



Micro- and mesozooplankton in Southwest Greenland waters in relation to environmental factors

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Abstract

Plankton samples and oceanographic data were obtained during transect studies across fishing banks over the Southwest Greenland shelf in June 1999, May, and July 2000. The study gives a detailed description of micro- and mesozooplankton distributions and community structures during spring bloom and post bloom periods. Plankton distributions were related to the physical environment described by a hydrodynamic ocean circulation model.

More than 30 species and a larger number of taxonomic categories were identified in the zooplankton samples. Large copepodites of *Calanus finmarchicus*, *Calanus glacialis*, and *Calanus hyperboreus* generally dominated the micro- and mesozooplankton biomass, with *Pseudocalanus* spp., *Metridia longa*, and *Oithona* spp. comprising most of the remaining biomass. By number, bivalves larvae and relatively large copepod nauplii (>200 µm) dominated the zooplankton community (>50 µm) in May, whereas smaller copepod nauplii (<200 µm) were dominating in June and July. In May during a spring bloom period, diatoms, *Thalassiosira* spp. and *Chaetoceros* spp., generally dominated the biomass of the plankton community of the upper 100 m followed by heterotrophic flagellates, copepods, other invertebrates, and ciliates. Conversely in June (and July) during post bloom, large copepods were dominating.

Hydrodynamic model simulations of ocean currents and trajectories of potential plankton transports showed differences in potential advection of plankton across shelf banks. The circulation around the banks seems to create retention areas entrapping plankton for periods. Model simulations predict that upwelling occurs west of the shelf banks and to a lesser extent in the deep channels separating the banks. This upwelling, caused by wind and tidal motions, probably increases productivity and carbon cycling over the shelf areas.

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1. Introduction

The Greenland economy and society depend to a large extent on harvesting fish and shellfish resources.

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In terms of marine resources the waters of Southwest Greenland are the most productive and most of the human population lives in this area (Born and Bøcher, 2001). Ocean currents that transport water from the polar and temperate regions increase the marine productivity in the shelf areas of Southwest Greenland. The watermass characteristics in the *West Greenland Current* are formed in the western Irminger Basin where the *East Greenland Current* and the *Irminger Current* meet and flow southward side by side (Fig. 1). As the currents round the tip of Greenland the Irminger water subducts the Polar Water and extensive mixing takes place (Buch et al., 2004). Hence, the waters of southwest Greenland are intermediate between cold Polar Water masses of the Arctic region and temperate water masses of the Atlantic Ocean.

During the last decades climate variability has created long periods of lower than normal temperatures in the Northwest Atlantic with major impacts on species distributions and harvestable resource yields (Serreze et al., 2000; Stern and Heide-Jørgensen, 2003; Buch et al., 2004; Heide-Jørgensen and Laidre, 2004). Over this period the dominant

resources for the commercial fishery in West Greenland has changed from fish, mainly Atlantic cod (*Gadus morhua*), to shellfish, mainly northern shrimp (*Pandalus borealis*) (Buch et al., 2004). Similar resource shifts have occurred in eastern Canada (Worm and Myers, 2003). Resource management requires improved knowledge of the structure and function of the marine pelagic ecosystem and mechanisms determining variability in fish and shellfish resources under changing climatic conditions (Pedersen and Rice, 2002; Pedersen et al., 2002; Buch et al., 2004).

Historic studies of plankton from Southwest Greenland give incomplete pictures of the plankton community structure at the lower trophic levels (MacLellan, 1967; Bainbridge and Corlett, 1968; Pavshits, 1968, 1972; Smidt, 1979; Jensen et al., 1999; Pedersen and Smidt, 2000). For example, simplified mass balance models for the West Greenland large marine ecosystem ignore fluxes through the lower trophic levels due to lack of information (Pedersen, 1994; Pedersen and Zeller, 2001). Smidt (1979) reported on the annual cycles of primary production and zooplankton in coastal/fjord areas of

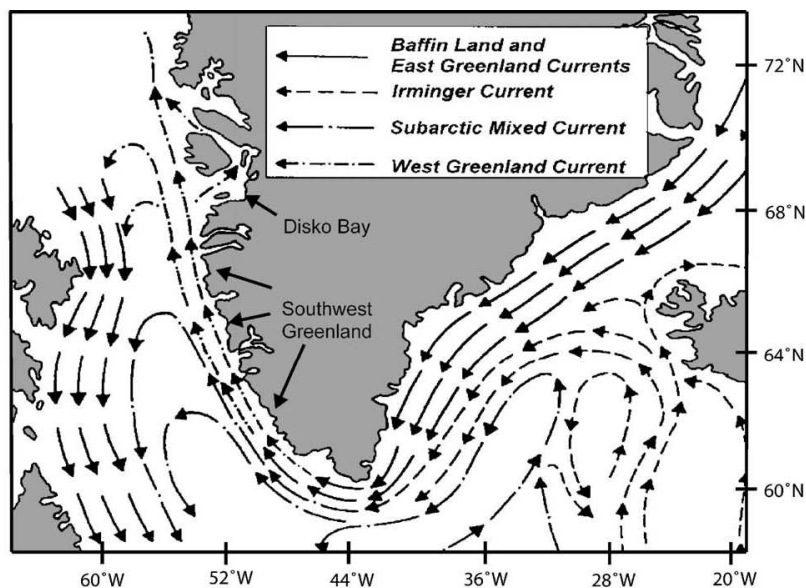


Fig. 1. Currents around Greenland (redrawn after Hachey et al., 1954).

Southwest Greenland based on studies during 1955–1967. Since Smidt's comprehensive description little information on the structure and function of the plankton community exists for Southwest Greenland.

Aquatic food webs have been studied intensively with respect to the interaction of consumer (“top-down”) and resource (“bottom-up”) effects on species composition and abundance. Variations in predator populations in the sea may have cascading effects across the food web, with implications for community structure and ecosystem functioning (Verity and Smetacek, 1996; Bundy, 2001; Pauly et al., 2001; Hunt et al., 2002; Pauly and Maclean, 2003). Worm and Myers (2003) found that overfishing on cod in the North Atlantic may have had cascading effects to lower trophic levels as indicated by an increase in northern shrimp populations. However, factors controlling the dynamics of shrimp populations include both “top-down” and “bottom-up” environmental mechanisms as well as commercial harvesting and their interactions are complex, dynamic, and poorly understood. For example Anderson (2000) suggested that larval emergence and recruitment success in northern shrimp are favoured by the relatively late zooplankton peak abundance observed during a cold ecosystem regime. A study by Parsons and Colbourne (2000) indicated that cold ocean conditions off Newfoundland and Labrador had a positive effect on shrimp production early in the life history. They speculated that the recruitment success of shrimp might be more related to nutrient supply for shrimp larvae in the upper water column than temperature. Recruitment success in Atlantic cod has been linked directly to plankton abundance, especially copepods genus *Calanus finmarchicus*, because cod larvae survival has been shown to depend on copepod abundance, size, and seasonal timing—a match in time and space between larvae and their prey organisms in the right concentrations, size, and energy value (Bainbridge and McKay, 1968; Sundby, 2000; Brander et al., 2001; Beaugrand et al., 2003).

The importance of “bottom-up” environmental mechanisms and hydrographical frontal processes for the variability in fish and shellfish resources in West Greenland ecosystems has been stressed in several studies (Pedersen and Storm, 2002; Munk, 2002; Munk et al., 2003; Hansen et al., 2003). Comprehensive investigations of pelagic productivity

and food web structure in Disko Bay (Fig. 1) have documented the dominance of large calanoid copepods and that bacterioplankton and unicellular zooplankton play a prominent role in the pelagic food web (Nielsen and Hansen, 1995, 1999; Madsen et al., 2001; Niehoff et al., 2002; Hansen et al., 1999, 2003).

A central theme in studies of marine plankton dynamics and higher trophic-level productivity is the efficiency and variability of linkages in the cycles of marine biological production (Runge, 1988; Kiørboe, 1993, 2001). According to Runge (1988) a link in the food chain from phytoplankton variability to fisheries is most likely to be detected via copepod productivity in systems dominated by the large grazer *C. finmarchicus* and fish populations that feed on eggs and juveniles of *C. finmarchicus* during the early larval stages. In West Greenland the latter may be the case for both Atlantic cod and northern shrimp (Bainbridge and McKay, 1968; Sundby, 2000; Harvey and Morrier, 2003).

Hansen et al. (2003) found an optimal match in time and space between the ascending from hibernation of the large dominating copepod grazers, *Calanus* spp., and onset of primary production in spring to be crucial for food web structure and energy transfer to higher trophic levels. For example if *Calanus* spp. were not able to change the behaviour and match the change in ice break and primary production as a consequence of rising temperatures, the consumers of the primary production may shift from large copepods to heterotrophic dinoflagellates or perhaps small, faster growing, copepod species. Hansen et al. (2003) speculate that such a shift could result in decreasing copepod production despite increased primary productivity in the system and possibly severely influence copepod predators such as fish larvae and planktivorous fish, thus generating a trophic cascade and influence the fisheries.

The distributions of fish and shellfish larvae are related to their spawning position at the shelf, water mass characteristics, and plankton productivity (Pedersen and Rice, 2002; Munk, 2002; Storm and Pedersen, 2003; Munk et al., 2003). Because plankton productivity is attached to the dynamics of hydrographical fronts marked deviations in frontal activity are likely to influence the survival probabilities of the different plankton organisms including fish and shellfish larvae with implications for ecosystem structure

and fisheries. Hence, understanding the hydrodynamic control of the pelagic food web structure is a key to understand changes in recruitment success for fish and shellfish (Pedersen et al., 2002; Nielsen and Hansen, 1999; Hansen et al., 2003; Buch et al., 2004). To improve the knowledge and understanding of the pelagic ecosystem over the Southwest Greenland shelf four research cruises collected hydrographical data and plankton samples in 1999 and 2000. The objectives of this study were (1) to give a detailed description of the micro- and mesozooplankton community, (2) to relate plankton distributions to the physical environment using a hydrodynamic ocean circulation model, and (3) to identify “bottom-up” environmental mechanisms and testable hypotheses determining variability in the fisheries resources.

2. Materials and methods

2.1. Study area and sampling

Sampling was carried out in June 1999, May, and July 2000 between 63°50'N and 66°50'N over the West Greenland shelf with the Greenlandic research vessels *Adolf Jensen* and *Paamiut* (Fig. 2; Table 1). In May and June, sampling was performed at stations along transects crossing Fyllas- and Sukkertop Bank. In July, sampling was out carried further north to include stations along transects crossing Lille- and Store Hellefisk Bank using the two research vessels at the same time. In May 6 coast/fjord stations were sampled in the inshore Nuuk-area (Fig. 2).

