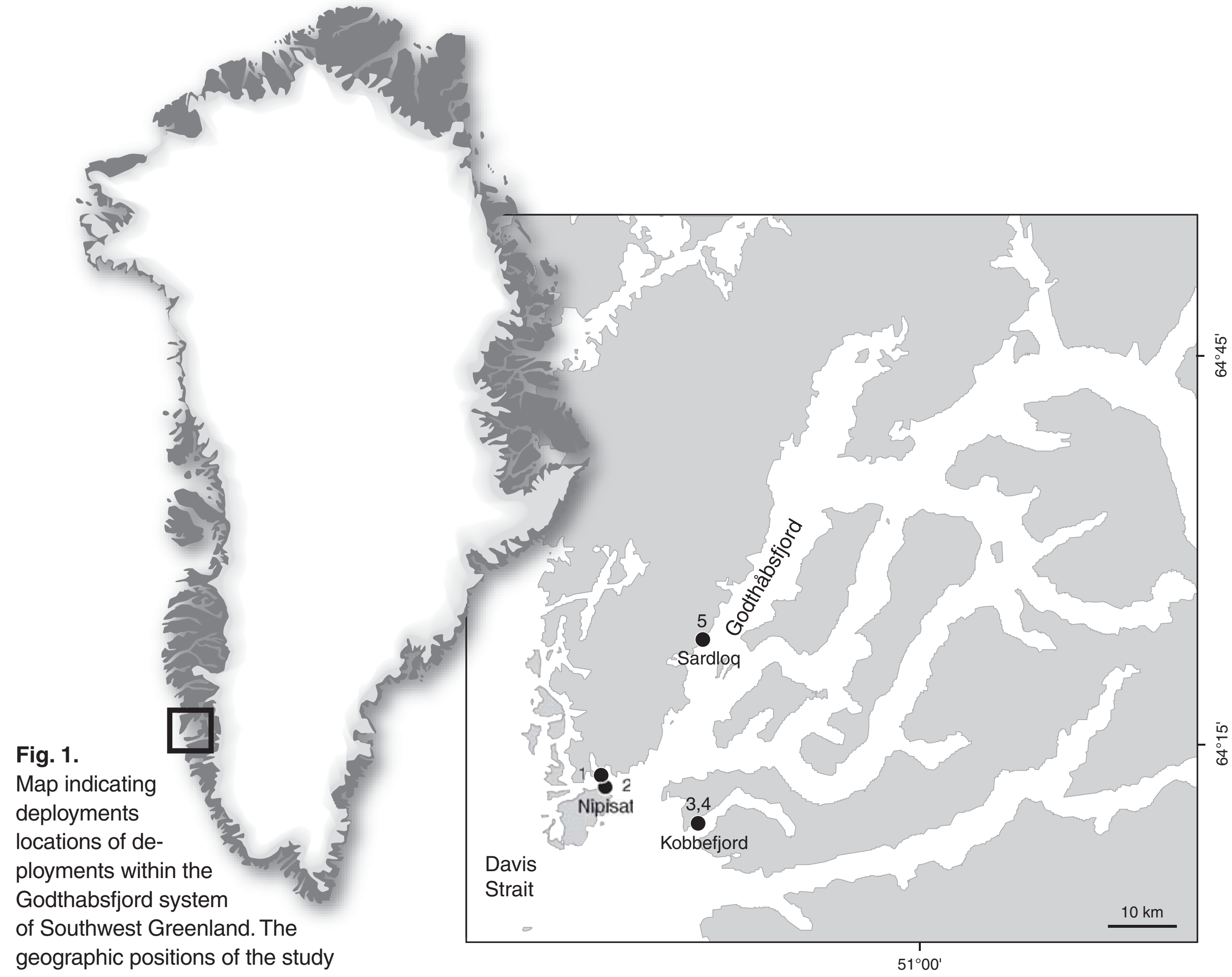


Fig. 1. Map indicating deployments locations of deployments within the Godthabsfjord system of Southwest Greenland. The geographic positions of the study sites were:
St 1) 64° 11.761N; 51° 54.607W,
St 2) 64° 11.598N; 51° 54.529W,
St 3) 64° 08.129N, 51° 39.386W,
St 4) 64° 08.121N, 51° 39.348W,
St 5) 64° 21.386N, 51° 40.508W.

5 the camera was diver operated and a rod was used to ensure a fixed distance to the vertical cliff during photography to scale photos. The density of identifiable faunal species was determined on the basis of the photographs each covering an area between 0.38 and 1.05 m^2 depending on the optical configuration of the camera. The silty-sand of Station 1 hosted little conspicuous epifauna and therefore no systematic photo investigations was carried out, but sediment inspection was complemented by van Veen grabs (n= 3, each 0.1 m^2). Samples were carefully sieved through a 1.0 mm mesh and collected specimens were fixed in 6 % borax-buffered formaldehyde and transferred to 70 % ethanol for later taxonomic determination.

Table 1. Station and deployment characteristics (± SD) for the 8 deployments. Station 1 and station 3 were investigated 3 and 2 times, respectively, while the remaining stations only were visited once.

Station	Depl. nr	Depth* (m)	Temp. (°C)	Sal	Oxygen (mmol L^{-1})	Depl.-time (hr)
1	3	6.6	1.6 ± 0.1	33.1 ± 0.1	363 ± 5	14.3
1	4	6.5	1.7 ± 0.2	33.1 ± 0.0	378 ± 5	0.8
1	8	5.4	3.0 ± 0.4	32.9 ± 0.1	424 ± 5	18.1
2	7	8.2	2.9 ± 0.3	33.0 ± 0.0	413 ± 8	12.5
3	1	6.3	0.3 ± 0.1	33.0 ± 0.1	346 ± 7	6.7
3	5	6.1	0.3 ± 0.1	33.0 ± 0.0	349 ± 7	19.6
4	2	11.7	0.3 ± 0.1	33.0 ± 0.1	344 ± 6	21.9
5	6	17.8	1.8 ± 0.1	32.7 ± 0.0	416 ± 14	12.1

*The tidal range during the study period was ~3.5 m and the values reflect mean value during the deployments.

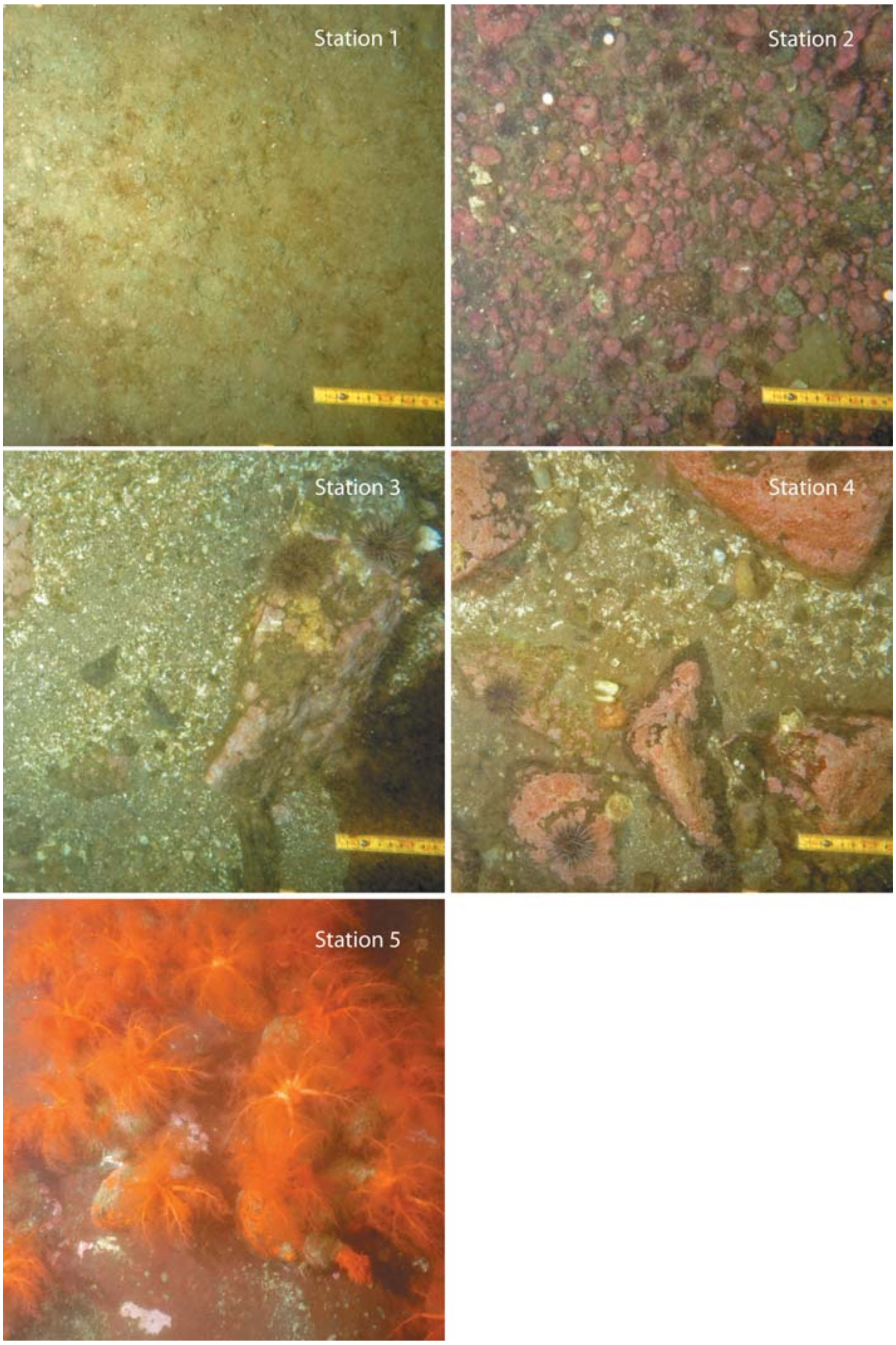


Fig. 2. Representative benthic photos from each station investigated.

Laboratory determined O_2 exchange rates

Sediment core sampling was only possible at Station 1 and by using a Kajak-sampler (KC-Denmark, Silkeborg, DK), a total of 6 sediment cores (inner diameter 5.3 cm) were successfully recovered. The cores were transported back to the laboratory in thermo insulated containers, where cores were uncapped and submerged in bottom water from the sampling site. The water was kept at in situ temperature and at O_2 concentration, and a rotating Teflon coated magnets attached to the inner wall of each core ensured a good mixing and exchange between the water phase of the cores and the exterior seawater. After overnight pre-incubation O_2 microprofiles and total O_2 exchange rates were obtained. In short, the 2-4 O_2 microprofiles were measured in each of the 6 cores using Clark type microelectrodes with an internal reference and a guard cathode (Revsbech 1989). The microelectrodes had tip diameters of 3-20 µm, stirring effects <1 %, and 90 % response time of <0.3 s (Gundersen et al 1998). The profiles were measured at a depth resolution of 100-200 µm in spots that were visibly unaffected by faunal activity. The microelectrodes were positioned by a motorized micromanipulator and the sensor current was measured by a picoampmeter connected to an A-D converter, which transferred the signals to a PC (Revsbech and Jørgensen 1986). The microprofiles had two inherent calibration points: The reading in the overlying water with a known O_2 concentration and the reading in the anoxic sediment. After microprofiling, sediment cores were capped with a gas tight glass plate, leaving an internal water height of 8-12 cm. On the underside of the glass plate an O_2 PreSens^{TM} optode patch (Ø 5 mm) was attached to allow non-intrusive periodic measurement of oxygen consumption in conjunction with a PreSens^{TM} optical fibre cable and Fibrox^{TM} 3 oxygen meter connected to a PC. During incubations 4-6 recordings were obtained at a regular interval in each core while the attached magnets continued to stir the overlying water phase (one core did not provide consistent results probably due to resuspension during incubations and these data were excluded). All measurements were done in darkness. After flux measurements sediment cores were sectioned for porosity determinations that were derived from a measured weight loss after 24h at 100°C and the specific density.

Diffusive O_2 exchange (DOE) of the sediment was calculated from the measured O_2 microprofiles as: $DOE = -D_o\, dC(z)/dz$, where, D_o is the temperature and salinity corrected molecular diffusion coefficient of O_2 and C is the O_2 concentration at a given depth, z, within the diffusive boundary layer (DBL). D_o was taken from Broecker and Peng (1974) and was temperature corrected as described by Li and Gregory (1974). The total O_2 uptake rate (TOU) was calculated from the linear O_2 decrease measured during the whole core incubation (Glud et al 2003).

Eddy-correlation measurements

A small stainless tripod (side-length 1.3 m; height 0.9 m) held a small CTD (Seabird SBE 19Plus) equipped with sensors logging temperature, conductivity, O_2 and scalar PAR (QSP-2300L) irradiance every 5 minutes. A vertically aligned acoustic doppler velocimeter (Vector, Nortek AS, Norway; referred to as the ADV) was placed centrally in the frame in such a way that the cylindrical measuring volume (1.5 x 0.6 cm) located along the ADV centerline was situated 8-10 cm above the seabed during deployments. The ADV was interfaced with a custom-built pressure compensated O_2 microelectrode (as described above) via a submersible picoampmeter (Unisense A/S Denmark). The picoamperimeter housing was positioned at a 45° angle relative to the ADV centerline and the position of the microelectrode tip adjusted to the edge of the ADV measuring volume (Berg et al 2003). The ADV and the O_2 microelectrode signals were sampled at a frequency of 32 Hz in bursts consisting of 14.5 min sampling followed by a 0.5 min "sleep" period. Total deployment times ranged from 18-22 h but unfortunately the majority of the deployments were truncated by microelectrode breakage caused by debris floating along with the bottom current. The periods of successful data recording ranged from 0.8 to 21.9 h with an average measuring period of ~14 h (Table 1).

The zero current of the oxygen microelectrode was determined prior to each deployment by dipping the sensor tip in an anoxic dithionate solution kept at 0°C. Further, the sensor signal during deployments was calibrated against the bottom water O_2 concentration determined by three approaches; 1) measured in sampled bottom water with a handheld Hach HQ40d optical DO meter (Hach Company, Loveland, Colorado) and 2) by Winkler titration and 3) the polarograhic DO sensor on the CTD attached to the measuring tripod. These values did not deviated by more than 2-3 %. Continuous recordings of the bottom water characteristics (temperature, salinity, O_2 concentration) reflected gradual changes related to tidal flow and light availability. Variations in temperature and salinity were considered insignificant while variations in the bottom water O_2 concentration (Table 1) were accounted for during eddy-flux calculations.

At Stations 1 to 4, the eddy correlation tripod was deployed using a winch whilst at the rock wall face (Station 5), the tripod was attached to the wall by bolts drilled into to the wall by a diver. We chose an area (~80 m long and ~10 m wide) covered by epi-macrofauna but without any significant topography. Due to the relative large size of the sea-cucumbers we adjusted the measuring volume to be 16.7 cm off the wall.