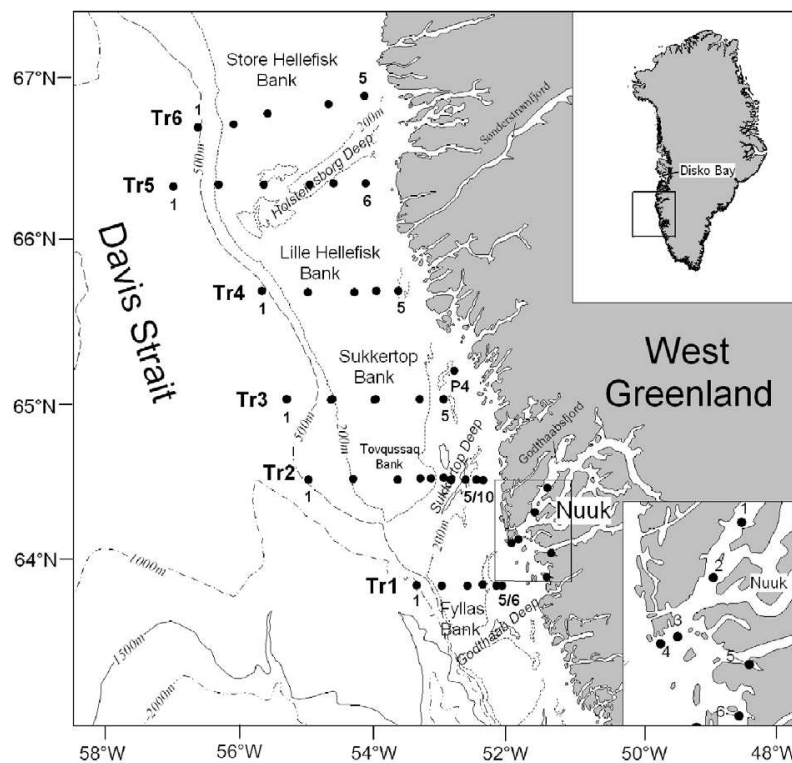


Fig. 2. Bathymetric chart of the West Greenland Shelf study area, with indication of sampling stations along 6 cross-shelf transects (Tr1–Tr6). Transects were sampled as follows: Tr1 and Tr3 in May 2000, Tr2–Tr3 in June 1999, Tr1–Tr6 in July 2000. Six inshore sampling stations were sampled in May 2000 only.

Table 1
Sampling data from the four research cruises

Period	Research vessel	Transect	Gear (net mesh size)
May 12–21 2000	RV <i>Adolf Jensen</i>	1, 3	Zooplankton pump (50 µm)
June 21–30 1999	RV <i>Adolf Jensen</i>	2, 3	WP2 (50 µm)
July 11–23 2000	RV <i>Adolf Jensen</i>	1, 4, 5	Zooplankton pump (50 µm)
July 12–27 2000	RV <i>Paamiut</i>	2, 3, 6	WP2 (50 µm)

Depth integrated micro- and mesozooplankton samples of the upper 200 m (or 2 m above bottom at shallower stations) were obtained from each station shown in Fig. 2. In June with *Adolf Jensen* and in July with *Paamiut*, samples were collected from one vertical haul with a WP-2 net (0.58 m diameter and 50 µm mesh size) retrieved at 10 m min⁻¹ assuming 100% filtration efficiency. In May and in July with *Adolf Jensen*, samples were collected using a submersible pump (900 l min⁻¹, HOMA-H500, DIFRES-design) equipped with a conical net of 50 µm mesh size. The pump or WP-2 net was lowered to max 100 m in May and July with *Paamiut* and max 200 m in June and July with *Adolf Jensen* started and retrieved to the surface at 10 m min⁻¹. Samples were preserved in 4–8% buffered formalin in seawater.

At each station, and at additional stations between these (not shown in Fig. 2), vertical profiles of temperature, salinity, and density were obtained with a Sea-bird SBE 9-011 sealogger CTD. Water samples were taken on stations with depths greater than 500 m and afterwards analysed on a Guildline Portosal 8410 salinometer for calibration of the conductivity sensor (Buch, 2000a; Buch and Nielsen, 2001). Fluorescence was measured with a HydroScat2 fluorometer from HOBI-Labs, except during the cruise with *Paamiut* in July. The fluorescence was calibrated against fluorometrically determined chlorophyll *a* content in water samples collected on selected stations in May and June (Poulsen and Reuss, 2002). The methods for calculation of biomasses and carbon contents of phytoplankton and protozooplankton are described in Poulsen and Reuss (2002). Biomasses were integrated to the depth where the in situ fluorescence was approximately zero by trapezoidal integration at four depths, ~5 m, fluorescence maximum, ~100 m, and the integrated depth (Poulsen and Reuss, 2002).

2.2. Taxonomic identification, abundance, and carbon content

Micro- and mesozooplankton were sorted and identified to the lowest possible taxon in the laboratory. Each species or taxonomic category was enumerated and length measured (Table 2). Within each copepodite stage up to 10 specimens were length measured. Abundance and length information was used to estimate the biomass as total carbon within taxonomic categories at each sampling station. Length-weight relationships (carbon content or ash-free dry weight) were obtained from the literature: *Calanus* (all three species) and *Metridia longa* from Hirche and Mumm (1992), *Acartia* spp. and all copepod nauplii from Berggreen et al. (1988), *Pseudocalanus* sp. from Klein Bretler et al. (1982), while for the smaller taxons *Oithona* spp., *Microcalanus* spp., *Oncaea* spp., and *Microsetella* spp., the relationship for *Oithona* spp. in Sabatini and Kjørboe (1994) was used. The carbon content of eggs

Table 2
Measurements by taxonomic category

Taxonomic category	Measurement
Copepoda–Calanoida and Cyclopoida	Length of Prosome
Harpacticoida	Total length (without setae)
Copepoda nauplii	Body length (without setae)
Euphausiacea, Amphipoda, and Mysidacea	Total length to the end of telson
Cirripedia nauplii	Body length (without spine)
Decapoda larvae	From posterior edge of orbit to the end of carapax
All eggs	Diameter
Egg sacks	Maximal length
Polychaeta, Bivalvia, Gastropoda larvae, and Cirripedia cypris	Maximal length
Echinodermata larvae (pluteus)	Length of armspan
Echinodermata larvae (others)	Maximal body length
Hydromedusae and Siphonophora	Maximal body length
Scyphomedusae	Diameter
Appendicularia	Maximal body length (without tail)
Tintinnidae	Total length
Chaetognatha	Total length to the end of tail, total length

(copepods and euphausiids) and egg sacks of copepods was estimated from egg/sack volume by assuming $0.14 \text{ pg C } \mu\text{m}^{-3}$ (Kjørboe et al., 1985). The carbon content of egg sacks is overestimated because they are not spherical. The carbon content of *Calanus* spp. stages CI to CIII and the smaller taxons was assumed to be 50% of dry weight, while a conversion factor of 60% was used for older stages of *Calanus* spp. (Hansen et al., 1999). For none copepods the reference in brackets was used to estimate carbon biomass: Appendicularia (Uye, 1982), Bivalvia (Fotel et al., 1999), Cirripedia (Turner et al., 2001), Euphausiacea (Lindley et al., 1999), Polychaeta (Hansen, 1999), Gastropoda (Hansen and Ockelmann, 1991).

The biomass structures of the plankton community in the upper ~100 m of the West Greenland pelagic food web were constructed from integrated values of carbon biomasses from this study and results by Poulsen and Reuss (2002).

2.3. Advection and hydrodynamic environment

The current transport of key plankton species was investigated using a 3D-ocean current model using a finite element mesh to increase the resolution on the shelf. The model setup was split into a diagnostic baroclinic simulation and a prognostic barotropic simulation. The diagnostic simulation calculates the baroclinic currents from a fixed temperature and salinity field constructed from observations centered at June–July (only used for horizontal velocities). For the shelf area off West Greenland south of 70°N hydrographic measurements were obtained at three different cruises in 2000 whereas for the rest of the area historical data were used. The prognostic simulation calculates the time varying currents resulting from tides and wind forcing calculated from the operational atmospheric model for Greenland. For a detailed description and discussion of the hydrodynamic model see Riber-gaard et al. (2004).

The calculated combined barotropic and baroclinic current fields were used as input in a particle-tracking model to simulate the possible transport of plankton. We conducted a number of drifter experiments to investigate possible effects on the plankton transport distances. Drifters were released on May 12

in 1999 and 2000 along three transects (Tr0, Tr1, and Tr3) across the southwest Greenland shelf, in four depths (10, 30, 50, and 80 m). Vertical migration behaviour was not included in the particle-tracking model, but particles were tracked in four different depths to evaluate possible effects on transport distances of vertical migration behaviour of plankton.

From the prognostic barotropic hydrodynamic model vertical current velocities and the locations of potential up- and downwelling areas were calculated and averaged over time. The locations of upwelling areas were assumed to be high productive areas and they were compared with our findings of plankton abundances. As we are only using a barotropic model for calculating the vertical velocities interpolated to 30 m and 60 m depths, the velocities are an upper limit, as the vertical stability in the model is neutral and not stable as is the case in the ocean. Thereby, lesser energy input is needed to raise a water parcel in the model than in the real ocean. Contrary, by neglecting the baroclinic response we exclude the possibility for neutral balanced up- and downwelling along steep sloping isopycnals, but we do not believe that these velocities are comparable to the vertical velocities found in the model (see later).

2.4. Statistical analysis

Sample data were analysed using the statistical package Plymouth Routines in Multivariate Ecological Research PRIMER 5.2.8 (PRIMER-E Ltd 2000; see Clarke and Warwick, 1994). Except for *C. finmarchicus*, copepodite stages of *Calanus glacialis*, *Calanus hyperboreus*, and other copepods were pooled within species or genus. *Calanus* spp. nauplii, small copepod nauplii, copepod eggs, and egg sacks were grouped, as were species within the different genus of bivalve, gastropod, echinoderm, and cirriped larvae. Rare taxa were excluded resulting in 22 taxa categories being used for subsequent analyses. The abundances (number m^{-2}) were log transformed ($x+1$). Bray–Curtis similarity was calculated between samples and used for nearest-neighbor cluster analysis. Station groups identified this way in May and June and group according to upwelling areas identified from our hydrodynamic model (mainly west of the banks at depths >150 m) were tested for significance using

ANOSIM (analysis of similarity, analogous to one-way ANOVA). ANOSIM was also used to test for significance in zooplankton data between sampling periods (May 2000, June 1999, and July 2000). Tests were also performed on more reduced data sets with data on *Calanus* spp., species of small copepods, and invertebrate larvae, respectively.

3. Results

3.1. Hydrography

From May to July, temperatures in the upper 50 m of the water column over the southwest Greenland shelf Banks (Tr1-3) increased from below zero to above 5 °C (Fig. 3a–d). During this period a thermocline developed at about 50 m and salinity dropped from 33.6 to below 33.2. The lowest salinities were found in the upper water column at the nearshore stations in May (Tr1 and 3), June (Tr3), and July (Tr1, 4, and 5). On Tr3 in June 1999, relative warm and low saline water was found east and on top of Sukkertop Bank, whereas a core of cold Polar water (<−0.5 °C) was seen west of the bank at depths between 25 and 125 m. In July 2000, cold Polar Water (<0 °C) was distributed at intermediate depths between 50 and 150 m over the shelf, and salinity showed an increasing trend from south to north (Tr1 to 6). Density lines (σ_t) varied between 25.6 and 28.4 and followed the salinity lines (data not shown).

3.2. Plankton distribution

Chl *a* concentrations were highest during the spring bloom in May with peaks (4–6 $\mu\text{g l}^{-1}$) over the shallow parts of Fyllas- and Sukkertop Bank along the offshore sampling transects Tr1 and Tr3 (Fig. 3a–b). The inshore coast-fjord stations, sampled in May only, showed similar high levels of chl *a* concentrations as at the offshore stations except at station 5 (>0.7 $\mu\text{g l}^{-1}$) (Fig. 3d). In June, a post-bloom situation prevailed resulting in low autotrophic biomass and low chl *a* values over Sukkertop Bank, but peak chl *a* values (1 $\mu\text{g l}^{-1}$) in the upper water column were seen at the westernmost stations of Tr3 (Fig. 3b). In July, subsurface chl *a* peaks (1–2 $\mu\text{g l}^{-1}$) at water depths of about 30 m were seen along Tr1, 4, and 5 (Fig. 3a,c).

Visual inspections of Fig. 3a–b showed higher abundance of *Calanus* copepodites and eggs/nauplii at stations west of the shelf banks in May and June. The small copepods and bivalves larvae were more abundant over the banks in May, in the cold Polar Water in June, and with no clear distribution patterns along transects in July.

More than 30 species and a larger number of taxonomic categories were identified in the zooplankton samples. Copepods dominated the zooplankton and the following species were identified: *C. finmarchicus*, *C. hyperboreus*, *C. glacialis*, *M. longa*, *Acartia longiremis*, *Microcalanus pusillus*, *Microsetella norvegica*, *Oithona similis*, *Oncaea borealis*, and *Pseudocalanus elongates*. The latter six species were grouped by genus, together with unidentified species of these taxa. A few specimens of *Euchaeta norvegica*, *Scolecithricella* spp., *Temora longicornis*, *Centropages hamatus*, and *Pleuromamma robusta* were identified.

The larger *Calanus* copepodites (CI–CV) showed an increasing abundance from May to July (Fig. 3a–d). *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* occurred in about equal abundance in May, whereas *C. finmarchicus* dominated in June and July. In *C. finmarchicus* and *C. glacialis*, CI was dominating in May, CI–CIII in June, and CIII–CV in July. In *C. hyperboreus*, CII was dominating in May, CI and CIII in June, and CIV in July. Abundance was highest over deep water east and west of the banks in May, June, and July. *Calanus* spp. abundance was low at the fjordic stations sampled in May, highest abundance (mainly CI) was found on the coastal stations 4–6 and females of *C. finmarchicus* only in Godthaabsfjord station 1 (Fig. 3d). In May there was relatively high abundance of *C. finmarchicus* females (few males) on especially the deeper stations west and east of the banks. In June and July the abundance of *C. finmarchicus* females was lower or nil. Generally no females or males of *C. glacialis* and *C. hyperboreus* were found. However, in July few *C. glacialis* females were identified at stations along Tr5. The low number of the *Calanus* spp. females, especially in June and July with “warm” water, may have been caused by under sampling of the large and more mobile zooplankton by the sampling gear used. The WP-2 net is originally constructed for net of 200 μm mesh size however in this study we used a 50 μm net in the

WP-2 frame and hence the slow towing speed may have caused under sampling of the largest most mobile individuals. Similarly, we cannot rule out that the zooplankton pump equipped with 50 μm mesh nets has undersampled the most mobile organisms.

The small copepod community (CI–CVI) consisted predominantly of *Oithona similis* and *Microsetella norvegica* during all sampling times. Total abundances were at similar levels in May and June, and highest in July. In May the fjordic stations were dominated by *Microsetella* spp. and *Pseudocalanus elongatus*. *Microcalanus* spp. was dominant at one station on Tr3 in May. *Pseudocalanus* spp. occurred in high abundance at the two shallow stations nearest to shore of Tr6 in July. The abundance of both large and small copepods was exceptionally high over deep water east and west of the bank on Tr2 and west of the bank on Tr3 in July (not shown). Copepod eggs showed highest abundance in May and June, whereas copepod egg sacks were dominating in July.

In June there was a trend of higher abundance of copepod eggs, nauplii, and “other zooplankton” west of the Sukkertop Bank (Fig. 3b). These findings west of the banks may indicate increased primary productivity, copepod egg production rate, and food for zooplankton due to mixing between cold water west of the shelf and warmer over the shelf.

The results of clustering on the aggregated data sets for May, June, and July are presented in Fig. 4. In May, the two western most stations on transect 1 and 3 group. In June, stations 1 and 2 on transect 2 and 3 grouped, however these transects were separated from each other. In July, it was impossible to find a pattern in the zooplankton data, which seemed to be randomly distributed. ANOSIM performed on the two western most stations (tr1-1 and tr3-1) in comparisons with other transect stations and fjord stations (f1–f6) in May showed differences ($p < 0.05$) between groups although a small number of samples.

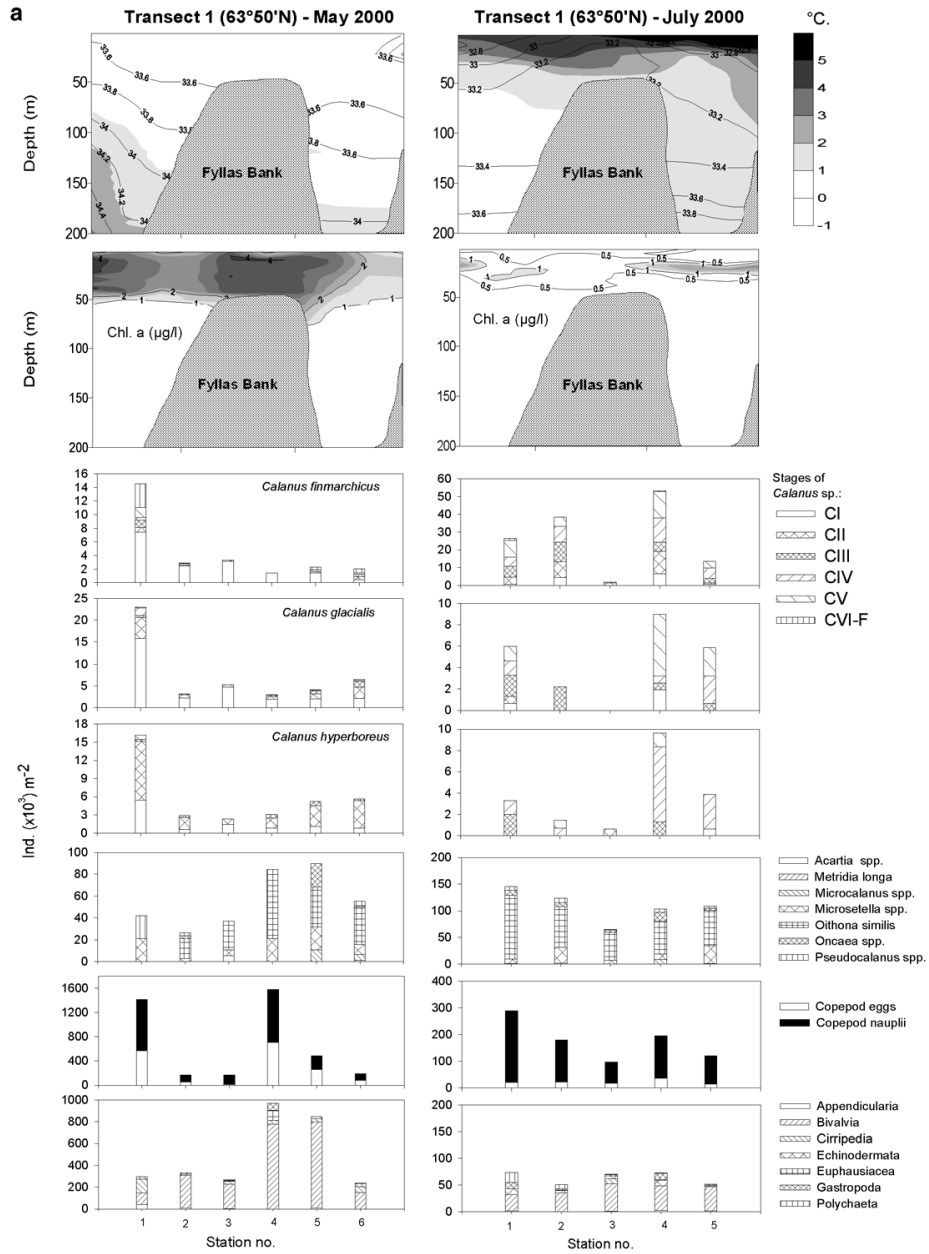
In June, two stations (tr2-4 and tr3-4) on top of the banks at depth < 45 m were similar and different ($p < 0.05$) from all other stations mainly due to low numbers of all plankton categories. In July, station tr3-3 and tr6-4 were different ($p < 0.05$) to all other samples by having no *C. finmarchicus* copepodites (CI–CII). ANOSIM on all samples from May, June, and July showed no difference ($p > 0.05$) between June and July, which both were different ($p < 0.05$) from May. The zooplankton data from June and July were tested for difference between stations west of the bank shelf (at depths > 150 m) and stations on the shelf bank and coast wards, respectively; however, these tests showed no significant differences. Test with more reduced data sets revealed no significant or clearer patterns in plankton distributions than described above. Hence, the hypothesis that upwelling areas identified by our hydrodynamic modeling structured the zooplankton community could neither be confirmed nor rejected by the zooplankton data (see later and Discussion).

3.3. Plankton community structure

By number, bivalves larvae and relatively large copepod nauplii (> 200 μm) dominated the zooplankton community (> 50 μm) in May, whereas smaller copepod nauplii (< 200 μm) were dominating in June and July (Fig. 5). In July high numbers of gastropod (pteropod) larvae were found especially along Tr2 and Tr3, and tintinnids on Tr1.

By weight, the large copepodites of *Calanus* spp. dominated the copepod and invertebrate biomass in all sampling periods, with *Pseudocalanus* spp., *Metridia longa*, and *Oithona* spp. comprising most of the remaining copepod biomass (Table 3). *Calanus* spp., especially *C. finmarchicus*, became increasingly dominant from May to July with exceptionally high biomasses over the shelf slopes along Tr2 and Tr3

Fig. 3. (a) Vertical sections of temperature ($^{\circ}\text{C}$), salinity, chlorophyll *a*, abundance indices of stage composition of *Calanus* spp., other copepods (CI–CVI), copepod eggs, nauplii, and other invertebrate larvae along transect 1 in May 2000 (left panels), and July 2000 (right panels). (b) Vertical sections of temperature ($^{\circ}\text{C}$), salinity, chlorophyll *a*, abundance indices of stage composition of *Calanus* spp., other copepods (CI–CVI), copepod eggs, nauplii, and other invertebrate larvae along transect 3 in May 2000 (left panels), and June 1999 (right panels). (c) Vertical sections of temperature ($^{\circ}\text{C}$), salinity, chlorophyll *a*, abundance indices of stage composition of *Calanus* spp., other copepods (CI–CVI), copepod eggs, nauplii, and other invertebrate larvae along transect 4 (left panels), and transect 5 (right panels) in July 2000. (d) Vertical profiles of temperature ($^{\circ}\text{C}$), salinity, chlorophyll *a*, abundance indices of stage composition of *Calanus* spp., other copepods (CI–CVI), copepod eggs, nauplii, and other invertebrate larvae at coast/fjord station 1–6 in May 2000.