Eddy correlation fluxes of O_2 were calculated based on the values of the two correlating parameters; the vertical velocity and the O_2 concentration, respectively, as described in Berg et al (2003, 2009). In short, the original 32 Hz recordings were lumped together by averaging into 16 Hz data and least-squares linear regression fits were used to define the mean vertical velocity and the mean O_2 concentration in each of the 14.5-min measuring segments (bursts). Then instantaneous deviations from these means were determined and multiplied to give the instantaneous O_2 fluxes that were finally averaged to give one value for each 14.5 min long burst.

Each time series of instantaneous velocities of O_2 concentrations and fluxes was carefully examined for “unnatural” disturbances, typically caused by a small piece of organic material hitting the microelectrode tip, or less frequently, a larger piece of debris momentarily corrupting the velocity readings. Disturbances unfortunately gives rise to a temporary change in an O_2 reading that most often lasts “several or many” data points and thus affecting the definition of the mean O_2 concentration, and ultimately the flux extraction. Through detailed visual inspection of the time series, minute for minute, such disturbances “or bad data sequences” were identified. In this process, and in addition to the instantaneous velocities and O_2 concentrations, the cumulative flux (the cumulation of instantaneous flux values) was a central variable because it exhibits an abrupt change at such disturbances. In the current study an average of 14 ± 7 % of the recorded data were regarded as “bad data” and were rejected from the analysis. For further information on eddy correlation data processing and quality control, see Berg et al (2003 and 2009).

We have expressed all flux measurements in the unit mmol m^{-2} h^{-1}, while values extrapolated to cover the diel cycle are expressed as mmol m^{-2} d^{-1}. We chose this to clarify the temporal scale on which the benthic productivity is expressed and to avoid some of the often seen confusion when productivity measurements are compared in the literature.

RESULTS

Parallel O_2 microprofiles, core incubations and eddy fluxes at Station 1

To evaluate how O_2 exchange as derived from the eddy-correlation approach compared with values obtained by more traditional measuring techniques we selected one of the few sites along the coastline of the Godthaabsfjord where it is possible to retrieve sediment (Station 1). The sediment was cohesive sandy mud with a surface (0-1.0 cm) porosity of 0.78 ± 0.01 (SE, n = 5) and an O_2 penetration depth of 2.3 ± 0.1 mm (SE, n = 15) as measured in recovered sediment cores. The diffusive O_2 exchange (DOE) as calculated from microprofiles measured in darkness was -1.1 ± 0.1 mmol m^{-2} h^{-1} (SE, n = 15), while the total O_2 exchange (TOE) measured in cores incubated in darkness amounted to -1.6 ± 0.1 mmol m^{-2} h^{-1}(SE, n = 5). Selecting data obtained during darkness from the in situ O_2 exchange measurements (EOE) provided an average O_2 exchange of -2.0 ± 0.2 mmol m^{-2} h^{-1} (SE, n = 61). Rates derived from the different approaches reflected a gradual increase in benthic O_2 exchange with increasing encompassed area (Fig 3). The benthic fauna at Station 1 was dominated by sediment-dwelling polychaetes that accounted for >70% of the total fauna abundance, however, their biomass was grossly exceeded by small bivalves (mainly *Macoma calcarea*) and medium sized sea-urchins (*Strongylocentrotus droebachiensis*) (Table 2).

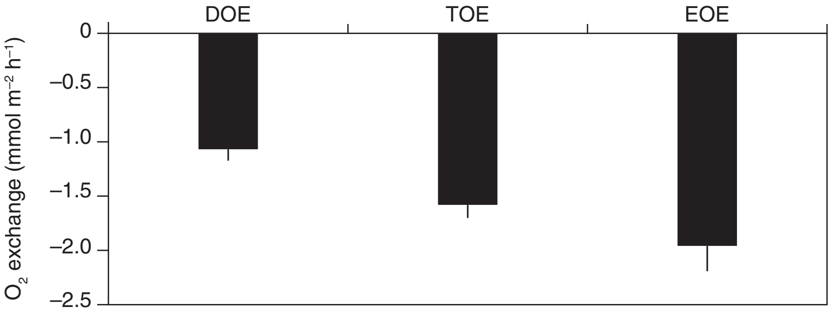


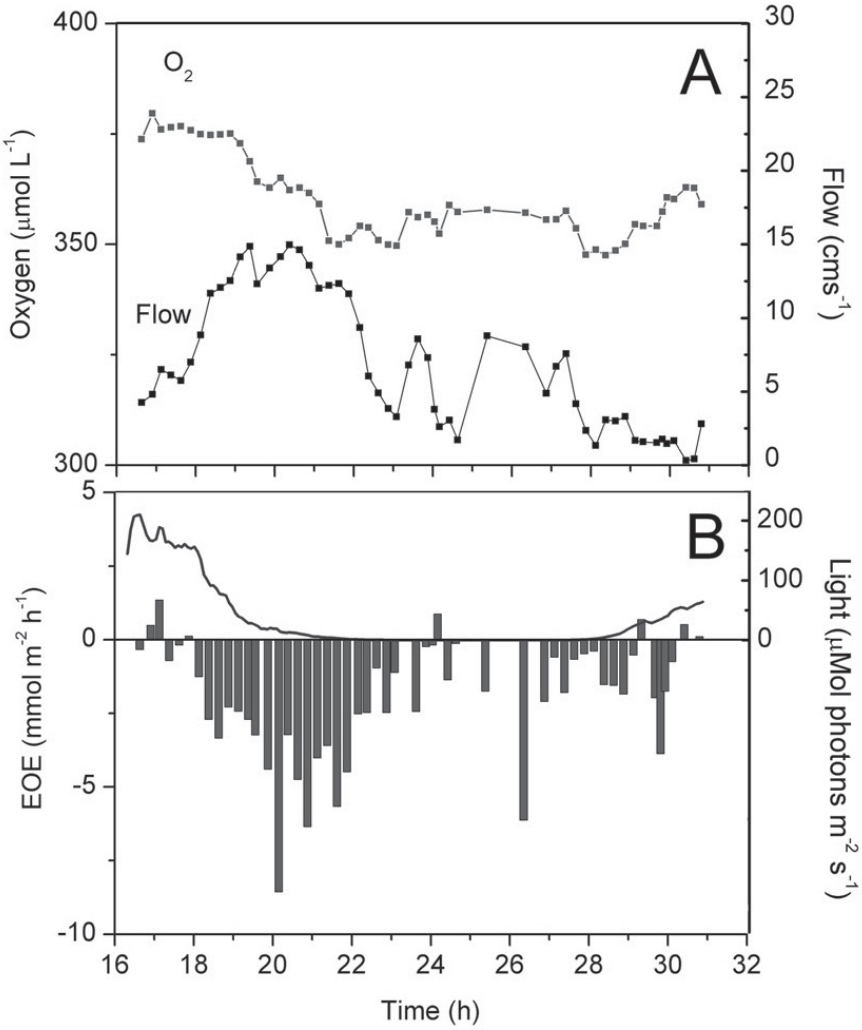
Fig. 3. The average O_2 exchange rates quantified in darkness (PAR <10 photons m^{-2} s^{-1}) from microelectrode profiles (DOE), total core incubations (TOE) and in situ eddy correlation (EOE). Error bars indicate the SE, n = 15, 5, 61 for DOE, TOE and EOE, respectively.

Table 2. Average (± SD) density and biomass (ash free dry weight, AFDW) of macrofauna as estimated from van Veen grab samples (St. 1, n = 3) and underwater photographs (St. 2-5, n = 10 to 20)

	Group/ species	**Density (Ind m^{-2})**	**Biomass (g AFDW m^{-2})**
St1	Polycheata	3147 ± 707	5.5 ± 2.2
	Bivalvia	497 ± 337	46.9 ± 79
	Crustacea	220 ± 66	0.2 ± 0.2
	Echnioderms (Total)	160 ± 131	19.8 ± 8.5
	Sea urchins (*S. droebachiensis*)	16.7 ± 5.8	17.3 ± 6.5
	others	453 ± 323	1.9 ± 1.7
St 2	Sea urchins (*S. droebachiensis*)	192.5 ± 61.9	20.9 ± 6.7*
	others	0.4 ± 0.7	–
St 3	Sea urchins (*S. droebachiensis*)	19.0 ± 8.1	32.5 ± 13.8*
	others	0.5 ± 0.7	–
St 4	Sea urchins (*S. droebachiensiss*)	25.1 ± 11.1	43.0 ± 19.1*
	others	3.1 ± 2.4	–
St 5	Sea urchins (*S. droebachiensis*)	3.7 ± 1.5	6.3 ± 2.6*
	Sea Cucumber (*Psolus fabricii*)	22.6 ± 8.1	–

*Biomass estimated from abundance and size distribution at the photos along with average individual biomass of specimens at the respective sites.

Fig. 4. Variations in bottom water O_2 concentration and horizontal flow velocities (Panel A) along with light availability and O_2 exchange derived by eddy correlation (EOE) in the respective 14.5 min bursts at Station 1 (deployment 3) (Panel B).



Three eddy deployments were carried out at station 1. Unfortunately one deployment (#4) only provided three consecutive burst values of 1.5, 4.9, and 2.0 mmol m^{-2} h^{-1} before the O_2 sensor broke. The values were obtained at an almost constant ambient light levels of ~250 μmol photons m^{-2} s^{-1} and at an average ambient horizontal flow velocity of ~2.4 cm s^{-1} (these values were included in the assessment of the benthic primary production –see below). The two other deployments at Station 1 were obtained at lower light levels but provided longer time series and reflected an extensive short term variations in the EOE as exemplified in (Fig 4). Variations in EOE did not show any direct relation to any single of the main controls that generally are considered to affect the benthic O_2 exchange; light availability, bottom water O_2 concentration and horizontal flow velocity. Neither was there a clear relation to the current direction (data not shown). However, high horizontal flow velocities around dusk did coincide with maximum O_2 uptake rates. Minimum O_2 uptake (and O_2 release) generally coincided with day time measurements (Fig 4). The variations in EOE are clearly regulated by the interplay of several variables that change on different timescales (see Discussion).

Eddy flux measurements across complex benthic substrates

At stations where the seabed consisted of rocks, stones and consolidated sand (Stations 2, 3, 4) the eddy correlation was the only possible way to measure the benthic O_2 exchange. As for the softer sediment the EOE also

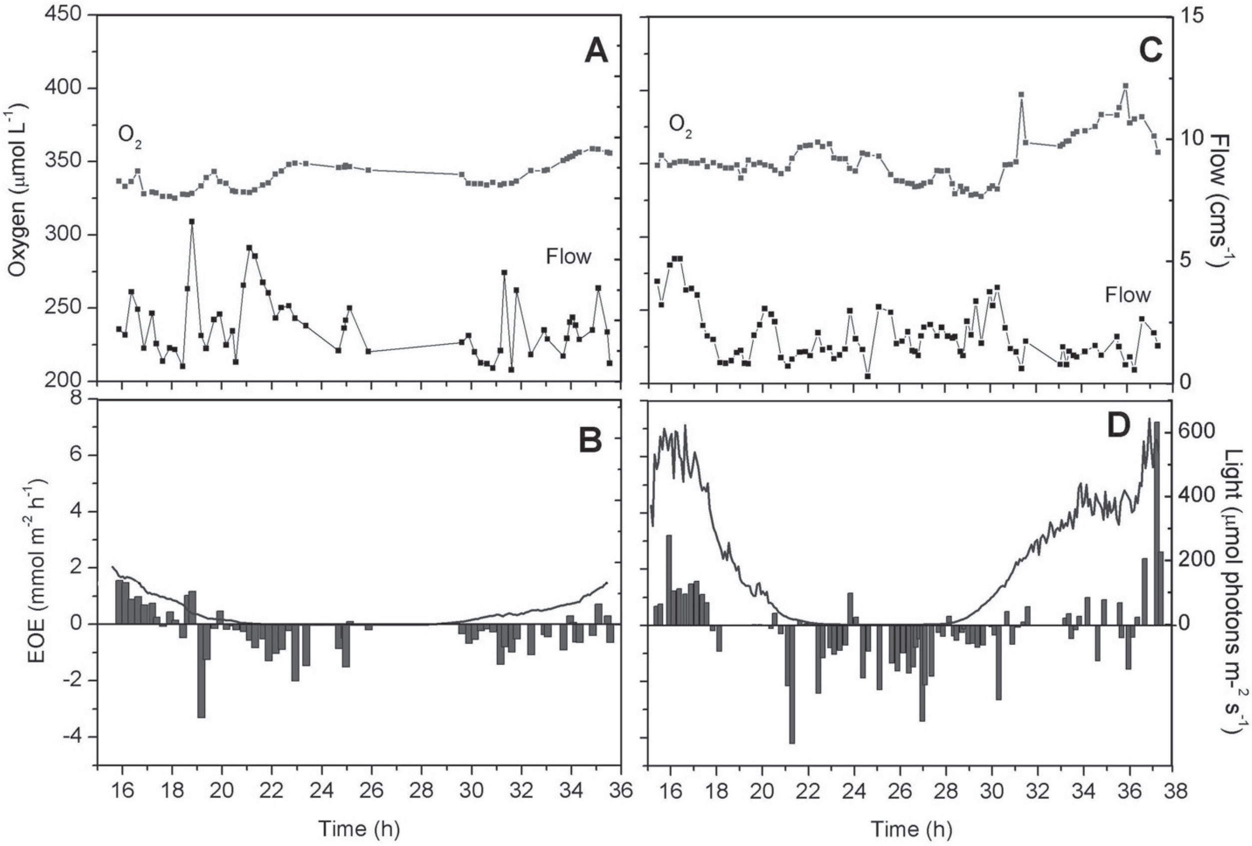


Fig. 5. Oxygen concentration and horizontal flow velocities at Station 3 and 4 (Panel A and C) along with the light availability and the O_2 exchange derived by eddy correlation (EOE) in the respective 14.5 min bursts for both stations (Panel B and D).

in these settings exhibited an extensive short term variation (Fig 5). Generally, however, periods with benthic O_2 release prevailed during daytime while maximum O_2 uptake rates were encountered just around dusk or at night time (Fig 5). While the average dark measurements for Station 3 ranged with those of the soft sediment at Station 1, Stations 2 and 4 exhibited somewhat lower rates (Table 3). For logistic and safety reasons we had to recover and redeploy the instrumentation during the middle of the day – a procedure that took 2-5 hours. Due to O_2 sensor breakage and deployment constrains, measurements during periods of maximum light were few, but in all instances average daytime measurements reflected a significantly reduced O_2 uptake (or even O_2 release) as compared to night time measurements (Table 3). To obtain a conservative estimate of the net benthic productivity (i.e. the daytime release of O_2) we extrapolated the average values obtained in light at the end and beginning of the individual deployments to account for the light period not covered for in the actual measurements. The estimates resolved an integrated O_2 exchange during 16 h of light ranging from -3.6 mmol m^{-2} d^{-1} at Station 1 to 6.9 mmol m^{-2} d^{-1} at Station 3 (Table 3).