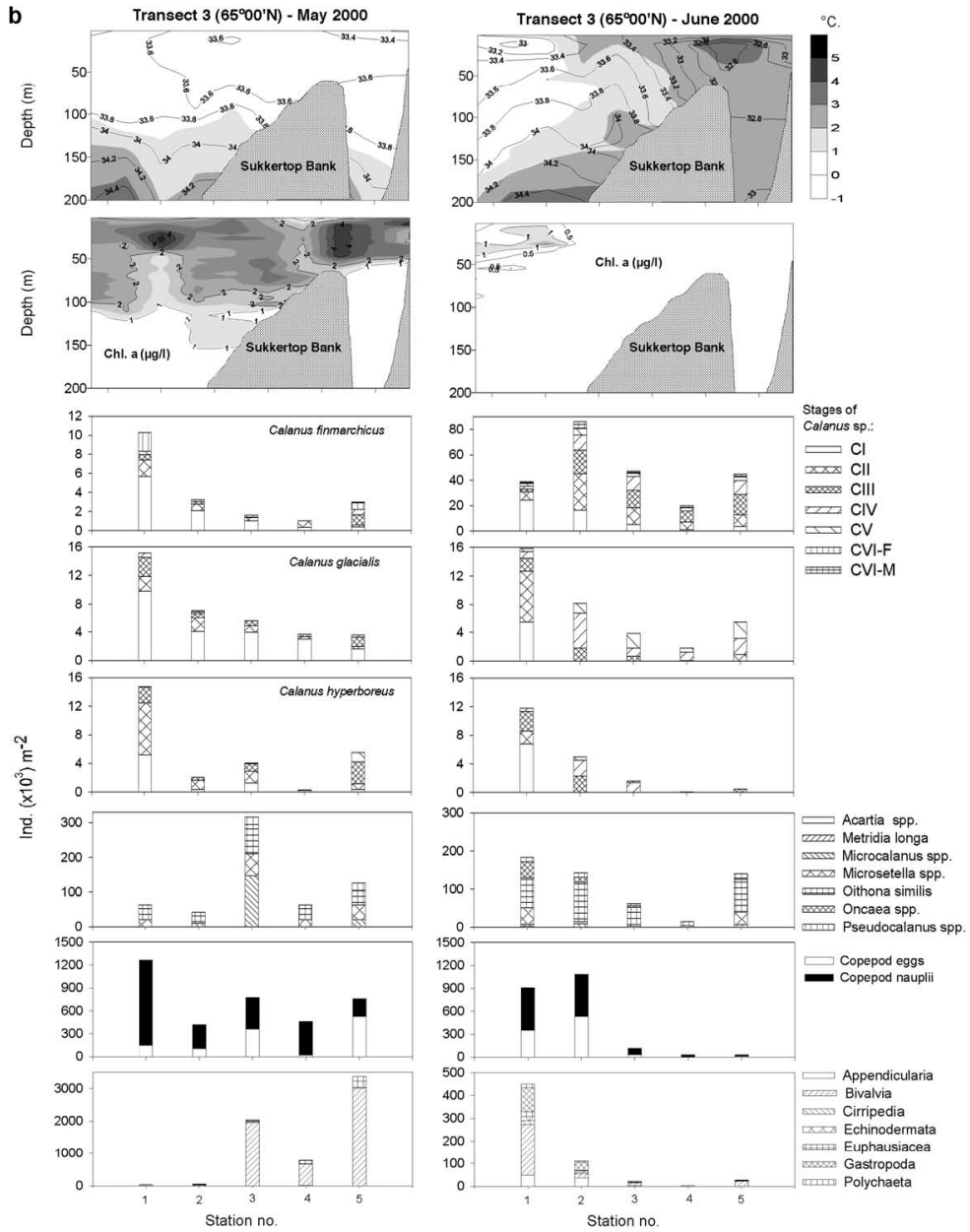


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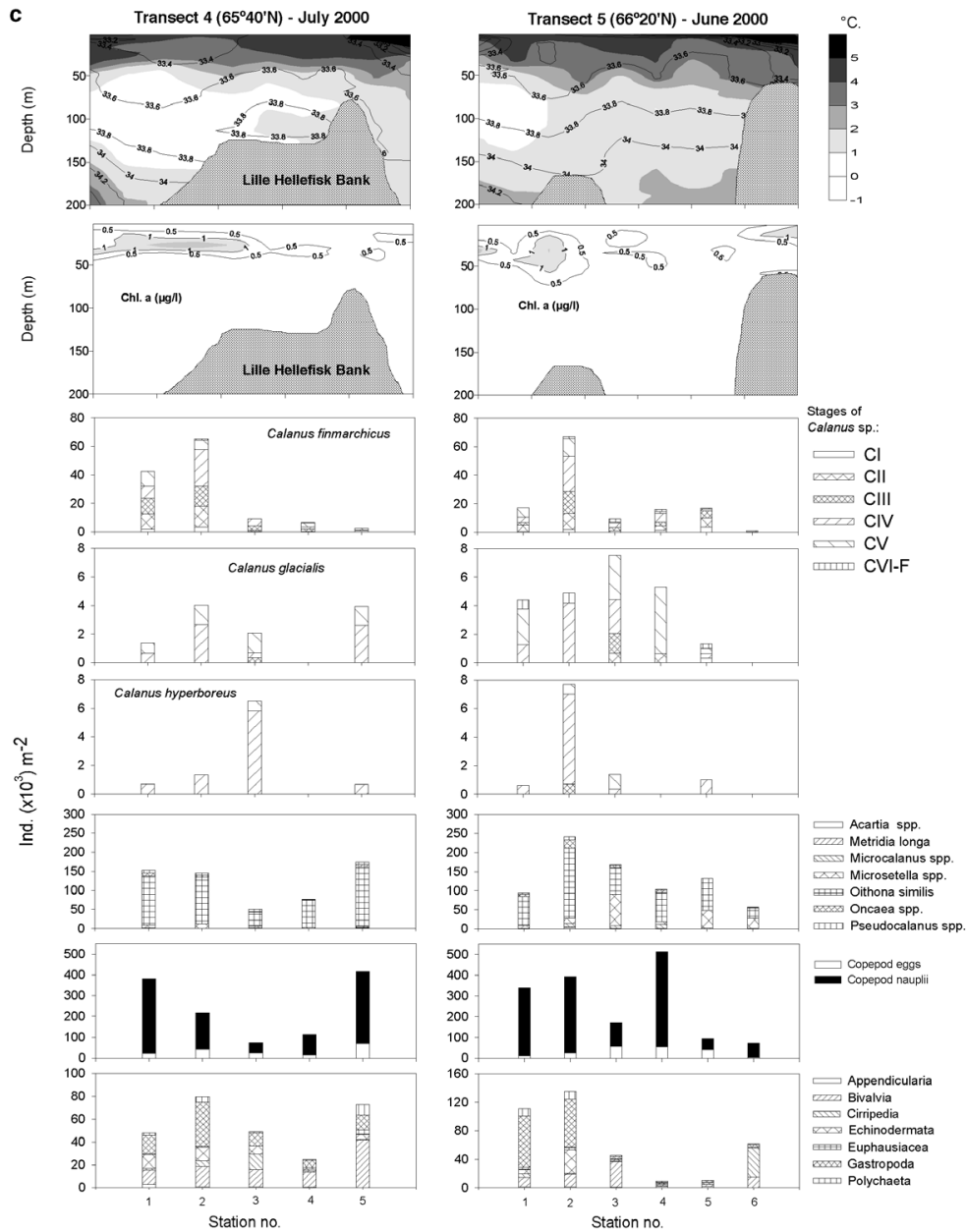


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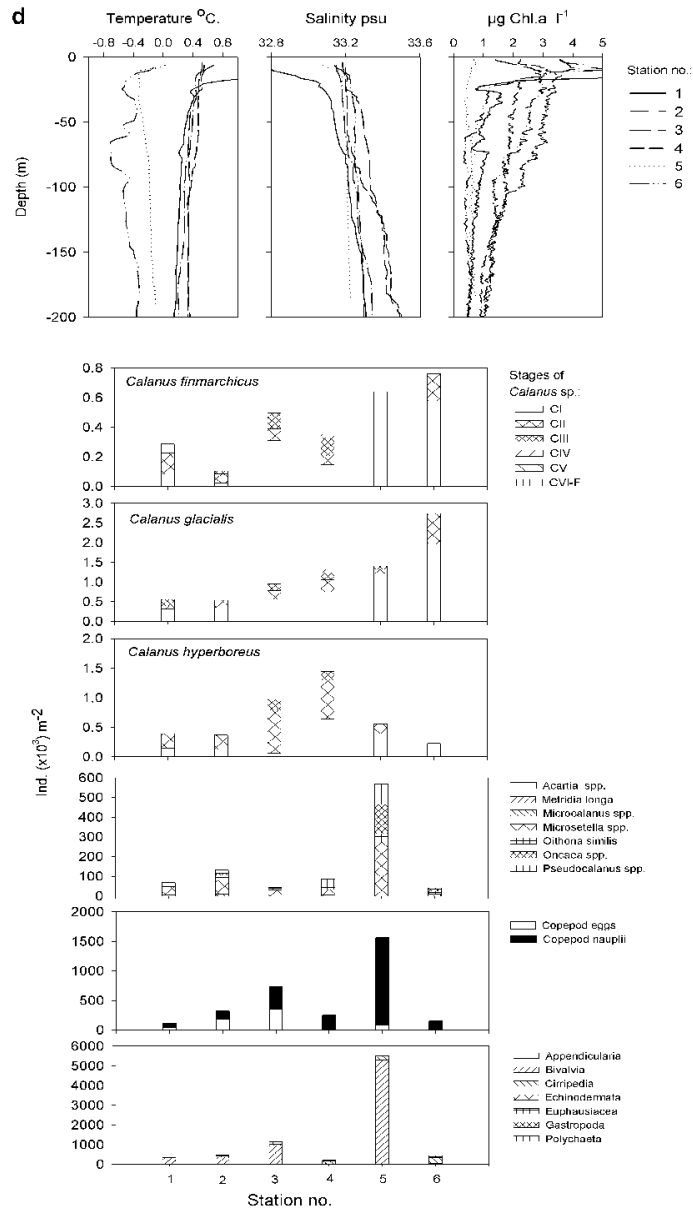