Integrating the benthic O_2 exchange for 24h (i.e. 16 light and 8 h darkness) the benthic communities were in all cases net heterotrophic with a daily O_2 uptake ranging between -0.4 to -19.6 mmol m^{-2} d^{-1} (Table 3)Assuming that O_2 consumption rate during night and day are similar, the difference in O_2 exchange rates express the benthic primary production during daytime and amounted to values from 17.5 to 37.1 mmol m^{-2} d^{-1} at the respective stations accounting for 16 h of light (Table 3). The photosynthetic activity was mainly related to the activity of benthic diatoms, but for Stations

Table 3. Average eddy-correlation derived O_2 exchange rates at each respective station (±SE), during darkness n= 63, 26, 48, 17 and 42 for the 5 respective stations while n= 66, 23, 58 and 41 for station 1 to 4, respectively. The table includes information on the day and night periods covered by each deployment and the proportion of the daily light that was encountered during the respective deployments. From the measurements of O_2 release rates the benthic primary production during 16 h of light was estimated by extrapolation (see text for details).

	St 1*	St 2	St 3*	St 4	St 5**
Measured dark EOE (mmol m^{-2} h^{-1})	–2.0 ± 0.2	–1.3 ± 0.2	–1.9 ± 0.2	–0.7 ± 0.1	–1.2 ± 0.1
Measured light EOE (mmol m^{-2} h^{-1})	–1.6 ± 0.3	–0.7 ± 0.3	0.3 ± 0.2	–0.1 ± 0.1	–
Night period measured (h)	8/0/8	8	8/8	8	–
Day period measured (h)***	5.6/0.8/9.3	6.0	0.8/14.6	10.1	–
Irradiance during measurements of total (%)	22.5	26.4	80.6	56.5	–
Estimated O_2 exchange during light (mmol m^{-2} d^{-1})***	–3.6	5.5	6.9	5.2	–
Total daily O_2 exchange (mmol m^{-2} d^{-1})	–19.6	–4.9	–8.3	–0.4	–
Daily primary production (mmol m^{-2} d^{-1})****	27.5	26.2	37.1	17.5	–

*Values for station 1 and 3 represent data from 3 and 2 deployments, respectively.

**Measurements were conducted at 17 m depth in the shadow of a high vertical cliff and maximum light recorded during the 12h deployment was 3 mmol photon m^{-2} s^{-1}.

***Day period define as period with light >10 mmol photon m^{-2} s^{-1} (i.e.~16 h).

****Assuming daytime O_2 consumption equals night O_2 consumption

2, 3, 4 where coralline algae covered up to 60-70% of the sea-bed (Fig 2) they could have made a significant contribution to the system production (Roberts et al. 2002). The primary producers were extensively grazed by the epifauna that on Stations 2, 3 and 4 was completely dominated by sea-urchins (*Strongylocentrotrus droebachiensis*) (Table 2).

Eddy flux measurements along a vertical cliff

The Godhaabsfjord, as most other deep glacial fjords, is characterised by many steep cliffs, often covered by filtrating epifaunal communities taking advantage of the continuous supply of particulate organic material. To the extent, that the prevailing current runs parallel to such cliffs the eddy correlation principle should work equally well here as it does for the horizontal sea-bed. Continuous recordings of the instrument packages mounted di-

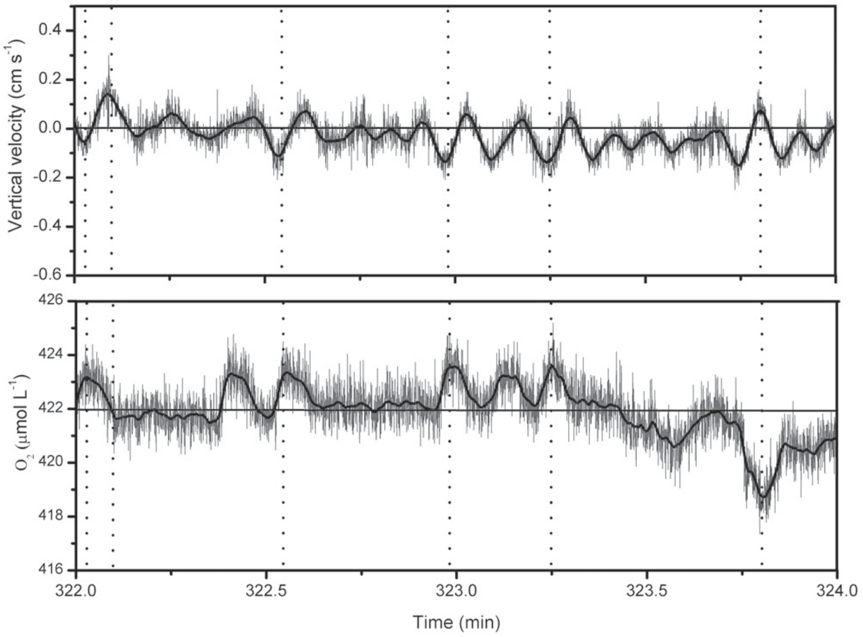
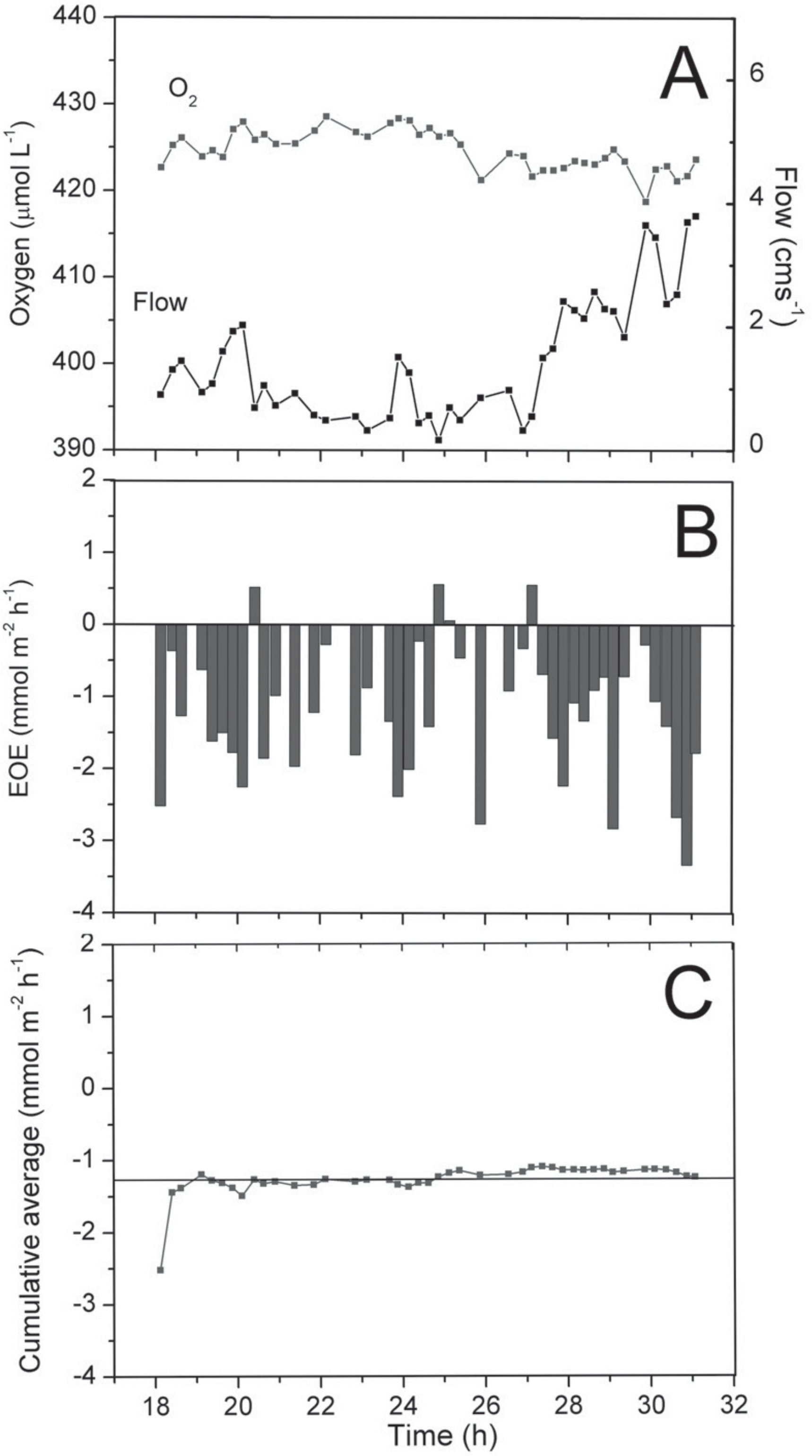


Fig. 6. Concurrent 32 Hz recordings of the horizontal flow component (i.e. perpendicular to the wall) and the O_2 concentration 16.7 cm off the wall. Horizontal flow jets coming off the wall (i.e negative values) coincide with minima in O_2 concentrations. The continuous lines indicate adjacent averages of to the respective data series using n = 10, while the horizontal line indicate the overall average.

Fig. 7. Oxygen concentration and horizontal flow velocities at Station 5 (Panel A) and the average O_2 exchange rate as derived by eddy correlation (EOE) in the respective 14.5 min bursts (Panel B). Panel C represents the cumulative average at the time points of each burst in Panel B along with the overall average (thin line).



rectly on the wall with the ADV pointing towards the cliff face in general confirmed a correlation between variations in the vertical flow velocity (i.e. the flow perpendicular to the cliff) and the O_2 concentration (Fig 6), consequently cumulative O_2 fluxes generally reflected a nice linear uptake during the respective bursts (data not shown). During the ~12 h deployment performed at ~17 m depth in the shadow of the high cliff, the maximum recorded light level was 3 µmol photon m^{-2} s^{-1}. The horizontal flow velocity (i.e. parallel to the cliff) was low ranging from 0.5 to 3.9 cm s^{-1} and there was no close relation between the EOE and flow velocity. However, maximum rates did coincided with maximum velocities measured towards the end of the deployment (Fig 7). The entire cliff was densely covered by sea cucumbers and to lesser extent with sea urchins (Table 2) and the average O_2 uptake of the community amounted to 1.2 ± 0.1 mmol m^{-2} h^{-1} (± SE, n = 42). The cumulative average expressing the average EOE value at any given time quickly approached the overall average value (Fig 7C).

DISCUSSION

Benthic primary production

Even though our measurements indicate that the different sea beds were net heterotrophic during the study period, they also reflected a significant benthic primary production ranging from 17.5 to 37.1 mmol O_2 m^{-2} d^{-1} (average 27.2 mmol O_2 m^{-2} d^{-1}). These values have to be regarded as minimum values as we only conservatively extrapolated the measured daytime values to also represent the mid-day period where no (or few) measurements were recorded. Further, similar day and night time O_2 consumption was assumed, but detailed microsensor measurements have documented that day time O_2 consumption typically exceed night time O_2 consumption by a factor of 1.4 to 1.8 (Fenchel and Glud 2000). This observation is mainly a result of efficient microbial turn-over of leaking photosynthesates and deeper O_2 penetration during the day time (Epping and Jørgensen 1996, Fenchel and Glud 2000, Tang and Kristensen 2007). The fact that we often observed maximum O_2 uptake rates just at dusk where the photosynthetic activity ceased indeed suggests that a labile pool of photosynthesates is quickly turned over and soon exhausted at the onset of darkness. Resolving the benthic primary production from the net O_2 exchange rates, therefore only provide a minimum value. Despite this, values range with that of the gross pelagic primary production measured just before and after our campaign in the central parts of the ~600 m deep fjord; integrating the activity in the ~50 m deep photic zone of the pelagic primary production at May 15 and June 17 2009 amounted to 35 and 15 mmol O_2 m^{-2} d^{-1}, respectively (Juul-Pedersen et al. 2010). The measurements suggest that the rugged seabed along such coastlines host a significant primary production driven by micro- and coralline algae that contribute significantly to sustaining microbial heterotrophic activity and the larger grazers of this zone.

Benthic O_2 consumption in the shallow water of the Godthaabsfjord

The difference between O_2 exchange as derived from porewater profiles and sediment core incubations has often been used to assess the non-diffusive O_2 exchange, which for most part has been ascribed to fauna activity (Archer and Devol 1992, Meile and van Cappellen 2003, Glud 2008). However, it has also been documented that small core incubations tend to exclude larger fauna species and consequently underestimate the true fauna mediated O_2 exchange (Glud and Blackburn 2002, Glud et al 2003). These observations are confirmed by the measurements at Station 1, where the eddy correlation exchange (EOE) exceeds the small core (inner diameter

5.3 cm) incubations by 25 %, most likely as EOE encompass the effects of larger in- and epifauna specimens like *Macoma calcarea*, *Mya neoovata* and *Strongylocentrotus droebachiensis* that are not represented in the core incubations. Over all the fauna mediated O_2 uptake averaged 0.9 mmol m^{-2} h^{-1} (i.e. EOE- DOE) equivalent to 46 % of the integrated O_2 uptake derived from eddy correlation. Both the absolute value and the relative proportion of fauna mediated O_2 uptake align well with similar estimates derived from concurrent in situ deployments of large-sized chambers and microprofilers in shallow water soft sediments (Glud 2008). Currently there only exists two studies with concurrent in situ measurements of large in situ chambers and eddy correlation and they suggest that in soft-bottom cohesive sediments and where the in situ fauna is proportionally represented during chamber incubation, the two approaches provide similar results (Berg et al 2003, 2009). However, in more complex environments characterized by advective porewater transport or dominated by mega fauna this may be very different (Berg and Huettel 2008).