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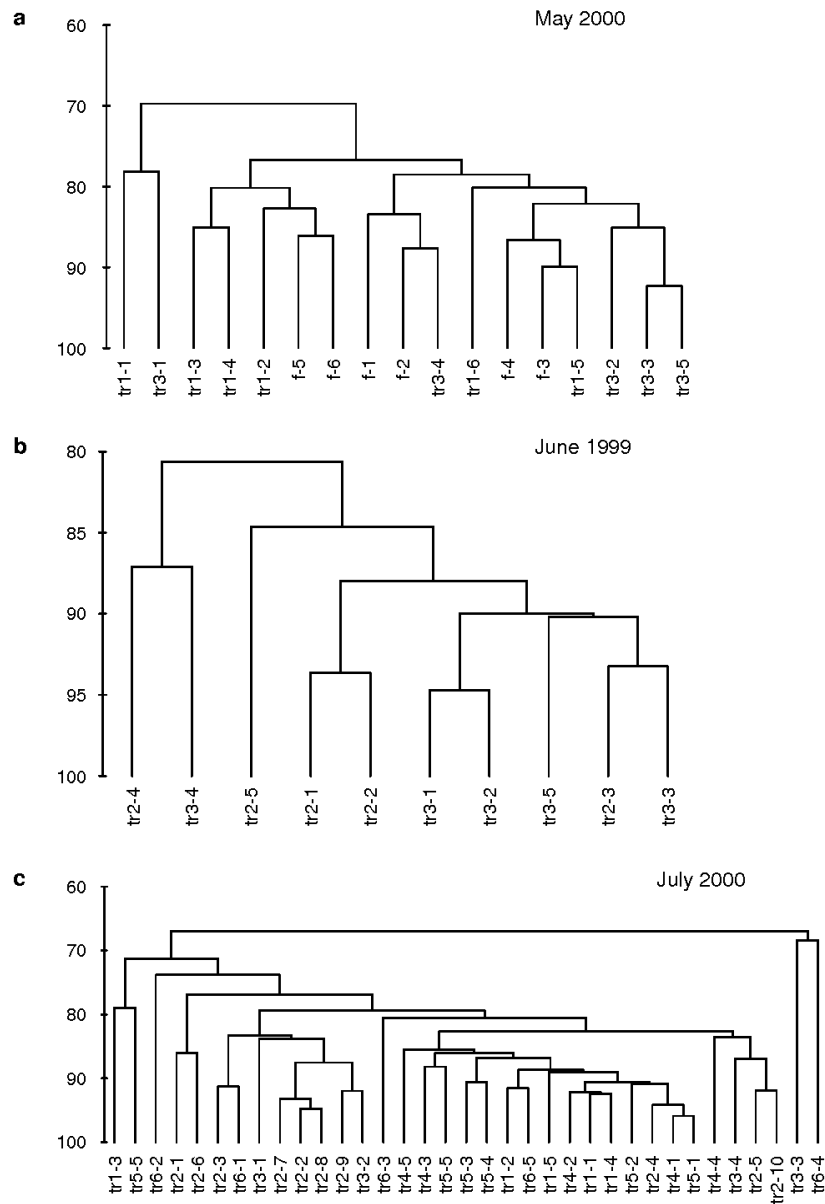


Fig. 4. Results of clustering performed on the Bray–Curtis similarity matrix created from the log-transformed zooplankton data by station and sampling periods (a) May 2000, (b) June 1999, and (c) July 2000. “tr”–transect and “f”–fjord station. For example “tr3-1” is station 1 on transect 3.

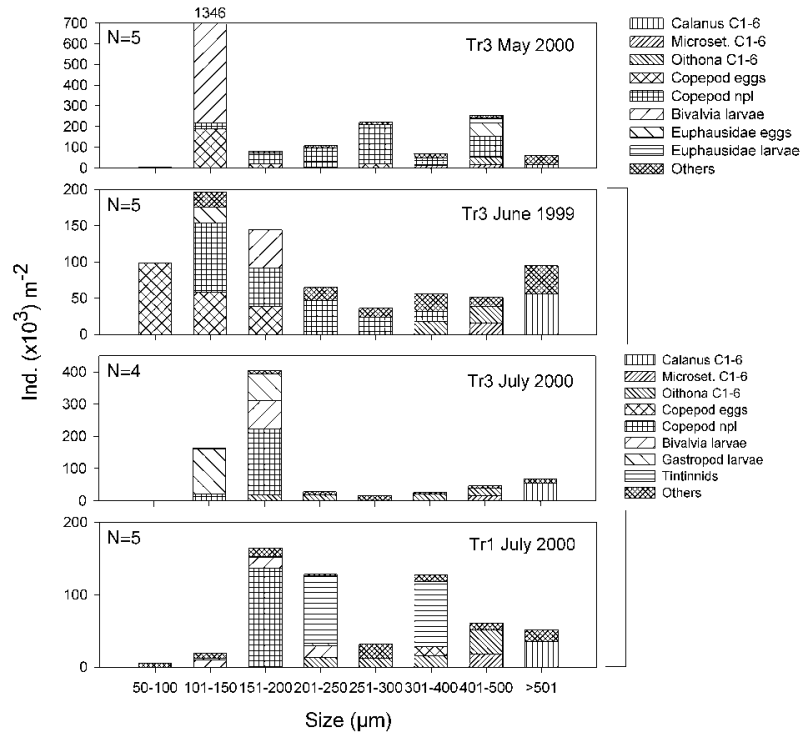


Fig. 5. Mean concentrations of micro- and mesozooplankton categories by size and sampling location in May 2000, June 1999, and July 2000.

(Fig. 6). In May, on the inshore stations (St. 1–6) other copepod species *M. longa*, *Pseudocalanus* spp., *Microsetella* spp. were dominating.

In May, diatoms, *Thalassiosira* spp. and *Chaetoceros* spp., dominated the biomass structure of the plankton community of the upper 100 m followed by heterotrophic flagellates, ciliates, and copepods (Tables 3 and 4). Conversely in June (and July) copepods dominated over heterotrophic flagellates, ciliates, autotrophic flagellates, and other invertebrate zooplankton. We have no information on the species composition and biomasses of phyto- and protozooplankton from July, however, tintinnids were very abundant on several stations.

3.4. Advection and hydrodynamic environment

Trajectories of particles by release locations (Tr0, Tr1, and Tr3) for 2 years, 1999 and 2000, were almost

identical in spite of some differences in the wind fields between years. Tracking of particles released in different depths (10, 30, 50, and 80 m) showed minor differences in transport patterns, indicating a strong barotropic component on the currents and a strong but relative depth independent baroclinic component in the top 80 m over the shelf break. This also suggests, that the wind forcing for the given period only have small influence on the horizontal currents. However, on short timescales (hours) the wind and the semi-diurnal tides dominate on the shelf, whereas on longer timescales (days) the barotropic currents forced by the interaction between the residual tides and topography dominate. The added diagnostic baroclinic component dominates independently on timescales over the continental shelf break as a significant increased northward flow. The strong baroclinic component indicates minor effects of adding vertical behaviour to the particles (plankton), over the shelf break. This

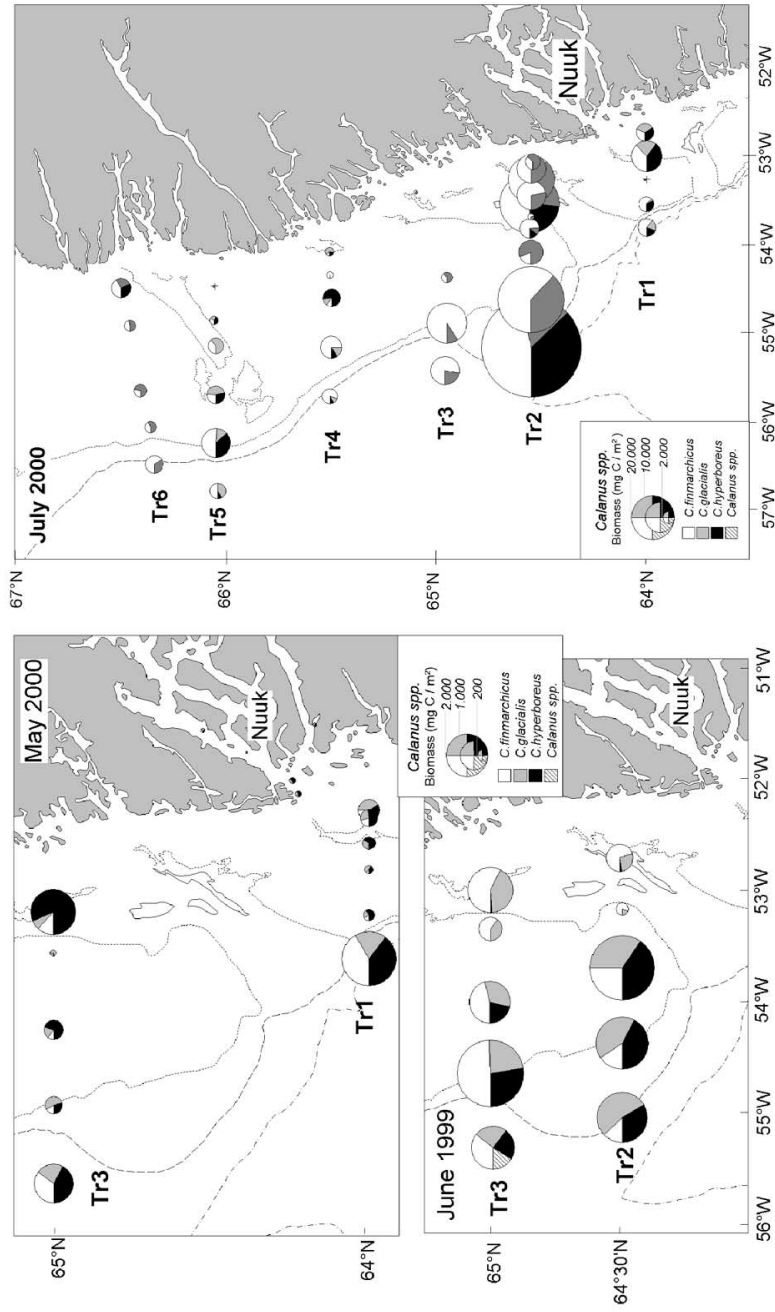


Fig. 6. Distribution and biomass (mg C m^{-3}) of *Calanus* spp. in May 2000, June 1999 (left panels), and July 2000 (right panels). Dot sizes are graduated by square root. Note different scales between left and right panel.

Table 3
Mean biomass (mg C m⁻²) the upper ~100 m of each zooplankton category by sampling location and period

Location	Transects 1, 3		Transects 2, 3		Transects 1–6		Fjord (St. 1–6)	
Sampling period	May 2000		June 1999		July 2000		May 2000	
Number of stations	11		10		36		6	
Plankton category	Mean	Std	Mean	Std	Mean	Std	Mean	Std
<i>Copepods</i>								
<i>C. finmarchicus</i>	160	266	764	534	3120	5509	4	3
<i>C. glacialis</i>	123	114	724	480	1858	2847	14	7
<i>C. hyperboreus</i>	304	385	563	584	1291	3875	16	15
<i>Acartia</i> spp.	1	4	0	0	1	4	2	5
<i>M. longa</i>	16	52	51	114	37	109	94	230
<i>Microcalanus</i> spp.	17	31	3	4	2	4	4	5
<i>Microsetella</i> spp.	12	10	9	12	17	27	54	75
<i>O. similis</i>	27	21	21	21	65	74	13	7
<i>Oncaea</i> spp.	0	0	3	3	5	12	11	22
<i>Pseudocalanus</i> spp.	66	82	22	20	49	54	74	62
Copepod eggs	88	63	22	40	34	34	56	63
Copepod nauplii	413	349	27	33	34	42	226	242
Total copepods	1229	1376	2210	1845	6513	12,592	566	736
<i>Other invertebrates</i>								
Appendicularia	16	22	24	29	7	11	4	4
Bivalvia	37	47	3	4	12	20	58	99
Cirripedia	103	190	63	115	45	85	301	315
Echinodermata	–	–	–	–	–	–	–	–
Euphausiacea	209	450	15	24	14	42	109	119
Gastropoda	13	33	11	19	56	95	4	7
Polychaeta	8	6	4	2	4	3	21	8
<i>Pandalus</i> larvae ^a	15	29	7	5	8	8	23	19
Total other invertebrates	401	776	127	198	146	263	520	570

^a From Pedersen et al. (2002).

might be complicated by baroclinic eddies formed in the front between the Polar Water and the Atlantic Water, which are not included in our setup, as the baroclinic forcing is treated diagnostic.

Simulations of particles released in 30 m along Tr0, Tr1, and Tr3 across the shelf showed clear differences in the transport patterns (Fig. 7). Drifters released in coastal areas and over the shelf were drifted north ending in the coast or caught in eddies over the shelf banks (south of 67°N). Hence, plankton tend to be drifted coastward or towards retention areas over the shelf banks. The westernmost drifters were either transported west to the Labrador shelf (Tr0) or north along the West Greenland shelf slope (Tr1 and Tr3).

In Fig. 8 the vertical velocities from the barotropic model are shown interpolated to 30 m depth and averaged over 6 months. Permanent upwelling was found to occur west of the shelf banks over model water depths between 150 and 500 m, on top of the

Banks crossed by transects Tr2, Tr5, and Tr6, and to a lesser extent in the deep channels separating the banks, which was often dominated by downwelling (Fig. 8). The up- and downwelling patterns were permanent in the hydrodynamic model and caused by the interaction between the strong tidal currents and the complex topography (Ribergaard et al., 2004). The magnitude of the vertical speeds is an upper limit, as the hydrodynamical model is run in barotropic mode, i.e. the water mass is neutral stable. Further, the vertical motion could be converted to vertical mixing of different watermasses, but we exclude this possibility by using a barotropic model. Wind speeds and wind directions have strong effects on the vertical velocities (up/downwelling). In Fig. 9 the vertical velocity at 60 m is shown from a location west of the Fylla Bank with a model depth of 312 m. From the end of April to mid-June 2000 wind from the north dominated the wind field resulting in upwelling (Fig.

Table 4
Mean depth integrated biomass (mg C m⁻²) of phytoplankton and protozooplankton by sampling location and period

Location	Transects 1, 3		Transects 2, 3		Fjord (St. 4)	
Sampling period	May 2000		June 1999		May 2000	
Number of stations	8		5		1	
Plankton category	Mean	Std	Mean	Std	Mean	Std
<i>Autotrophic organisms</i>						
Flagellates<10 µm	90	39	185	86	107	–
Flagellates>10 µm	16	23	44	64	0	–
Euglenophyceae	16	45	0	0	0	–
<i>Phaeocystis pouchetii</i>	436	341	–	–	4010	–
A. Dinoflagellates	44	42	37	50	83	–
<i>Ceratium arcticum</i>	0	0	94	209	0	–
Centric diatoms	339	339	18	22	8	–
<i>Chaetoceros</i> spp.	3567	2171	395	881	2327	–
<i>Thalassiosira</i> spp.	4985	1792	25	53	1716	–
Pennate diatoms	332	363	29	51	99	–
<i>Mesodinium rubrum</i>	7	6	5	3	0	–
Total autotrophic biomass (mg C m ⁻²)	9831	3420	831	1224	8349	–
<i>Heterotrophic organisms</i>						
Nanoflagellates<10 µm	32	22	94	47	132	–
Nanoflagellates>10 µm	1	3	6	7	0	–
Coanoflagellates	108	70	34	39	58	–
A. Dinoflagellates<20 µm	95	65	149	101	294	–
A. Dinoflagellates>20 µm	948	656	205	205	1683	–
T. Dinoflagellates	136	66	32	27	107	–
Ciliates<50 µm	252	115	109	72	322	–
Ciliates>50 µm	392	363	115	61	151	–
<i>Laboea strobila</i>	77	91	18	21	25	–
Tintinnids	12	27	2	3	3	–
Total heterotrophic biomass (mg C m ⁻²)	2053	1108	763	376	2775	–

Data recalculated from mg C m⁻³ presented in Poulsen and Reuss (2002). Depth integrations were from surface to depth of zero “in situ” fluorescence.

9). By using a barotropic model to calculate vertical velocities, we exclude the possibility of up- and downwelling along isopycnals, but this does not have the same magnitude as the vertical velocities found in the model.

4. Discussion

4.1. Hydrography

The upper 200 m during May, June, and July were dominated by Polar Water, which is characterized by temperatures below 0 °C (increasing to 3–5 °C in the surface layer during summer) and salinities below 34.4 (Buch, 2000b). A hydrographic frontal zone between cold Polar Water and warmer mixed shelf

water over the bank was most clearly seen in June on the western part of Tr3 (Fig. 3b). In May and July, fronts were difficult to identify across transects. However, watermasses along the coast was influenced by freshwater runoff and smaller fronts were observed adjacent to these. The coarse spatial and temporal resolution of hydrographical data measurements made detection of the small scale frontal processes difficult. Furthermore, fronts may only occur periodically and might not have been detected. We found no clear relationship between zooplankton abundance and water mass characteristics.

4.2. Plankton distribution

The onset of the seasonal phytoplankton development (spring bloom) begins in Southwest Greenland

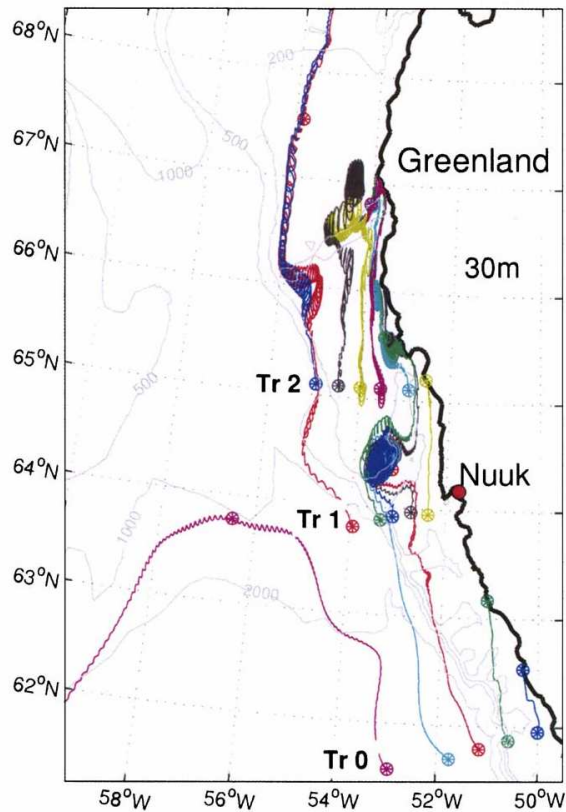


Fig. 7. Model calculated tracks of particles released in 30 m depth on May 12, 2000 along three transects across the shelf (Tr0, Tr1, and Tr3). Additional marks on the calculated particle tracks indicated position on July 12, and the tracking was stopped on September 12.

in April and it is delayed from south to north due to later increase in day-length and withdraws of the West-Ice covering the Baffin Bay and Davis Strait during winter (Pavshitsk, 1968, 1972; Jensen et al., 1999; Head et al., 2000). However, duration and extent of the ice cover are related to climatic conditions, and, consequently, onset and development of the spring bloom vary from year to year. In May and June, chlorophyll *a* was concentrated in the relatively cold Polar Water mass. During the spring bloom in May the phytoplankton biomass ($9.8 \pm 3.4 \text{ g C m}^{-2}$) was dominated by diatoms of *Thalassiosira* spp. and *Chaetoceros* spp. (Table 4). In June, a post-bloom situation prevailed on most of Tr3 resulting in a very

low phytoplankton biomass ($0.8 \pm 1.2 \text{ g C m}^{-2}$). However, peak phytoplankton biomasses (3.0 g C m^{-2}) were found at the western part of Tr3 where diatoms of *Chaetoceros* spp. dominated (Fig. 3b). In July pronounced subsurface concentrations of chlorophyll *a* were observed in the upper 50 m of the water column on Tr1, Tr4, and Tr5. In all cases the blooms extend down to the depth of the upper thermocline. The phytoplankton composition of these subsurface blooms was not investigated, but diatoms probably dominated (Nielsen and Hansen, 1999). According to Nielsen and Hansen (1999), subsurface blooms develop after the spring bloom caused by intrusions of nutrients due to temporal mixing of the surface water.

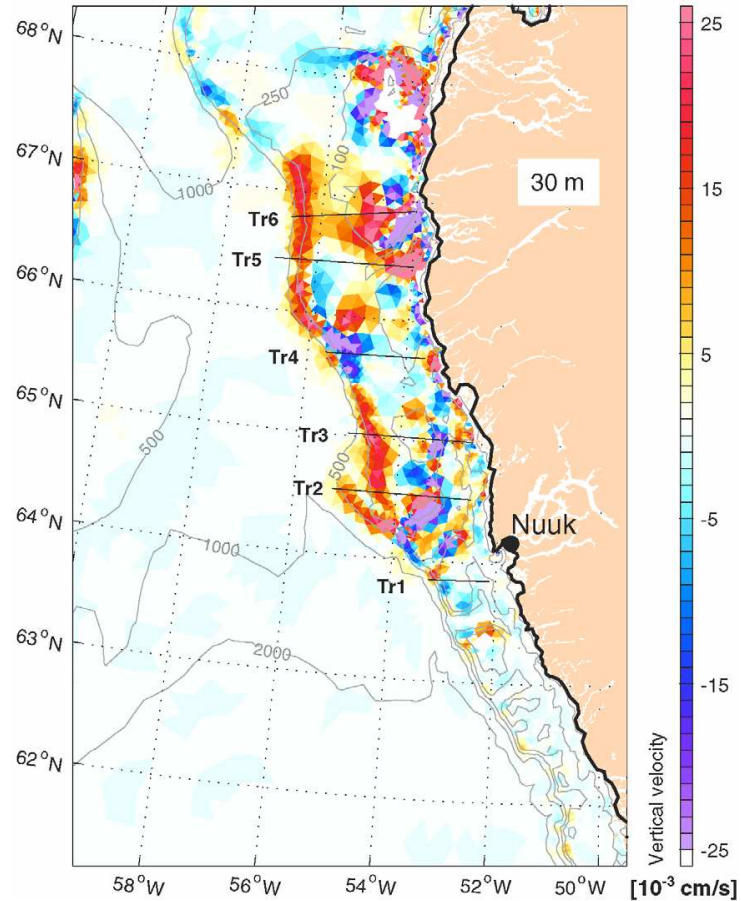


Fig. 8. Locations of potential up-/downwelling areas calculated from the hydrodynamic model. The field is a 6 monthly mean calculated from April to October 2000. Location of sampling transects indicated.

In May and June, high abundance of copepods and invertebrates seemed to coincide with high chl *a* concentrations, which may indicate increased growth and survival in high productive areas. In July, we were unable to find a clear pattern in zooplankton community structure. The lack of a clear pattern is probably caused by the high hydrodynamic activity due to tidal motions, regional pressure response to wind, and wind mixing over the shelf banks with complex topography. The hydrodynamic activity may generate subsurface blooms as indicated in Fig. 3c. Such subsurface blooms may be driven by “tidal

pumps” and may influence zooplankton growth distant from banks where it is generated (Richardson et al., 1998, 2000).