The EOE as measured on hard-bottom Stations (i.e. 2, 3 and 4) was surprisingly high considering little sediment accumulation. Actually, the O_2 uptake measured in darkness scale with chamber measurements in many shallow-water, carbon- and fauna rich depository sediments (Moodley et al 1998, Rowe et al 2002, Laursen and Seitzinger 2002, Glud et al 2003). In recent years there has been increasing evidence that despite low carbon content, permeable sands can have high O_2 turn-over rates due to an efficient entrapment and recycling of particulate carbon (Huettel et al 1996, 2007, Cook et al 2007). The capability for such sands to work as biocatalytic filters facilitating an efficient carbon-turn over does, however, require an occasional wave induced "resetting" as they otherwise gradually consolidate and clough up (Huettel and Webster 2001). We can not assess the permeability of the complex substrates of these stations (as recovery is impossible), but the fact that stones are covered by slow growing coralline algae and the dense coverage of shells suggest that the intervening sediment rarely is resuspended or redistributed. Even though material can be trapped in the complex topography most of the O_2 consumption is probably occurring at the substrate surface and a significant fraction reflect turn over of local benthic primary production. The main macrofauna grazers at these sites are *S. droebachiensis* (Table 2) that transverse over the surface rasping off any coverage and ingest the diatom enriched surface sediment. In Kobbefjord (see Fig 1) the average annual carbon demand of the *S. droebachiensis* community was estimated on the basis of growth rates (including gonad production) and amounted to ~61 g C m^{-2} yr^{-1} at station 3 of this study (Blicher et al 2009). Assuming that 30 % of the ingested carbon is respired (Miller & Mann 1973) and a respiratory coefficient of 0.7 (Grebmeier et al 2006), and converting the values to O_2 equivalence the average contribution of the community at 0-10 m amounted to 0.25 mmol O_2 m^{-2} h^{-1} equivalent to 19-35 % of the night time O_2 uptake at stations 2, 3, 4 (Table 3). Apart from the respiratory O_2 demand of *S droebachiensis* the considerable faecal production of these animals, amounting to 60 % of their ingestion (Miller and Mann 1973), must stimulate a patchy microbial driven remineralization leading to further O_2 consumption. Clearly these complex benthic substrates host dynamic communities with high carbon turn over rates. The average rate scale with those of soft depository sediments, but the activity is merely driven by local benthic primary production.

Whereas the communities at Stations 1-4 presumably get a significant faction of their carbon demand covered by local benthic primary production, the filter feeding sea-cucumbers of Station 5 depend on a pelagic food source that is advected to the community. The actual O_2 uptake of the epifaunal covered cliff is also similar to that of the hard-bottom stations (i.e. Stations 2-4). In fact, per m^2 the respiratory activity of the epifauna (including any microbial biofilms) on a 24 h basis is only slightly less than that of the daily pelagic primary production of the entire 50 m deep photic zone during the same period (i.e. 1.3 – 2.9 mmol m^2 h^{-1} (Juul-Pedersen et al. 2010). This demonstrates that the epifaunal covered cliffs of the narrow fjords can efficiently graze on the pelagic production, but their relative importance will obviously depend on the geometry of the fjords and on the frequency of such dense epifaunal assemblages – a topic for further studies.

Oxygen exchange rates as derived by eddy correlation

The introduction of the eddy correlation technique to aquatic research allows quantification of O_2 exchange rates across benthic interfaces that in praxis are impossible to investigate with chambers and microelectrode profiling. Further, the approach non-invasively integrates O_2 exchange of a large area (Berg et al 2007). However, the actually location and size of this measuring area or foot print in a dynamic environment can be difficult to define. With constant changes in the direction and the velocity of flow passing a highly heterogeneous seabed, the derived O_2 exchange is bound to exhibit high variation. Further, water bodies passing the measuring volume may express an O_2 balance that has accumulated over time scales that are longer than the temporal resolution of the bursts. For instance water that has been isolated over a highly O_2 consuming (or producing) patch of the seabed and then advected into the measuring area results in a instantaneous unrepresentative high (or low) O_2 exchange rate for the measuring area. Derived fluxes may even temporarily exhibit the opposite sign of the overall average flux. This is exemplified by the incubations at the vertical cliff where the derived O_2 exchange rate varied between 1.0 and -6.7 mmol m^{-2} h^{-1} during the ~12 h incubation (Fig 7). However, the cumulative average (i.e. the average exchange rate obtained at any given time after deployment) quickly approached the overall average of -1.2 mmol m^{-2} h^{-1}, but it never reached a true steady level (Fig 7C) presumably as the environmental controls; the free flow velocity and the particle density (which could affect fauna activity), changed with the tidal current. For coastal environments in general, the ever changing free flow velocity (or better turbulent dissipation energy) will regulate the DBL thickness which again will affects the benthic O_2 distribution, and consequently the benthic O_2 exchange rates will exhibit a high degree of variability reflecting concurrent changes in the local hydrodynamics (Lorke et al 2003, Røy et al 2004, Glud et al 2007). For heterogeneous environments it is therefore imperative to obtain long time series in order to resolve the correct average O_2 exchange. Even though eddy derived fluxes can reflect distinct changes in environmental controls like light or flow velocity (Berg and Huettel 2008), the interplay of several controls and the general short term variations in the eddy flux can mask such relations.

The eddy correlation approach is in many ways superior to other approaches for resolving the benthic O_2 exchange. However, from a practical point of view one key issue is frequent sensor breakage, and for future research the development of more robust sensors would be highly advantageous. Sturdy fast responding mini electrodes with outside diameters ranging from 0.1 to a few mm of have been used for benthic investigations (Wenzhoefer et al 2000, de Beer et al 2005, Cook et al 2007) and robust optodes have also proven themself for in situ operation in different benthic environments (Glud et al 1999, Wenzhoefer et al 2001). Novel highly O_2 sensitive chemi-luminescent indicator complexes (Mayr et al 2009) potentially opens up for a new generation of fast responding mini-optodes which could prove themselves as a good, sturdy and cheap alternative to electrochemical sensors for eddy correlation O_2 measurements.

ACKNOWLEGDEMENTS

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Paper VII

ABUNDANCE, OXYGEN CONSUMPTION AND CARBON DEMAND OF BRITTLE STARS IN YOUNG SOUND AND THE NE GREENLAND SHELF

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Key words: Arctic, macrobenthos, epifauna, respiration, sea floor photography, megafauna

Running head: Functional role of brittle stars in NE Greenland

ABSTRACT

We used sea floor photography to estimate brittle star abundance in Young Sound, NE Greenland and the adjacent shelf. From photos covering a total area of 78 m^2 and spanning a depth range from 20 to 310 m we found maximum average densities of >400 ind. m^{-2} at 40 to 80 m depth. *Ophiocten sericeum* was the dominant species. However, gradual changes in species and size composition with depth were observed. Average biomass was ~600 mg C m^{-2} with highest values at sites dominated by the large *Ophiopleura borealis* (up to 2190 mg C m^{-2}). We measured average individual oxygen consumption of three dominant species at ambient temperature (-1.0°C) and salinity in incubation chambers using a fiber-optic oxygen sensor enabling continuous measurements. We established a general relation between individual disc diameter (D, mm) and oxygen consumption (R, µmol O_2 h^{-1} ind^{-1}): $R = 6.0 \times 10^{-4} D^{2.60}$ ($R^2 = 0.96$, n = 33), which facilitated the estimation of community respiration and carbon demand from sea floor images. Maximum carbon demand by brittle stars was found in the fjord at 30 m depth (14 mg C m^{-2} d^{-1}) and at 160 m (13 mg C m^{-2} d^{-1}). At the rest of the stations values ranged from 0.5 to 8 mg C m^{-2} d^{-1}. Overall, our results demonstrate that brittle stars, despite very low individual energy requirements, contribute significantly to marine carbon cycling in Young Sound as well as in the shelf areas off Northeast Greenland.

INTRODUCTION

Brittle stars (Echinodermata; Ophiuroidea) form dense assemblages in several marine habitats and in the deep sea around the world (e.g. Tyler 1980, Smith 1983, Brey & Clarke 1993, Quiroga & Sellanes 2009). Despite their widespread occurrence in coastal areas in the Arctic (Piepenburg 2000) few studies have focused on the ecology of brittle stars and therefore little is known about the significance of brittle stars in ecosystem carbon cycling. Respiration is a very fundamental parameter that can be used to estimate the population energy demand and role in carbon cycling. To our knowledge, only three studies have estimated respiration rates of Arctic brittle stars. In the Beaufort Sea, Renaud et al. (2007) measured oxygen consumption of several dominant species, including several species of brittle stars, but specific oxygen consumptions rates for brittle stars were not presented. In the Chukchi Sea, Ambrose et al. (2001) estimated oxygen consumption of *Ophiura sarsi* with a mean disc diameter of 2.2 cm with and without the addition of algae, but relied on a general relation between mass-specific respiration and biomass (Mahaut et al. 1995) to calculate population respiration due to uncertainties as to the reliability of their measurements. The most detailed study was performed by Schmid (1996), who estimated oxygen consumption of 33 specimens belonging to 4 different species within a relatively narrow size interval.

In Young Sound, NE Greenland, brittle stars have been registered as a dominant epifaunal group at shallow depths (<60 m) with densities up to several hundred individuals per square meter (Sejr et al. 2000). In this study, we complement previous studies by estimating abundance of brittle stars in the deeper part of the fjord and along a transect into the Greenland Sea. We then measure oxygen consumption of the dominant species and produce an estimate of the daily carbon demand by brittle stars in the study area.

MATERIALS & METHODS

The study was conducted in the outer part of Young Sound (74°18´N, 20°15´W) and outside the fjord entrance on the continental shelf in the Greenland Sea, NE Greenland, in August 2009. Young Sound is a 90 km long and 2-7 km wide sill fjord, with a mean depth of 100 m. The fjord is ice-covered from October/November to July and water temperatures never exceed -1.0°C below the subsurface layer (>20 m) (Bendtsen et al. 2007). Phytoplankton production is confined to the ice-free period, and characterised by a peak subsequent to the break-up of sea ice, usually lasting a few weeks until nutrients are depleted in the surface layer.

Abundance, biomass and size frequency

A series of high-resolution digital photos (Ocean Imaging Systems, USA) of the sea floor were taken along three depth-transects in Young Sound at 20, 30, 40, 50, 60, 80, 100 and 160 m depth, and at 4 stations on the Greenland Sea shelf ranging in depth from 200 to 310 m. Ten photos from each station (26 stations in total, each photo covering 0.3 m^2) were used to quantify the abundance of brittlestars. Using the image processing software ImageJ 1.43r, we measured the disc diameter of brittlestars in the photos in order to describe the size frequency distribution. Biomass was estimated on the basis of the allometric relationship between disc diameter, D (mm) and individual body mass, M (mg org. C) for *Ophiocten sericeum* in the Barents Sea: $M = 0.016D^{2.622}$. The relationship for *Ophiura sarsi*: $M = 0.019D^{2.796}$ was used to convert disc diameter to biomass for *Ophiopleura borealis* (Piepenburg 2000).

Oxygen consumption

Brittle stars were collected with a small dredge at 20, 60 and 160 m depth in Young Sound. Specimens were transferred to an aquarium containing bottom water and returned quickly to the laboratory, where they were carefully sorted with respect to species and size. To allow time for recovery from handling they were held in open incubation chambers in aerated seawater at ambient temperature (-1.0°C) and salinity in approximately one hour before metabolic measurements were initiated. Due to the relatively short recovery periods specimens were assumed to have been actively feeding until shortly before the beginning of our measurements. We measured oxygen consumption, R (µmol O_2 h^{-1}), of *O. sericeum*, *O. robusta* and *O. borealis* in closed incubation chambers kept in the dark using a fiber-optic oxygen sensor (FIBOX, PreSens, Germany) and oxygen-sensitive optode patches calibrated to zero oxygen (sodium dithionite solution) and air saturated water. This system enabled continuous measurements of oxygen concentration in the closed chambers. Chamber volumes ranged from 240 to 360 mL. The water was stirred by a 20-mm Teflon-coated magnet (60 rpm) fixed at the centre of the chambers. To reduce incubation times (average of the experiments was approximately 4 hours), we measured total oxygen consumption of batches of 4 to 13 individuals of similar disc diameter (± 1 mm), corresponding to previous observations of brittle star densities in the Arctic (Piepenburg 2000, Sejr et al. 2009). Thus, we obtained an average estimate of individual R (corrected for a control without brittlestars). For the large *O. borealis*, only one specimen was included in each incubation chamber.

Carbon demand

Total oxygen consumption of the brittle star community, R_{total}, was calculated by a combination of 1) the size frequency, 2) the abundance (ind. m^{-2}), and 3) the relation between disc-diameter and individual oxygen consumption:

$$R_{total} = \sum N_i \times R_i \qquad (1)$$

where N_i and R_i are the number of brittle stars and the average individual oxygen consumption, respectively, in size class i (1-mm intervals). Thus, an average R_{total} was estimated for each station.

Oxygen consumption was converted to carbon mineralisation by assuming a respiratory coefficient, RQ of 0.7 (Grebmeier et al. 2006). An assimilation efficiency of 0.8 and a net growth efficiency of 0.3 (e.g. Navarro & Thompson 1996, Sejr et al. 2004) result in 56% of the ingested carbon being mineralised. Thus, estimates of carbon requirements could be obtained by multiplying the respiration-derived mineralisation rates by a factor of 1.79.

RESULTS

Abundance and biomass

Peak abundance of brittle stars was found at 40-80 m depth in Young Sound (Fig. 1a) with an average abundance of at least 200 ind. m^{-2}. Maximum abundance was 445 ind. m^{-2} at 60 m. At depths <100 m *Ophiocten sericeum* prevailed. *Ophiura robusta* was occasionally found at 30-60 in the fjord but never constituted more than 1-2% of total abundance. At two stations (100 m and 160 m) only the very large *Ophiopleura borealis* was observed. On the shelf, abundance decreased steadily with depth, from 162 ind. m^{-2} at 200 m to 9 ind. m^{-2} at 310 m, coinciding with a change in dominance from *O. sericeum* to *Ophiacantha bidentata* and *O. borealis*. Maximum biomass (average 2190 mg C m^{-2}) was found at 160 m in Young Sound due to the dominance of the very large species *O. borealis* (Fig. 1b). High biomass was also found at 30 m (1088 mg C m^{-2}) due to high abundance of relatively large *O. sericeum*. Lowest biomass was found at the deepest station in the Greenland Sea (36 mg C m^{-2}).

Size frequency

The size distribution of the dominant species, *O. sericeum*, changed with depth. Median disc diameter ranged from 10.3 mm (20-30) to 5.0 mm at 40-80 m (Fig. 2a). At 100-160 m, median disc diameter was 9.9 mm and 6.9

Fig. 1. A). Average abundance (± 95 % CI) of brittle stars in Young Sound and the Greenland Sea obtained from sea floor photography, and **B)** estimated biomass (average ± 95 % CI).

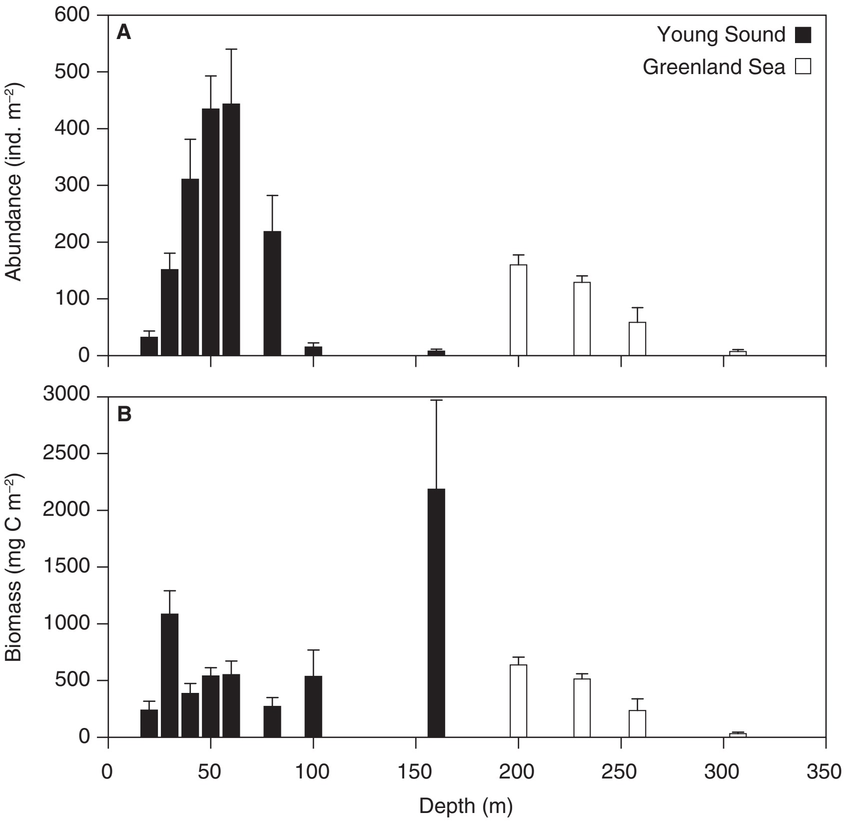
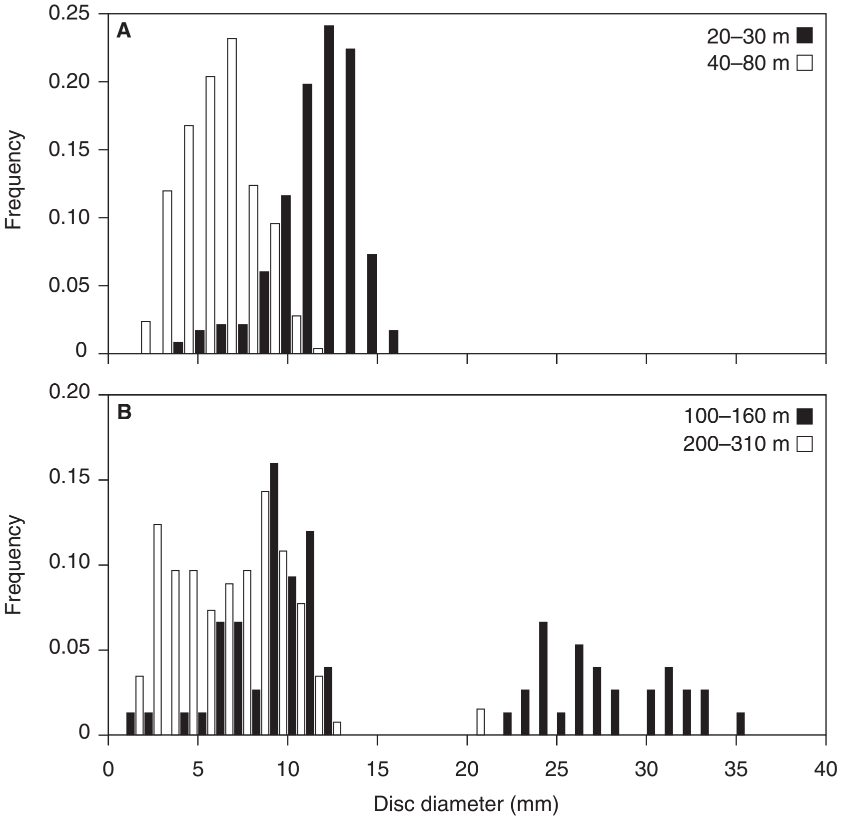
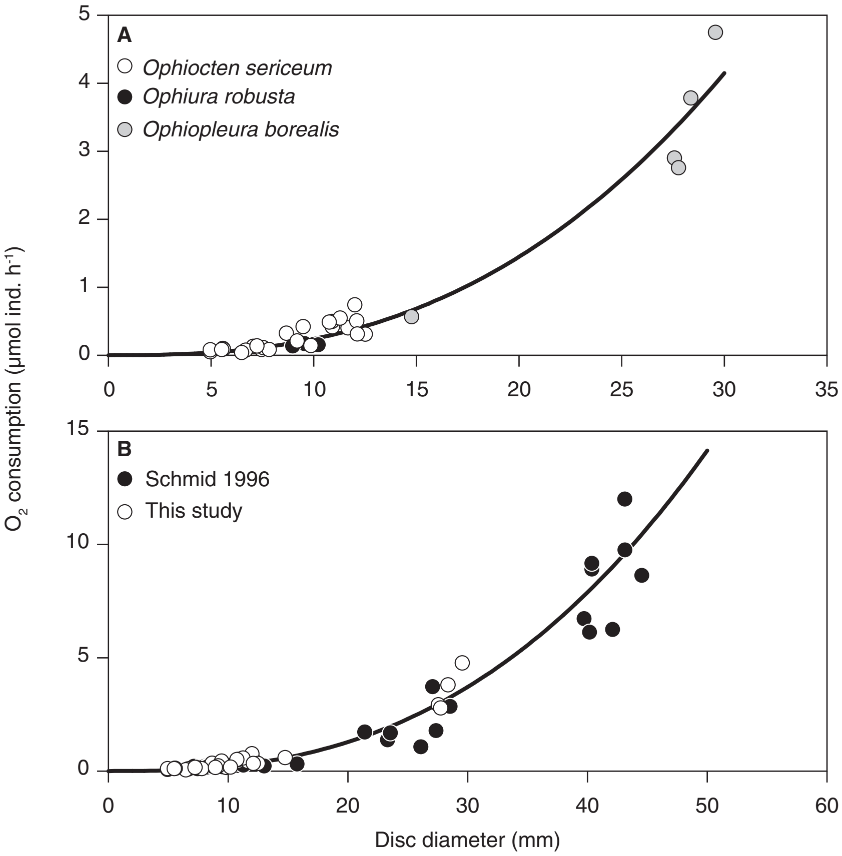


Fig. 2. Size frequency distributions of brittle stars from **A)** 20-80 m depth, and **B)** 100-310 m depth in Young Sound and the Greenland Sea. All specimens >20 mm are *Ophiopleura borealis*.



mm in the Greenland Sea (200-310 m). The occurrence of *O. borealis* is seen in the bi-modal distribution of size frequencies (Fig. 2b) at the 100-160 m depth interval. The median disc diameter of *O. borealis* was 27.6 mm.

Fig. 3. A) Average individual oxygen consumption rate, R (μmol O_2 h^{-1}) of three different species of brittle stars as a function of disc diameter, D (mm): $R = 0.006D^{2.60}$. **B)** General relationship between disc diameter, D (mm) and individual oxygen consumption rate, R (μmol O_2 h^{-1}) in six species of Arctic brittle stars: $R = 0.0005D^{2.62}$.



Oxygen consumption

The average individual oxygen consumption rate ranged from 0.04 μmol ind.$^{-1}$ h^{-1} in *O. sericeum* with an average disc diameter of 5.0 mm (13 individuals in chamber) to 4.7 μmol ind.$^{-1}$ h^{-1} for *O. borealis* with a disc diameter of 29.6 mm (Fig. 3a). In the three species investigated, no apparent difference in the relationship between consumption rate and size were observed. Hence, oxygen consumption (R, μmol O_2 h^{-1} ind^{-1}) increased allometrically with increasing disc diameter (D, mm) across species according to: $R = 6.0 \times 10^{-4}D^{2.60}$ ($R^2 = 0.96$, n = 33).

Carbon demand

Maximum carbon demand was found in the fjord at 30 m (14 mg C m^{-2} d^{-1}) and at 160 m (12.9 mg C m^{-2} d^{-1}). At the remaining stations, values ranged from 3 to 8 mg C m^{-2} d^{-1} except at the deepest station (310 m) where carbon demand was 0.5 mg C m^{-2} d^{-1} (Fig. 4).

DISCUSSION

The estimated carbon demand for brittle stars in Young Sound and the nearby shelf in August 2009 is among the highest reported from the Arctic (Table 1). Average carbon demand for the depth intervals studied range

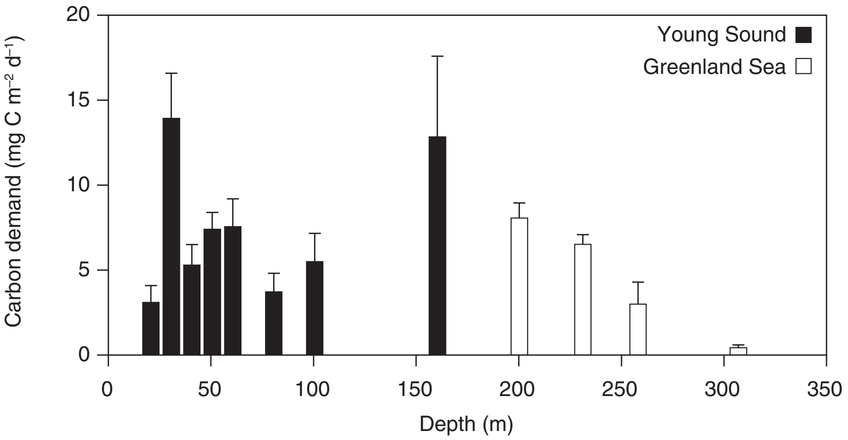


Fig. 4. Average carbon demand (±95 % CI) of brittle stars estimated from individual respiration rates, abundance and size frequency distribution.

from 4.5 to 9.2 mg C m^{-2} d^{-1}. Comparable estimates have only been obtained at shallow sites in NE Greenland and in the Laptev Sea. Estimates of total mineralisation in the sediment in summer, as obtained from sediment cores (5.3 cm diameter), range from *c.* 30 mg C m^{-2} d^{-1} (100 to 165 m depth) to 240 mg C m^{-2} d^{-1} (20 m) (Glud et al. 2000). Thus, brittle stars contribute with an additional 1-25% (average of all stations = 8%) to the sediment exchange estimated by Glud et al. (2000), which predominantly included bacterial mineralisation. This is comparable to the contribution from brittle stars in the Barents Sea (depths <200 m, Piepenburg et al. 1995) and the maximum contribution in the Chukchi Sea (Ambrose et al. 2001). Estimates of the annual average carbon demand of three other dominant macrobenthic species are available from Young Sound (Table 1). Although their carbon demands are significant, their distribution is limited to shallow depths (<60 m). In Young Sound, approximately 70% of the sea floor

Table 1. Estimates of average carbon demand of brittle stars in the Arctic and of other dominant macrobenthic species in Young Sound. *Carbon demand estimate obtained by multiplying respiration rates by 1.79 (see Materials and methods).

Site/species	Depth	Carbon demand (mg C m-2 d-1)	Reference
Carbon demand by Arctic brittle stars			
Young Sound	20-30	8.5	this study
Young Sound	40-80	6.0	this study
Young Sound	100-160	9.2	this study
NE Greenland shelf	200-310	4.5	this study
NE Greenland, banks	40-150	5.3	Piepenburg (2000)
trough slopes	100-580	1.0	Piepenburg (2000)
trough bottoms	180-440	0.4	Piepenburg (2000)
upper slope	80-770	<0.1	Piepenburg (2000)
Barents Sea	80-100	3.6	Piepenburg (2000)
Barents Sea	150-360	1.8	Piepenburg (2000)
Laptev Sea	14-23	0.1	Piepenburg (2000)
Laptev Sea	30-45	6.2	Piepenburg (2000)
Chukchi Sea	29-212	16.2*	Ambrose et al. (2001)
Carbon demand by other species in Young Sound			
Hiatella arctica	0-60	2.5	Sejr et al. (2002)
Mya truncata	10-60	6.8	Sejr & Christensen (2007)
Strongylocentrotus sp.	5-65	4.2	Blicher et al. (2007)

is found at depths >60 m (Bendtsen et al. 2007). When the shelf areas in the Greenland Sea are taken into account, our results demonstrate that brittle stars in NE Greenland are clearly a dominant macrofaunal group in terms of abundance and carbon mineralisation, and an important contributor to marine carbon cycling as such.

Due to the large standing stock of brittle stars, their carbon demand in Young Sound was relatively high despite low individual respiration rates. The grand average biomass across all depths (600 mg C m^{-2}) is comparable to maximum values from shelves and slopes in NE Greenland and the Laptev Sea, and exceeds values from the Barents Sea (Piepenburg 2000). However, the maximum biomass of 2190 mg C m^{-2} at 160 m depth is well below the 3388 mg C m^{-2} reported from a single station in the Chukchi Sea (Ambrose et al. 2001). The other component used to estimate carbon demand is the average individual respiration rate. To compare our rates with those of Schmid (1996), we converted individual biomasses given in that study to disc diameter using the allometric relationships between disc diameter and body mass provided by Piepenburg (2000). The individual respiration rates measured by Schmid (1996) are comparable to our estimates and indicate a general relationship between disc diameter and individual respiration across six species of brittle stars encompassing a wide range in size (Fig 3b). It should be noted that values are approximate as they are based on several general conversion factors to make data directly comparable (from wet weight to disc diameter). Moreover, a general relationship such as this does not consider the potential seasonal variation in macrobenthic activity, which has been reported in other studies in polar areas (Brockington & Clarke 2001, Blicher et al. 2010). However, it can be used to produce a preliminary estimate of the carbon requirements of this abundant taxon in the Arctic using a more general approach based on size structure and abundance, which can be effectively described using seafloor images.

Different sediment composition or water mass characteristics are likely to be responsible for the observed patterns in the general abundance of brittle stars as well as the depth-zonation of species. *O. sericeum*, *O. robusta* and *O. borealis* are cold-water species mainly occurring in the Arctic (Piepenburg 2000 and references therein). Hence, entrainment of relatively warm Atlantic Water (>2°C) across the shelf break (Sejr et al. 2009, J. Mortensen, *unpubl.*) might be responsible for the abundance of *O. bidentata* at the deep stations in the Greenland Sea. However, at present our knowledge of the factors controlling the distribution of different species of brittle stars in the Arctic is very limited. Piepenburg (2000) combined data from several Arctic and sub-Arctic regions and found brittle star biomass to peak in the range of 40-150 with peak abundance at 50-100 m, and our data does not deviate from this very general pattern. The dominance of the species *O. sericeum* has also been found at depths <150 m in NE Greenland at 78 to 81°N, the Barents Sea and the Laptev Sea (Piepenburg 2000).