In May, in this study, there was about equal abundance of the three *Calanus* species with stage CI being dominating in *C. finmarchicus* and *C. glacialis*, whereas CII dominated over CI in *C. hyperboreus*. Females of *C. finmarchicus* were abundant, whereas no females of *C. glacialis* or *C. hyperboreus* were observed (maximum female abundance of *C. finmarchicus* was 3458 ind. m⁻² in May). High abundances of CIV and CV of all three *Calanus*

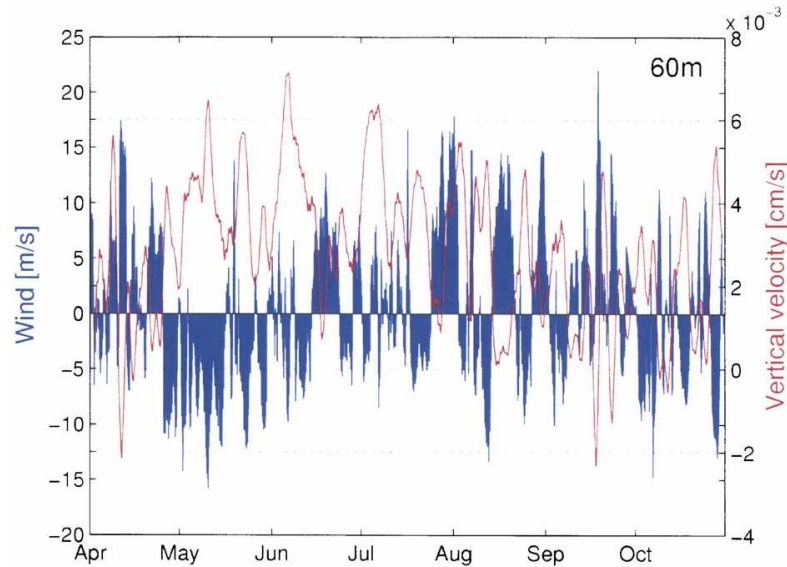


Fig. 9. Wind speeds (blue line) and vertical velocities (red line) at 60 m depth at a station west of Fyllas Bank on Transect 1 (Tr1) (depth to bottom 312 m) from 1 April to 31 October, 2000. Negative wind speeds indicate winds blowing from north to south. Positive wind speeds indicate winds blowing from south to north. Winds from the north result in upwelling as indicated in the figure (positive vertical velocities).

species were observed in July. The abundance and demographic structure indicate that the three species of *Calanus* have developed from CI–CII to CIV–CV between the sampling in May and July.

In Disko Bay, *C. finmarchicus* outnumbers both *C. glacialis* and *C. hyperboreus* by up to a factor of three throughout the year, indicating that this species can reproduce and recruit successfully in ecosystems strongly influenced by polar conditions (Madsen et al., 2001; Niehoff et al., 2002). Madsen et al. (2001) deduced the life cycle of *C. finmarchicus* to be 1 year and at least 2 year for *C. glacialis* and *C. hyperboreus*. This is similar to findings at North Iceland by Astthorsson and Gislason (2003). At Svalbard and in the marginal ice zone of the Barents Sea in northeast Atlantic, Scott et al. (2000) and Falk-Petersen et al. (1999) found *C. finmarchicus* to have a 1 year life cycle, *C. glacialis* 1–2 year life cycle, and *C. hyperboreus* a 3–5 year life cycle. These generation times may fit for *Calanus* in southwest Greenland waters. However, based on only three sampling periods and possibility of undersampling of mature individuals in this study it is impossible to deduce the

development and life cycles of the three *Calanus* species, because one has to take into account advection by currents and possible mixing of different populations over the southwest Greenland shelf.

We found relatively high numbers of *Calanus* nauplii, low numbers of *Calanus* copepodites in stage CI mainly, few females of *C. finmarchicus*, no females of *C. glacialis* or *C. hyperboreus* in the coast and fjord samples in May. We hypothesise that the young *Calanus* stages have drifted into the fjord from offshore areas. The latter is supported by plankton drift simulations using a hydrodynamic model (Fig. 7). According to Smidt (1979) some zooplankton species occur mainly in the inner fjord regions, while others mainly occur closer to Davis Strait, and are uniformly distributed. Among the copepods, *Pseudocalanus* spp., *M. longa*, *O. borealis*, and *M. norvegica* were most frequent in the inner fjord regions, while species of *Calanus* and *Microcalanus* were mainly or exclusively found in coastal regions (Smidt, 1979). MacLellan (1967) found few young stages of *Calanus* in the fjord and suggests that they may have been advected out of the fjord with the runoff melt water. It

seems therefore likely that for example the *Calanus* spp. populations in the fjord are sustained by inflow of progeny from offshore and coastal populations.

4.3. Plankton community structure

During the May survey phytoplankton (diatoms) dominated the plankton community structure of the upper ~100 m whereas during June (and July) heterotrophic organisms were dominating (Fig. 10). In terms of biomass ($C\ m^{-2}$), the three species of large copepods *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* were generally dominating the heterotrophic community. In May and June the three *Calanus* species were of about equal biomass, but in July *C. finmarchicus* was dominating. These findings are similar to findings from the Disko Bay area (Nielsen and Hansen, 1995; Hansen et al., 1999, 2003).

In terms of numbers, the small copepods, *Oithona similis*, *Microsetella* spp., and *Oncaea* spp. were dominating in July in addition to high numbers of pteropods, pelagic snails, and tintinnids. This is similar to Pavshikov (1968, 1972) who describes *O. similis* and pteropods to be dominant taxa over the West Greenland shelf in July–September. The small sized copepods *Oithona* spp., *Microsetella* spp., *Oncaea* spp., pteropods, and tintinnids have been described to be vertical flux feeders associated with marine snow particles, feeding on flagellates, fecal pellets, and various detritus particles (Kjørboe, 1998). The small copepods are important links in marine food webs, serving as major grazers of phytoplankton, as components of the microbial loop, and as prey for ichthyoplankton and other larger pelagic carnivores (Turner, 2004; Simonsen et al., 2004).

The shift in the phytoplankton community from a spring-bloom to a post-bloom community was most likely due to nutrition limitation of the phytoplankton, and the dominance of small autotrophic flagellates in June suggested reliance upon recycled nutrients in the euphotic zone (Poulsen and Reuss, 2002). The spring-bloom biomasses of protozooplankton and heterotrophic nanoflagellate (HNAN) were comparable to biomass reported from Disko Bay (and temperate areas), however the June post-bloom biomasses of protozooplankton and HNAN were lower than earlier reported. Poulsen and Reuss (2002)

suggest that the low June protozooplankton and HNAN biomasses were due to the absence of phytoplankton subsurface blooms and the associated decrease in food availability. The microbial food web most likely played an important role in carbon cycling as indicated by the large standing stocks of primarily bacterivorous HNAN especially during the post-bloom situation in June. We have no information on bacterial biomass from this study. However, Hansen et al. (2003) report the bacterial biomass to vary between 40 and 150 $mg\ C\ m^{-3}$ during summer (during spring-bloom and post-bloom periods) in Disko Bay, at the same level of autotrophic biomass during the spring-bloom as in May in this study. In Disko Bay, Nielsen and Hansen (1995) found an increase in bacterial production after the phytoplankton bloom but no increase in HNAN most probably due to grazing by planktonic ciliates. According to Poulsen and Reuss (2002) it seems unlikely that the low biomass of small autotrophic flagellates presented in June would be able to fuel a bacterioplankton community large enough to sustain the heterotrophic biomass present. However, DOM produced during the bloom may be the resource the bacterioplankton are utilizing during the post-bloom situation in June, which in turn is passed up the food web (Møller and Nielsen, 2000; Poulsen and Reuss, 2002).

In May the phytoplankton biomass and production were able to sustain the heterotrophic plankton community but probably not in June (or July) during the post-bloom situation (Fig. 10). In the latter situation copepod feeding may have been supplemented or dominated by heterotrophic food (ciliates and heterotrophic dinoflagellates) as found in Disko Bay by Hansen et al. (1999). According to Poulsen and Reuss (2002) a skewed size distribution of the heterotrophic dinoflagellates towards smaller species indicated top-down regulation by copepods in the post-bloom period. From a study of microzooplankton grazing of phytoplankton in the Barents Sea during early summer Verity et al. (2002) concluded that it may be that, except during the peak of the vernal bloom, microzooplankton is a major food source for mesozooplankton in the Barents Sea, and the importance of top-down influences on community structure and ecosystem function may be a general feature of these waters. This also seems to be the case in West Greenland waters as indicated by this and recent studies here (Hansen et al.,

1999; Turner et al., 2001). In Disko Bay in June, Turner et al. (2001) found that the dominant part of the total food intake by *Calanus* spp. nauplii in the surface water was composed of ciliates and dinoflagellates, most of which were phagotrophic.

Abundances and biomasses of shrimp larvae were generally low compared to potential prey items (see Table 3). Fish larvae were much less abundant than shrimp larvae and very few Atlantic cod larvae were caught (Simonsen et al., submitted, unpublished data). Larval shrimp food may consist of mainly copepods (*C. finmarchicus*) for larger larvae (ZII–ZVI) although phytoplankton may be important for smaller larvae (ZI–ZII), see Pedersen and Storm (2002) and Harvey and Morrier (2003) for larval shrimp lipid contents, growth, food, and feeding. Studies of larval shrimp feeding, food selection (energy value of food items), and growth rates during larval development in the natural environment are lacking and needed. However, a study of the feeding ecology of larval fish, Greenland halibut (*Reinhardtius hippoglossoides*), and Sandeel (*Ammodytes* sp.), shows the importance of match in abundance and size of copepods for potential larval survival in different areas of their distribution (Simonsen et al., 2004).

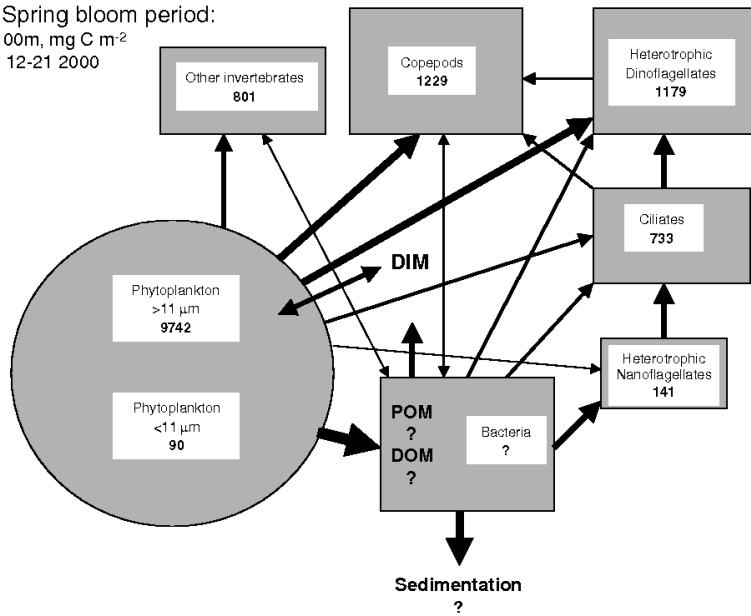
From this study we have no information on primary productivity, carbon transfer routes, and rates in the pelagic food web and this information is needed to calculate realistic carbon budgets and food production for fish and shellfish larvae (Fig. 10). For example for *C. finmarchicus* the variability in specific egg production rate (eggs female⁻¹ day⁻¹) is determined by the variability in phytoplankton production and hence the variability in phytoplankton production may be directly linked to fish productivity by determining abundance of copepod eggs, nauplii, and small copepodite stages which are food for fish larvae and juveniles (Runge, 1988; St. John and Lund, 1996). A recent study by Irigoien et al. (2003) in the Irminger Sea has shown that *C. finmarchicus* may rely on phytoplankton blooms for recruitment from nauplius to the first copepodite stage.