In summary, the data presented add to existing examples of how macrofauna in general and brittle stars in particular are important components of benthic carbon cycling in Arctic fjords and shelves, potentially adding up to 25 % to the mineralisation of bacteria and meiofauna. Also, the general relationship between disc diameter and individual respiration across six species of brittle stars may prove useful to future studies, as it allows a preliminary estimate of brittle star oxygen consumption, mineralisation and carbon demand to be made from sea floor photos.

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Paper VIII

MACROBENTHIC SPECIES COMPOSITION AND DIVERSITY IN THE GODTHAABSFJORD SYSTEM, SW GREENLAND

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ORIGINAL PAPER

Macrobenthic species composition and diversity in the Godthaabsfjord system, SW Greenland

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Abstract The southwest Greenland coast is made up of large and deep sill fjords. On the shelf, a number of shallow banks separated by deep troughs are located 20–50 km from the coast. We collected three 0.1-m^2 van Veen grabs at nine stations along a transect spanning from the inner Godthaabsfjord influenced by glaciers, across the shallow Fyllas Bank and out to the slope of the continental shelf at approximately 1,000 m depth. Along this transect, we explored patterns of macrobenthic diversity, species composition, abundance and biomass. The sampled stations were very different in terms of environmental variables, resulting in large differences in species composition primarily related to differences in depth, silt–clay fraction and chl *a* content of the sediment (BIO-ENV analysis). Habitat differences also reduced species spatial ranges and the majority of species were found at only one (49%) or two (20%) stations and, consequently, species turnover or beta diversity was high and correlated to differences in depth, silt–clay fraction and median sediment grain size. Species richness and diversity were lowest in sites exposed to sediment disturbance: near the glaciers in the inner fjord (physical disturbance by mineral sedimentation) and at selected stations on the shelf (bioturbation by burrowing sand eel). Alpha diversity and richness were only weakly correlated to environmental parameters, indicating that alpha richness and diversity are influenced by several factors or that relationships are non-linear as was found for species richness and silt–clay fraction.

Keywords Soft bottom · Spatial patterns · Benthos · Macrofauna · Biodiversity · Arctic · Diversity

Introduction

It is estimated that roughly 75% of all animal species in Greenland are marine invertebrates, of which the majority are benthic species (Jensen and Christensen 2003). Despite their dominance, few studies of benthic diversity have been conducted around Greenland and the information is limited to individual fjords (e.g. Schmid and Piepenburg 1993; Sejr et al. 2000) or confined areas of the shelf (e.g. Piepenburg et al. 1997). The Greenland coast spans more than 22° of latitude representing a climatic gradient from the sub-Arctic south influenced by warm Atlantic water to the high-Arctic north with pronounced influence from sea ice. Along this gradient, annual growth rates of bivalves and sea urchins show large differences related to food conditions and temperature (Blicher et al. 2007; Sejr et al. 2009). At present, no information is available on how benthic species composition and diversity varies along this climatic gradient. The need for such baseline information is increasing. Climate change, oil exploration and trawling are all factors expected to affect species composition and diversity of the Greenland benthos in the coming decades. With the predicted reduction in sea ice cover around Greenland, commercial activities will become logistically less demanding. The shelf areas around Greenland are estimated to contain

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large reservoirs of undiscovered oil and gas (Bird et al. 2008) and large areas off East and West Greenland have been opened for oil and gas exploration (Mosbech et al. 2007). Climate change and increasing commercial activity are likely to influence the structure, functioning and biodiversity of the marine ecosystem around Greenland. This study is the first to contribute to baseline information of benthic diversity along the climatic gradient along the West Greenland coast. Additional cruises have been conducted in 2008 and 2009 covering the coastal zone from approximately 66 to 77°N.

The coastal waters of southwest Greenland (60–70°N) represent the most productive marine region of Greenland, and the area is important for fisheries, e.g. shrimp, halibut and crabs, and serves as an important feeding ground for sea birds and mammals (Mosbech et al. 2007). Very few quantitative studies have been conducted on the macrobenthos in this part of Greenland, and to our knowledge, studies of macrobenthic species composition and diversity have never been undertaken near the capital city of Nuuk. This area is of interest because a long-term monitoring program of the marine environment in the fjord and on Fyllas Bank has been initiated (Jensen and Rasch 2008). A recent study from shallow parts of the fjord system documented high carbon demand of the two dominant benthic species, indicating that the benthos is important for ecosystem carbon flow (Blicher et al. 2009). The aim of the present study was to provide a description of the macrobenthos along a transect from the inner part of the fjord to the continental slope. The transect is approximately 200 km long and covers several distinct benthic habitats, such as the continental slope, shallow shelf banks, outer parts of the fjords and inner fjordic basins influenced by glaciers. These habitats are expected to vary with respect to disturbance level, hydrographic regimes and grain size composition of the sediment, all factors which are known to influence macrobenthic species composition and diversity (Sanders 1968; Etter and Grassle 1992). Along this transect, we quantify species richness, diversity, biomass and abundance, describe changes in species composition and attempt to establish relationships between biological and environmental variables.

Materials and methods

Study site

The Godthaabsfjord system (Fig. 1) is located off southwest Greenland (64°N). The distance from the inner basins to the coast is approximately 100 km with a maximum depth of approximately 600 m. Several glaciers feed into the inner part of the fjord system. Approximately 20 km off the coast, the shallow Fyllas Bank rises to depths of about 50 m. West of the bank the sea floor drops down to the central Davis Strait. The surface circulation off the coast is dominated by the northward-flowing West Greenland Current. It is a mixture of cold low-saline water of polar origin transported south by the East Greenland Current and Irminger water of Atlantic origin (Buch et al. 2004). As the distance from the coast and depth increase, the influence of polar water diminishes, resulting in warmer and more saline water. The surface water temperature within the fjord varies seasonally from 0 to 5°C, while the temperature at the bottom is relatively constant at 0–1°C (Jensen and Rasch 2008). Primary productivity in the water column at the fjord entrance in 2006 and 2007 was 75 and 92 g C m^{-2} $year^{-1}$, respectively, with peak productivity in July (Jensen and Rasch 2008).

Sampling

Nine stations were visited in May 2006. At each station, macrobenthos was sampled by collecting three replicate

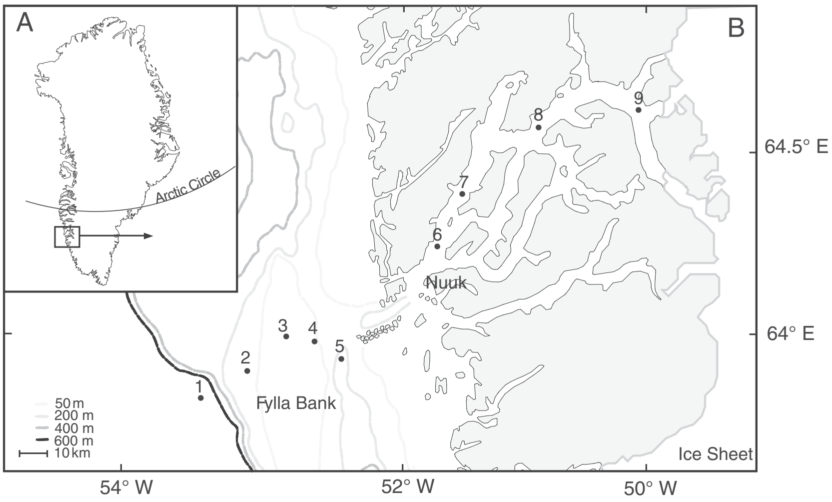

Fig. 1 The Godthaabsfjord system with positions of sample stations and depth contours

samples using a 0.1-m^2 van Veen grab. The retrieved sediment was sieved through a 1.0-mm sieve and the retained material was fixed in approximately 4% borax-buffered formalin. Several weeks later, the animals were transferred to 70% ethanol. Organisms were identified to the lowest possible taxonomic level and counted, and the wet weight including shells was determined for the following groups: polychaetes, molluscs, crustaceans, echinoderms and others. At each station, a separate van Veen grab was collected and used for subsampling for sediment characteristics: sediment chlorophyll *a* content (chl *a*), grain size composition and total organic carbon (TOC) content. Three samples for sediment chlorophyll content were collected through the sampling ports of the closed van Veen grab using a 100-ml plastic cut-off syringe (upper 3 cm of the sediment was collected). Three samples of the upper 10 cm of sediment were collected for grain size analysis, while three samples of the upper 5 cm of the sediment were taken for TOC content analysis. Chl *a* content was determined fluorometrically. Pigments were extracted in the freezer in the dark for 48 h, during which time tubes were shaken periodically. Sediment was then centrifuged (4,000 rpm for 10 min at 0°C) and the supernatant was analyzed (Turner Designs model 10-AU) before and after acidification with 20% HCl. For grain size analysis, approximately 200 g of sediment was wet sieved through a set of sieves (63, 125 and 250 μm). Samples for TOC analysis were freeze dried, homogenized and weighed into sample boats. Analysis was performed on a C/N elemental analyzer (RoboPrep-C/N, Europa Scientific).

Data analysis

Alpha (α), beta (β) and gamma (γ) diversities (as defined by Whittaker 1960) were quantified. We estimated α diversity at two scales: (1) in single grab samples and (2) at single stations by pooling the three replicate grab samples. For both data sets, we calculated species richness and three different measures of species diversity: (1) the Shannon–Wiener diversity index using $\log_e(H')$, (2) the Hurlbert index, i.e. the estimated number of species per 100 individuals (ES_{100}) and (3) Pielou evenness (J'). Gamma diversity was defined as the total species richness of the sample area (Gray 2000). The total species richness in collected samples was presented as species accumulation curves. The estimated total species richness of the studied communities including species not present in the data set can be estimated by the non-parametric Chao2 method (Chao 1987) where Chao2 = S_{obs} + (Q1/2Q2), where S_{obs} is the species observed in the total data set and Q1 and Q2 are the number of species found at only one (Q1) or two (Q2) stations. Beta diversity is a term that is not related to scale such as α and γ diversities. Here, it is used as a measure of the extent of change in species composition between samples or stations (Whittaker 1975). Beta diversity was measured in two ways: (1) complementarity (C_{jk}; Colwell and Coddington 1994) which is measured between pairs of stations as the number of unshared species divided by the total number of species at the two stations multiplied by 100. It can range from 0 (two identical samples) to 100 (two samples with no shared species). (2) The Bray-Curtis coefficient of similarity based on square root transformed abundances. The Bray-Curtis similarity between two samples *j* and *k* is defined as $S_{jk} = 100[1 - \sum|y_{ij} - y_{ik}|/\sum(y_{ij} + y_{ik})]$ with the summation being over species $i = 1, \ldots, p$ and y_{ij} and y_{jk} being the square root transformed abundance of species *i* in samples *j* and *k*, respectively. The Bray-Curtis similarity ranges from 0 (no shared species) to 100 (identical samples). The Bray-Curtis similarity and complementarity between stations were calculated based on pooled replicates.

Correlation analysis between measures of α and β diversities and environmental variables was conducted using non-parametric Spearman rank analysis on untransformed data.

The spatial patterns of species distributions were explored by use of multivariate analyses. Bray-Curtis similarities between individual grab samples were depicted through ordination by non-metric multidimensional scaling (nMDS). The differences between stations were tested with use of one-way ANOSIM test. The data were square root transformed prior to the analyses. Relationships between species distributions and environmental variables were examined using the BIO-ENV procedure, which calculates the Spearman rank correlations between the biotic Bray-Curtis similarity matrix and abiotic matrices including all possible combinations of the considered environmental factors (Clarke and Warwick 1994). BIO-ENV, ANOSIM and nMDS analyses as well as calculation of α diversity measures were performed using the PRIMER software ver. 5.1. Chao2 and complementarity were calculated using Estimate S (ver. 8.0, Colwell RK 2006 available at http://purl.oclc.org/estimates).

Results

Environmental data

Sediment chlorophyll *a* showed a maximum of 4.1 μg g^{-1} at station 4 and a minimum of 0.16 μg g^{-1} at station 1 (Table 1). Highest sediment content of TOC was found at stations 5 and 6 (from 1.1 to 1.8%). Intermediate levels of 0.5–0.7% were recorded at stations 1, 2, 3 and 4. Low carbon content (less than 0.1%) was found in sediments at stations in the inner fjord (7, 8 and 9). Large variation in grain size composition was observed. At the shallow station on

Table 1 Depth, grain size composition, total organic carbon (TOC) and chlorophyll a (chl *a*) content of sediment at sampling stations

Station	Depth (m)	Sediment type	<63 μm (%)	63–125 μm (%)	125–250 μm (%)	>250 μm (%)	TOC (%)	Chl *a* (μg g^{-1})
1	956	Clay	73.1	18.8	5.8	2.1	0.54	0.16
2	72	Clay	6.6	62.3	29.8	1.2	0.53	0.40
3	47	Shell gravel	0.8	0.2	4.7	94.3	0.70	1.04
4	102	Clay	8.2	25.1	65.5	1.2	0.63	4.10
5	273	Sand, gravel	27.0	1.2	13.9	57.9	1.78	1.54
6	357	Clay, sand	33.6	18.9	42.7	4.8	1.11	1.32
7	626	Silt	99.0	0.4	0.3	0.3	0.08	0.50
8	579	Silt	93.8	1.4	1.4	3.3	0.04	0.45
9	476	Silt	98.4	1.2	0.2	0.3	0.01	0.23

Fyllas Bank (3), the sediment consisted almost entirely of shell gravel (the >250 μm fraction constituted 94%). In contrast, the sediments at the stations closest to the glaciers (7, 8 and 9) were dominated by silt. All pair-wise correlations between environmental variables were tested and highest correlation coefficients were found for depth versus <63 μm size fraction ($\rho = 0.82$) and 125–250 μm size fraction versus chl *a* ($\rho = 0.83$). Salinity within 5–10 m of the bottom ranged from 33.3 PSU at station 3 to 34.9 at station 1. Due to the limited range, salinity was not included in the analysis.

Alpha and gamma diversities

We found a total of 339 species and 14,834 specimens. Of these, 206 species were polychaetes, 51 molluscs, 71 crustaceans, 6 echinoderms and 5 species belonging to other groups. Sampling efficiency of the van Veen grab was generally very good due to the silty substrate at most stations. Several attempts were required at station 3 to collect adequate samples. Sample and station species richness showed large variability ranging from 11 to 87 species per grab sample and from 30 to 140 species per station (Fig. 2; Table 2). The highest richness was found at stations 1, 2, 5 and 6 and the lowest richness at stations 3, 4 and 9. At stations with lower species richness, the numbers of species were only slightly above values recorded for individual grab samples. At stations with high richness, the values calculated after pooling replicates were considerably higher than that of individual samples. The spatial distribution of species diversity mirrored the pattern described for species richness; higher values at stations 1, 2 and 6 and lower

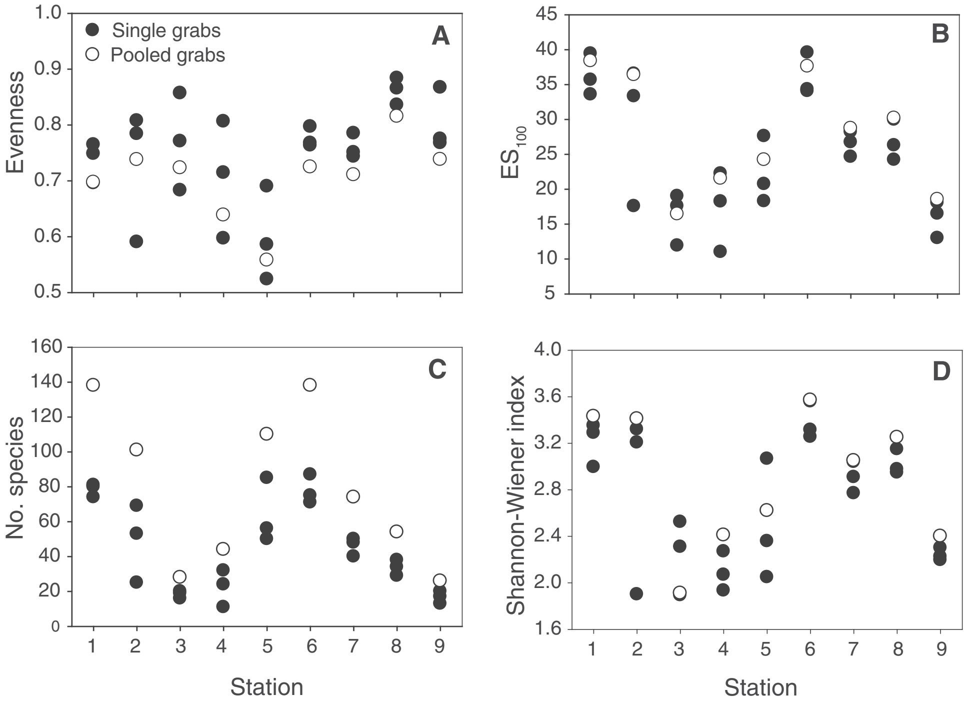

Fig. 2 Macrobenthic α diversity along a transect on the SW Greenland coast and shelf: Pielou index (evenness), number of species per 100 individuals (ES_{100}), sample species richness (no. species) and Shannon–Wiener index. Values for samples and for stations (pooled samples) are presented

Table 2 Abundance (*N*, individuals per 0.1-m^2 grab), biomass (*B*, g wet weight per 0.1-m^2 grab), number of species per sample (*S*), number of species per 100 individuals (ES_{100}), evenness (J') and Shannon–Wiener diversity index (H') in 0.1-m^2 samples

Station	*N*	*B*	*S*	ES_{100}	J'	H'
1	445	3.4	74	34	0.70	2.99
	540	3.5	81	36	0.75	3.29
	378	3.4	80	39	0.76	3.35
2	182	4.1	25	18	0.69	1.90
	217	8.4	52	37	0.81	3.20
	573	37.7	69	36	0.79	3.32
3	135	0.2	20	19	0.59	2.31
	218	4.3	16	12	0.52	1.90
	81	0.1	19	18	0.77	2.52
4	116	17.6	24	18	0.71	2.27
	58	2.4	11	11	0.80	1.93
	331	10.7	32	22	0.60	2.07
5	1,507	16.9	85	28	0.69	3.07
	3,480	10.3	56	21	0.59	2.36
	1,602	4.7	50	18	0.62	2.52
6	532	29.8	87	40	0.76	3.56
	429	17.4	71	34	0.77	3.25
	579	13.6	75	34	0.78	3.31
7	492	12.5	48	28	0.74	3.04
	475	8.5	40	25	0.75	2.77
	556	4.6	50	27	0.79	2.91
8	179	24.0	38	30	0.87	3.15
	186	0.6	29	24	0.84	2.98
	238	10.0	34	26	0.88	2.95
9	81	1.4	13	13	0.87	2.22
	109	3.0	17	17	0.77	2.20
	143	1.3	20	18	0.77	2.30

Table 3 Results of Spearman rank correlation analysis between indices of richness and diversity (*S*, number of species per sample; ES_{100}, the estimated number of species per 100 individuals; J', Pielou's evenness; H', the Shannon–Wiener diversity index) in individual grab samples and environmental and biological variables

	S	ES_{100}	J'	H'
Biomass	**0.54**	**0.50**	−0.19	**0.43**
Abundance	**0.82**	**0.55**	**−0.49**	**0.47**
Depth	0.37	**0.43**	0.11	**0.41**
<63	0.03	0.11	0.33	0.17
63–125	0.29	0.34	−0.01	0.26
125–250	0.32	0.12	−0.32	0.12
>250	0.21	0.09	−0.11	0.12
Median	−0.20	−0.21	0.10	0.09
TOC	0.28	0.14	−0.31	0.07
Chl *a*	−0.05	−0.21	−0.29	−0.26

Significant correlations ($P < 0.05$) are printed in bold

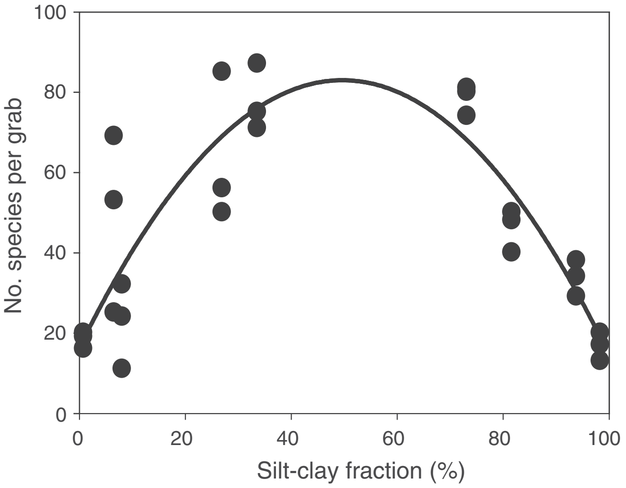

Fig. 3 Relationship between sample species richness (No. species per grab) and silt–clay fraction in sediments. Fitted curve given by $S = 16.39 + 2.68[\text{silt–clay}] - 0.02[\text{silt–clay}]^2$ ($R^2 = 0.74$, $P < 0.01$)

values at stations 3, 4 and 9. For evenness, the pattern was different. The lowest evenness (<0.6) was found at station 5 (due to the dominance of *Polydora* sp.) and the highest at station 8 (>0.8). No significant correlation between diversity and richness and environmental parameters was found except for depth and ES_{100} and H' (Table 3). However, all measures of diversity and richness were significantly correlated to abundance and biomass, except for evenness, which was not correlated to biomass. A significant non-linear relationship between species richness and silt–clay fraction was found with highest values of species richness recorded at intermediate levels of silt–clay fractions (Fig. 3).

The species accumulation curves plotted for the whole material reached an asymptote neither in case of observed numbers of species nor in case of the estimated total species richness (Fig. 4). The Chao2 estimate of total species richness gave an estimate of 498 species ± 38 (SD).

Abundance, biomass and species range

The abundance varied greatly among stations (Fig. 5a). The highest abundance (and very high between-replicate variability) was found at station 5 where large numbers of *Polydora* sp. were found (up to 1,389 in one grab). Intermediate abundance (378–579 ind. 0.1 m^{-2}) was found at stations 1, 6 and 7. Low density (58–331 ind. 0.1 m^{-2}) was found at stations 3, 4 and 9. At all stations, polychaetes were most abundant (from 54 to 93%). At station 2, molluscs constituted 36% of total abundance. The five most abundant species were all polychaetes and they constituted 38% of total abundance (Table 4). Biomass also showed considerable variation along the sampled stations (Fig. 5b). Low biomass

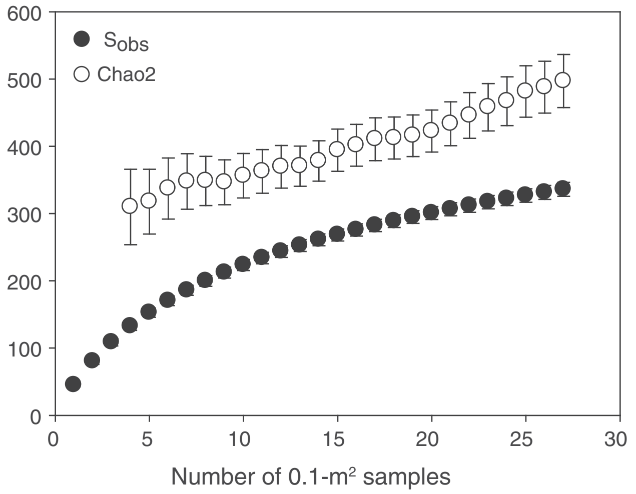

Fig. 4 Species accumulation curves. S_{obs}, observed numbers of species. Chao2, estimated maximum number of species. For Chao2, mean ± SD (based on 100 randomizations without replacement) are presented. The fitted regression is $S_{obs} = 200 + 135.1 \ln([\text{sample area}] + 0.19)$, $R^2 = 0.999$, $P < 0.001$

(<5 g ww 0.1 m^{-2}) was found at stations 1, 3 and 9. High biomass (15–20 g ww 0.1 m^{-2}) was found at stations 2 and 6 and intermediate values of biomass (8.5–11.5 g ww 0.1 m^{-2}) were recorded at the remaining stations. At several stations, one or two individual echinoderms (*Ophiura* sp., *Ctenodiscus* sp.) constituted much of the biomass, e.g., at stations 6, 7 and 8. Molluscs dominated the biomass at station 2. Most species occurred at only one (49%) or two (20%) stations (Fig. 6). None of species was found at all of nine stations. Polychaetes had the widest spatial range and species belonging to this group were the only ones found at five sites or more. The five most abundant polychaetes generally had large distributional range being present at four stations or more (Table 4).

Table 4 The five most abundant macrobenthic species found along a transect off SW Greenland

	N	*D* (%)	Stations
Polydora sp.	2,553	18	5
Prionospio steenstrupi	1,143	25	8
Euchone sp.	872	31	4
Heteromastus filiformis	605	35	7
Exogoninae indet.	453	38	5

Total number of individuals found (*N*), the cumulated proportion of the abundance of the five most abundant species in relation to the total abundance in all samples (*D*) and the number of stations at which each species was found

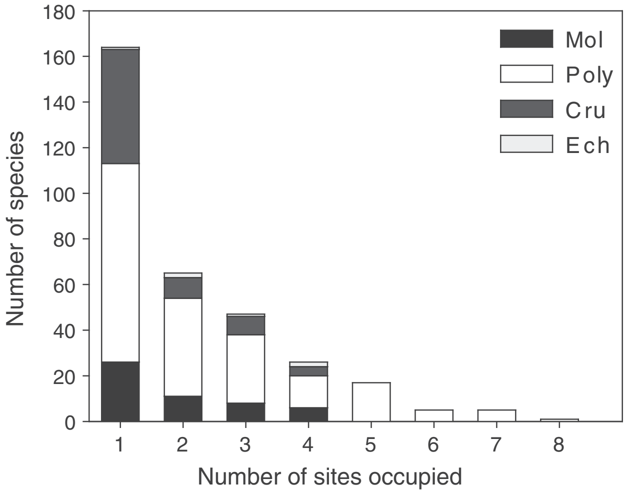

Fig. 6 Macrobenthic species habitat range within major taxa. Habitat range given by the number of stations occupied by a species. See Fig. 5 for abbreviations of taxonomic groups

Beta diversity

The Bray-Curtis similarity is depicted on nMDS plot (Fig. 7) showing highest similarity between replicates collected at the same station. In general, the similarity between station replicates ranged from 50 to 70% except for stations 2 and 4 where similarity between replicates was around 40%. Highest similarity between stations was found at stations 7 and 8 (approx. 40%). Two measures of β diversity (Bray-Curtis similarity and complementarity) were calculated from the data set obtained by pooling the three replicates at each station. The similarity between all possible pair-wise comparisons of stations ranged from 0 (no common species) to 48% with an average of 18.1 ± 4.0 (95% CI). Complementarity ranged from 57 to 100% with an

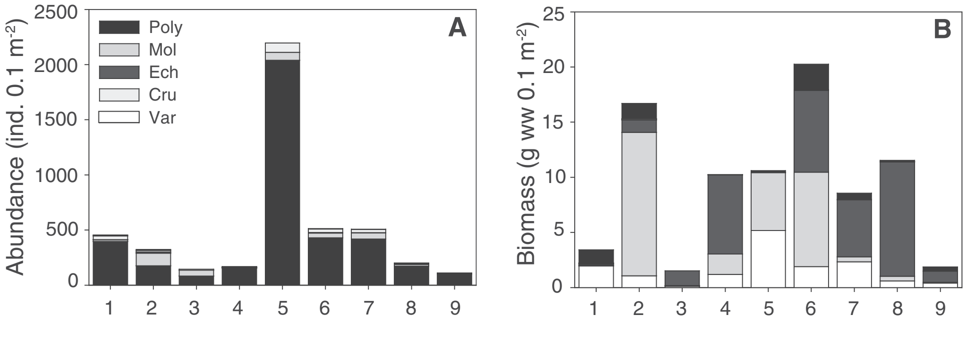

Fig. 5 Macrobenthic abundance and biomass (wet weight) at stations. Percentages of major taxa are also presented (*Poly* polychaeta, *Mol* mollusca, *Ech* echinodermata, *Cru* crustacea, *Var* various taxa)

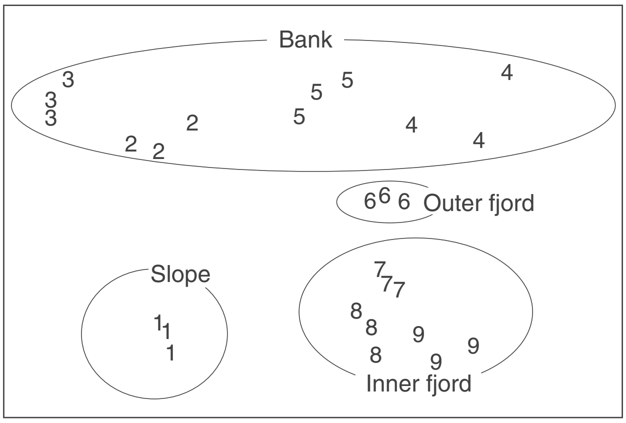

Fig. 7 Multidimensional scaling ordination for square root transformed macrobenthic species abundance data. Stress = 0.11

Table 5 Results of correlation analysis (Spearman rank) between two measures of beta diversity and environmental parameters

	Bray-Curtis	Complementarity
Depth	**−0.46**	**0.45**
<63	**−0.45**	**0.43**
63–125	−0.7	0.07
125–250	0.01	0.01
>250	−0.15	0.05
Median	**−0.54**	**−0.46**
TOC	−0.06	−0.07
Chl *a*	−0.06	−0.05

Significant correlations ($P < 0.05$) shown in bold

average of 84.8 ± 3.2 (95% CI). Both measures of β diversity were significantly correlated to differences in depth, silt–clay fraction and median grain size between stations (Table 5).