Using a dynamic pelagic food web model in Disko Bay, Hansen et al. (2003) found that warming due to climate change resulted in an early ice break generating more primary productivity, an early spring bloom without large copepods (*Calanus* spp.), and a protozoan dominated microbial food web, transferring the primary production through ciliates and/or dinoflagellates before ingestion by copepods. In such a situation the vertical carbon fluxes were reduced compared to a normal present day situation with a match between primary productivity and ascending from hibernation by large *Calanus* spp. grazers. According to Hansen et al. (2003) it is not known whether copepods will be able to respond to earlier spring blooms by ascending earlier from hibernation. If the ascent is controlled by photoperiod, *Calanus* spp. will not respond to a change in ice cover. If the ascent is controlled by maturation, although at reduced rates, the future hibernation pattern of the large copepods may depend upon the temperature effect of global change at their overwintering depths or possibly their food intake in the previous seasons. If lipid storage determines the ascent, a few years with an early spring bloom would probably reduce their stored reserves due to decreased production, and maybe they would ascend sooner due to starvation.

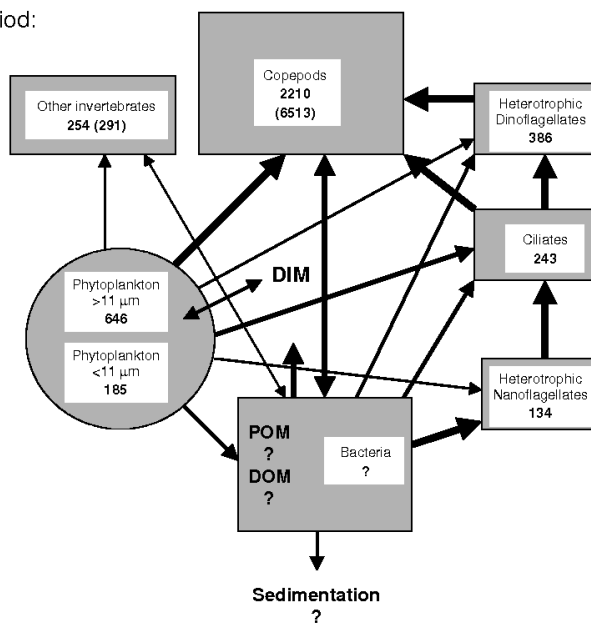
Water temperature exerts a strong influence on the growth rates of zooplankton, and is often thought of as more important than food availability for limiting the growth rates of for example bacteria and copepods (White et al., 1991; Huntley and Lopez, 1992; Hunt et al., 2002). Hence, temperature has a profound effect on carbon transfer routes, rates, and structure of the pelagic food web, and in areas where interannual (and longer-term) variability in temperature is large, as in West Greenland, it is likely to play a major role in variation in copepod production. In the southeastern Bering Sea ecosystem, a sub-arctic ecosystem comparable to the Southwest Greenland ecosystem in this study, coupling between meso-zooplankton and phytoplankton stocks is likely to be particularly weak in years when ice-associated spring blooms dominate the

Fig. 10. Simplified schematic representation of community structure (biomass in mg C m⁻²) during the spring-bloom period in May 2000 (A) and the post-bloom period in June 1999 (B) (data from Tables 3 and 4). DIM—dissolved inorganic material (C, Ca, Si, N, P, ...), POM—particulate organic material, DOM—dissolved organic material, and bacteria were not measured and therefore are unknown. Carbon transfer routes and rates were not measured and therefore the energy transfer and carbon budget are unknown. However, possible carbon and nutrient transfer routes are indicated by arrows and main routes are graduated based on information from Nielsen and Hansen (1995), Hansen et al. (1999, 2003), Poulsen and Reuss (2002), and Verity et al. (2002).

A - Spring bloom period:
0-~100m, mg C m⁻²
May 12-21 2000



B - Post-bloom period:
0-~100m, mg C m⁻²
June 21-30 1999
(July 11-27 2000)



annual total primary production (Hunt et al., 2002; Hunt, 2003). When water temperatures during the spring bloom are cold (<2 °C), as occurs when there is an ice-edge bloom, zooplankton reproduction and population growth will be retarded and the spring phytoplankton bloom will be less vulnerable to control by zooplankton grazing and sink ungrazed to the bottom to support a rich benthic food web. In contrast, during spring blooms when water temperatures are relatively warm (>4 °C) as is the case when an open-water spring bloom occurs in May or June, meso- and microzooplankton reproduction and population growth will occur at higher rates. However, the connection between physical aspects of the marine environment such as wind mixing, sea ice cover, and water temperature and the responses of the biota need to be investigated (Hunt, 2003). The timing of sea ice retreat affects the timing and possibly the fate of the spring bloom, but the ecosystem consequences of different modes of bloom need to be determined. According to Hunt et al. (2002) a decoupling between primary production and zooplankton production may be seen as interannual and interdecadal variation in zooplankton biomass tied to either water temperature or predator demand, but not to annual primary production rates. Conversely, the variability in the flux of phytoplankton to the benthos may be strongly correlated with spring primary production and summer winds. Testing these relationships will require development of a rigorous time series of zooplankton production over the shelf and monitoring with sediment traps (Hunt et al., 2002).

In Southwest Greenland waters there is a need for monitoring programmes of plankton and pelagic food web dynamics over the shelf to describe the lifecycles of copepods and seasonal changes in productivity, community structures, and carbon cycling due to changes in sea-ice, wind, temperature, and hydrodynamics using methods described by Gislason and Astthorsson (1998), Astthorsson and Gislason (2003), Hunt et al. (2002), and Rysgaard et al. (1999).

4.4. Advection and hydrodynamic environment

Our hydrodynamic model simulations demonstrated that wind fields and tidal motions were important in the generation of up- and downwelling, advection,

and retention of plankton over the Southwest Greenland shelf. In particular, the strong tides generate strong and permanent vertical motion which has a large 14 days cycle, as the difference between spring and neap tides is high in this area (Ribergaard et al., 2004). Drift simulations that started in May showed generally northward drift and close to the coast coastward drift as well. Northerly winds prevailed during this period and offshore Ekman drift in the upper layer replaced by water upwelled west of the banks. As the coastward drift is also seen from simulations at 10 m depth (not shown), which is within the Ekman layer, it is most likely caused by the added baroclinic velocity field. During June and July plankton sampled on the westernmost stations on transect Tr1–Tr6 may have high probability of following currents north whereas plankton sampled on stations over and east of the shelf banks may have high probability of being trapped in tidal induced eddies, baroclinic eddies, or hydrographic fronts. However, better spatial and temporal coverage of hydrographical and biological data will be required to confirm this and its biological implications. In particular, the baroclinic forcing has to be treated prognostic in the hydrodynamic model, and the vertical distributions of plankton need to be found from in situ plankton sampling programmes.

Transport by the *West Greenland Current* has strong impact on species distributions, life cycles, and production over the Southwest Greenland Shelf (Petersen, 1966; Pedersen and Rice, 2002; Pedersen et al., 2002; Ribergaard et al., 2004). As the individual life cycle of plankton increases in time the importance of the advection term increases. For *C. finmarchicus* with a life cycle of several months, the advection term may become very important (Pedersen et al., 2000; Sundby, 2000). Micro- and mesozooplankton in the survey area e.g. *Calanus* spp. may potentially have been drifted to the area from South or East Greenland. Head et al. (2000) found high concentrations and productivity of *C. finmarchicus* in Southwest Greenland (south of 62°N). It seems likely that *C. finmarchicus* populations over the West Greenland shelf to a large extent are sustained from the main *C. finmarchicus* distribution area south of Greenland and that the variability in advection transport to Southwest Greenland could have implications for Atlantic cod and northern shrimp recruitment (Sundby, 2000;

Beaugrand et al., 2003; Pedersen and Storm, 2002; Ribergaard et al., 2004).

Our hydrodynamic modeling identified circulations around shelf banks, up- and downwelling areas, and “tidal pumps”. Our findings of hydrodynamic features and their biological implications for plankton growth and pelagic–benthic coupling should be verified and studied by high resolution sampling programmes and process studies of hydrodynamics and biological production using methods described by for example Richardson et al. (1998, 2000). Time series of water temperature salinity, current speeds, and directions from bottom mounted ADCP and moorings located in central positions over the West Greenland shelf could provide data to validate and improve models of ocean circulation and hydrodynamics. Satellite observations and images, for example SeaWiFS, may be useful tools in identification of onset and distributions of surface phytoplankton blooms, sea-ice retreats, polynias, and biological “hot spot areas”, but not in the identification of subsurface blooms or food web structure and functioning. For example subsurface blooms may be important for the overall primary-, secondary productivity and links to fisheries resources (Nielsen and Hansen, 1999; Richardson et al., 1998, 2000). Measurements of fluorescence, phyto- and zooplankton production over the shelf could be monitored using moorings and sedimentation traps as described by Hunt et al. (2002). In “hot spot areas” high resolution models for biological production and simple pelagic food web dynamics should be coupled to the ocean circulation model. Complex models of interactions (Fig. 10) are not easily tractable in hydrodynamical models (Rice, 1995; Carlotti, 2003). It will be necessary to extract from complex interactions, those processes which are the most relevant for the population dynamics of the selected species and for the ecosystem dynamics.

Ways towards predictions of changes in copepods and fish production at higher trophic levels under climate change seem to be a development of coupled bio-physical models (Miller et al., 1998; Fennel, 2001, 2003; Werner et al., 2001) and hybrid recruitment models (Bailey et al., 2003). The value of models that incorporate individual biological model and physical habitat modeling techniques consists not only in increasing our understanding of the link between

spatial and temporal dynamics of zooplankton/fish populations but also in allowing exploration of potential environmental variations in this habitat on these populations (Carlotti, 2003). According to Carlotti (2003) the inclusion of zooplankton community models in whole ecosystem models should end with regional models of zooplankton production and fish recruitment.

One major difficulty in studying the impact of climate change on any species is to know the degree of adaptability of the life cycle in response to environmental variability (e.g. Hansen et al., 2003). A relatively simple but rarely possible approach to estimate the adaptability of a species is to study a population over a long period encompassing important environmental fluctuations. A more feasible approach could be to anticipate (rather than to follow) the local response of a species to the predicted climate changes by development of coupled physical–biological models based on results from studies of the dynamics of populations in different areas along latitudinal environmental gradients. Such models could be adapted, validated, and improved against monitoring of hydrodynamics, the structure, and function of the pelagic food web and variability in year-class strengths of the species in focus (e.g. Pedersen et al., 2002; Bailey et al., 2003).

We believe that development of individual based models coupled to hydrodynamic models will be useful in predicting the ecosystem response to the anticipated warming for example changes in productivity and recruitment of key species such as *C. finmarchicus*, northern shrimp, and Atlantic cod.

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