Spatial variation in species composition

We found a significant difference in the species composition between stations (ANOSIM, $R = 0.982$, $P < 0.001$). Samples representing the main habitats were grouped together on the nMDS plot: shallow bank (stations 2, 3, 4 and 5), inner fjord (stations 7, 8 and 9), outer fjord (station 6) and continental slope (station 1). The fauna found on the continental slope was dominated by the polychaetes *Ceratocephale loveni*, *Terebellides stroemi*, *Heteromastus filiformis* and *Lumbrineris* sp. and the crustacean *Ampelisca spinipes* (Table 6). On the bank, several species of molluscs were abundant (*Boreocingula globulus*, *Crenella decussata*, *Limatula hyperborea* and *Margarites* sp.). The outer fjord stations were dominated by the polychaetes *Polydora* sp., *Prionospio steenstrupi* and *Euchone* sp. and the inner fjord stations were characterized by high dominance of *Lumbrineris* sp., *Prionospio cirrifera* and *Myriochele heeri*. The environmental variables that best explained the pattern of macrobenthic species distribution (BIO-ENV analysis) were the combination of silt–clay fraction, depth and chl *a* (spearman rank correlation coefficient: 0.791). The single factor that best explained variation was the silt–clay fraction (spearman rank correlation coefficient: 0.762).

Discussion

Alpha and gamma diversities

The observed variation in α diversity was only weakly related to the measured environmental variables, as significant correlations were found only between H' and ES_{100} and depth (Table 3). No clear relationship was found between α diversity and the similar set of environmental factors on the Norwegian shelf (Ellingsen and Gray 2002), whereas other studies have shown relationships between α diversity and depth (Włodarska-Kowalczuk et al. 2004), grain size (Etter and Grassle 1992) or silt–clay fraction and total organic matter content (Ellingsen 2002). The weak correlation between single environmental parameters, species richness and diversity indices (Table 3) suggests that a multitude of factors together influence small-scale diversity, or that relationships could be non-linear. Low values of diversity indices and species richness were found at stations assumed to be subject to elevated levels of disturbance. At station 9, three glacial fronts within a 3-km radius most likely resulted in very high deposition rates of inorganic particles. In Svalbard, a similar reduction in both biomass and diversity close to glaciers has been described (Włodarska-Kowalczuk et al. 2005). At stations 3 and 4, sand eels (*Ammodytes* sp.) were abundant in the grab samples (average 12 per grab in six samples). Sand eels stay buried in the sediment during the day to avoid predators and are active at night. Their burrowing activity could cause sufficient levels of disturbance to reduce diversity and richness of benthos. An intermediate level of disturbance is generally found to enhance species richness and diversity (Petraitis et al. 1989), whereas a high level of disturbance from, e.g., trawling (Thrush and Dayton 2002) or river run-off (Thrush et al. 2004) reduces diversity. At the disturbed stations, biomass and abundance was low, indicating sub-optimal condition that was most likely related to high disturbance levels. Also, the low abundance and biomass at these stations contributed to the significant correlation between measures of diversity and biomass and abundance (Table 3). Species richness is generally found to increase with depth from about 200 m to maximum values at 1,500–2,500 m (Etter and Grassle 1992; Gray 2002). We found highest species richness and diversity at the deepest

Table 6 The ten most abundant species and their average abundance (ind. 0.1 m^{-2}) shown for each of the four assemblages (slope, bank, outer fjord and inner fjord)

	Slope 64%	Bank 72%	Outer 73%	Inner 60%
Ceratocephale loveni (P)	**34.3**			
Lumbrineris sp. (P)	**20.0**		2.9	**17.6**
Aphelochaeta sp. (P)	**9.7**	0.2	0.9	0.6
Terebellides ströemi (P)	**38.3**	0.2	0.4	2.1
Heteromastus filiformis (P)	**125**		**21.3**	4.0
Clymenura lankesteri (P)	**17.3**			
Notoproctus oculatus (P)	**8.7**			
Asclerocheilus sp. (P)	**6.3**			
Paraonis sp. (P)	**16.3**	0.2		
Ampelisca cf. *spinipes* (C)	**14.7**			
Boreocingula globulus (M)		**34.2**		
Crenella decussata (M)		**245**	1.0	
Limatula hyperborea (M)		**8.7**		
Margarites sp. (M)		**4.8**	0.1	
Exogoninae sp. (P)		**39.5**	3.0	
Ophryotrocha sp. (P)		**8.8**	0.2	
Polydora sp. (P)		**6.5**	**279**	
Macrochaeta sp. (P)	0.3	**6.3**		
Leitoscoloplos mammosus (P)		**6.3**	7.8	**14.4**
Oligochaeta indet.	3.0	**17.7**	0.3	0.3
Prionospio steenstrupi (P)		0.2	**118**	**7.9**
Pygospio elegans (P)		1.8	**38.8**	
Spio sp. (P)			**46.0**	
cf. *Asabellides* sp. (P)		1.0	**19.0**	
Galathowenia oculata (P)	1.0		**28.6**	**11.1**
Euchone sp. (P)			**96.8**	0.1
Cossura pygodactylata (P)			**27.2**	
Harpinia plumosa (C)		0.5	21.1	
Thyasira dunbari (M)	3.3		0.1	**10.0**
Aglaophamus malmgren (P)	1.7		0.2	**8.0**
Prionospio cirrifera (P)	0.7		6.6	**29.7**
Spiophanes kroeyeri (P)	2.0		5.7	**12.6**
Myriochele heeri (P)	2.3		3.8	**45.1**
Cossura longocirrata (P)				**7.9**

Abundance are given in bold when a species is among the ten most abundant. For each assemblage, the relative contribution of the listed species to the total abundance is given

P polychaeta, *C* crustacea, *M* mollusca

station, but the effect of depth was confounded by the reduction in diversity indices and richness at relatively deep stations in the inner part of the fjord towards the glaciers. The reduction was most pronounced for richness. Species richness showed a non-linear relationship with the fraction of silt–clay with maximum values at intermediate fractions (Fig. 3). This indicates that high species richness is found when sediments are not dominated by a single size fraction and supports evidence from the deep sea that sediment particle size diversity is positively related to species diversity (Etter and Grassle 1992). At station 5 with high species richness, we also found very high abundances of *Polydora* sp., indicating that high abundance of tube-building polychaetes can increase species richness by stabilizing the sediment and increasing habitat heterogeneity as was also observed at single stations on the Norwegian shelf (Ellingsen 2002).

The number of species found in three pooled replicates at stations 1 and 6 is relatively high and matches the maximum number of species in 5 replicate samples at 101 sites on the Norwegian shelf (Ellingsen and Gray 2002). Species richness in individual samples is also greater than values from the Svalbard shelf where maximum richness of 55–65 species was found at 300–550 m depth (using a 0.5-mm sieve) (Włodarska-Kowalczuk et al. 2004). Although comparison is not straightforward due to slight differences in methodology, levels of alpha richness in this study seem to match and possibly exceed values from Svalbard and the

Norwegian shelf. In a benthic study of another shallow bank (Store Hellefiskebanke) off West Greenland at 63–68°N (Anonymous 1978), average species richness across the bank was approximately 120 species in 5 pooled van Veen grabs (range, 60–180 species in 5 grabs at 10 stations; depth range, 20–90 m). The total species richness (γ diversity) of 339 species in 2.7 m^2 is in the upper range of values reported from much larger surveys on the Norwegian shelf (177–477 species in sample areas of 8–12.5 m^2; Ellingsen and Gray 2002) and the Canadian Arctic (104–434 species; Cusson et al. 2007). The presented data set from the Godthaabsfjord system is too limited for a comparison of richness and diversity between shelf regions. However, one other study from West Greenland (63–68°N) reported a total species richness of 496 species at 31 stations (Anonymous 1978) indicating that total species richness or γ diversity is at least in the upper range of values reported from the shelves of Arctic Canada and Norway.

Our sampling stations were located along a transect from the inner fjord to the continental slope at depths ranging from 47 to 956 m. A wide range of environmental conditions explains both the high total species richness and the limited spatial range of species distribution. Forty-nine percent of the species were found only at one site and 20% at only two sites. The relatively high proportion of species with limited species range is mainly produced by species occurring at station 1. Half of the species occupying only one site (68 species) was found at station 1, which was situated at greater depth and in water more dominated by Atlantic water than the other stations. A positive relationship between habitat heterogeneity and diversity often exists (Rosenzweig 1995). In this study, the physical settings of the individual stations were so different that they represent different habitats rather than heterogeneity within the same habitat. The limited number of samples distributed among different habitats appears to be the most likely explanation for the high γ diversity found in this study. Gray (2002) suggested that food resources control population levels at a variety of scales, which set the maximum species richness, but whether this maximum is reached depends on the spatial and temporal heterogeneity in sediment structure. The complex bathymetry of the southwest Greenland shelf creates areas of upwelling, which stimulates primary production (Pedersen et al. 2005). The favorable food conditions combined with variable bathymetry and heterogeneous sediments along the West Greenland coast (Rvachev 1963) could create favorable conditions for high benthic species richness. The available data suggest high α and γ species richness but additional studies are needed before it can be determined if species richness is higher than in other shelf areas of comparable latitude.

Beta diversity

The different habitats that were sampled in this study caused β diversity to be high. The average Bray-Curtis similarity between stations (18%) was lower than that recorded on the Norwegian shelf (range 26–63%) and the average complementarity (85%) was above that of the Norwegian shelf (range 53–81%) (Ellingsen and Gray 2002). A contributing factor to the difference between the two studies is the different numbers of replicates per station. Ellingsen and Gray (2002) used five replicates, while only three replicates per station were sampled in our study. Fewer samples increase the effect of small-scale variability on differences between stations, which could contribute to the higher β diversity observed in this study. The significant correlation between both measures of β diversity (similarity and complementarity) and depth and silt fraction indicates that habitat heterogeneity is associated with β diversity. This also agrees with the result of the BIO-ENV analysis, which showed that differences in depth and silt fraction were best associated with differences in species composition. The high β diversity is translated into the high γ richness recorded in the study. The indication of a positive relationship between high β and γ diversities supports the observation from the Norwegian shelf (Ellingsen and Gray 2002) that areas that are environmentally heterogeneous have higher β and γ richness.

Spatial variation in species composition

Multivariate correlation analysis (BIO-ENV) suggested that differences in depth, particle fraction <63 μm and chl *a* between stations were best correlated to differences in species composition. Grain size distribution, depth and chl *a* content have been shown to be important factors affecting the spatial variability in diversity and species composition of macrobenthos in coastal regions (e.g. Glockzin and Zettler 2008 and references therein). Depth is often identified as the key environmental parameter because macrobenthos often display a significant depth zonation related to indirect effects of depth on a range of environmental factors such as food availability, grain size composition and disturbance level (Snelgrove and Butman 1994; Glockzin and Zettler 2008). Depth is also a key parameter along the sampled transect as it is correlated to both abiotic (grain size distribution, physical disturbance, temperature) and biotic factors (food supply). The distance to the glacier front is another key factor here, as the glacier-proximal areas are affected by high inorganic sedimentation, iceberg scouring and low amounts of organic matter (Włodarska-Kowalczuk and Pearson 2004). The set of species dominating in the inner basin of Godthaabsfjorden (polychaetes *Lumbrineris* spp., *Aglaophamus malmgreni* and *Chaetozone* spp. and small detritus-feeding bivalves *Thyasira dunbarii*) was very similar to those dominating the glacial bay macrobenthic communities in Svalbard (Włodarska-Kowalczuk et al. 1998, 2005). Several of the dominant species in this study have been reported as being dominant in other Arctic areas. Especially polychaetes of genera such as *Lumbrineris*, *Heteromastus*, *Terebellides*, *Polydora*, *Euchone*, *Myriochele*, *Chaetozone*, *Cossura* and *Prionospio* were reported to be abundant in other areas of the SW Greenland shelf (Anonymous 1978) as well as fjords of West Greenland (Schmid and Piepenburg 1993), East Greenland (Sejr et al. 2000) and Svalbard (Włodarska-Kowalczuk and Pearson 2004). Glacier ice is not considered to directly affect the sampled station by scouring mainly due to the depth of the stations.

In conclusion, this study offers a first description of the composition of the benthic fauna in the Godthaabsfjord system. The dominant species in the area are similar to those reported from other fjords in Greenland and in Svalbard. Distinct habitats such as the continental slope, the shallow Fyllas Bank and the inner fjord with glaciers displayed different physical settings and consequently different benthic species composition and diversity. This study combined with one other available study from the West Greenland shelf indicates that species richness at α and γ levels is in the upper range of values reported from the Norwegian and Canadian shelf. However, additional studies are needed before the benthic diversity of the West Greenland shelf can be compared to other regions.

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STRUCTURE AND DYNAMICS OF MARINE MACROZOOBENTHOS IN GREENLAND

– AND THE LINK TO ENVIRONMENTAL DRIVERS

The marine ecosystem off Greenland is poorly described. Due to ongoing climate changes and oil explorations in the area there is an urgent need for basic ecological research to be able to document potential changes in the future as well as to identify environmental drivers of ecosystem dynamics.

This PhD study describes macrozoobenthic structure and dynamics on different temporal and spatial scales, and on levels of biological organization ranging from cell to community. Besides providing baseline knowledge on the macrozoobenthic community structure in a number of different biotopes in Greenland, the combined results indicate that benthic fauna play a central role for marine carbon cycling. Further, the study presents novel findings on how temporal and spatial growth variations of benthic macro-invertebrates in Greenland are linked to environmental controls, supporting a general hypothesis of food limitation of Arctic macrobenthos. Variations in temperature, seasonal sea ice distribution and fresh water runoff from land are likely to affect benthic productivity directly and indirectly through its potential effect on primary production and pelagic-benthic coupling. Therefore, the benthic community is expected to be sensitive to environmental change with potential implications for animals on higher trophic levels, such as several bottom foraging bird and fish species.

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