Horizontal and vertical dynamics of zooplankton and larval fish communities during mid-summer in Disko Bay, West Greenland

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Disko Bay is a highly productive inlet at the border between high- and low-arctic sectors of west Greenland. The physical/chemical conditions in the bay have changed during recent decades, specifically during an inflow event in 1996–1997 that led to increased deep-water temperatures. To further understand the consequences of physical changes to the plankton community in the bay, we examine findings from a field study on mesozooplankton and fish larvae in the areas of Disko Bay and Disko Bank carried out in 1997. We sampled 31 stations over 5 days along four transects and assessed horizontal and vertical distribution patterns, community composition and plankton trophodynamics. Plankton abundance was enhanced near-coast and across the pycnocline, and communities differed between regions. Polar cod (*Boreogadus saida*) and the sandeel (*Ammodytes* sp.) were among the abundant fish larvae. Productivity/growth estimates of key species of copepods and fish larvae showed no apparent relationship to food availability; they reached weight specific values of ~6% day^{-1} for copepods and ~14% day^{-1} for fish larvae. Overall, we found a rich and dynamic plankton community, strongly influenced by the complex hydrography of the area. Thus, changes in physical characteristics of the bay could threaten the resilience of its ecosystem.

KEYWORDS: arctic Greenland; frontal hydrography; plankton communities; growth variability; *Boreogadus saida*

INTRODUCTION

Archived series of observations indicate that oceanographic characteristics off West Greenland have changed markedly during recent decades. Temperature has been increasing in surface waters, and the physical/chemical characteristics in the deeper parts of the water column have also changed (Holland *et al.*, 2008; Hansen *et al.*, 2012). The subsurface characteristics depend on currents flowing along the coast of Greenland, especially a relatively warm and saline branch of the Irminger current (Holland *et al.*, 2008). This flows northward at several hundred meters depth, below colder and less saline surface waters (the Greenland Coastal current and the Baffin Current in more polar areas), and is known to impact greatly the marine life of West Greenland. For example, variations in the West Greenland stocks of cod (*Gadus morhua*) and shrimp (*Pandalus borealis*) have been related to the northward extent of this current and its interfacing with other water masses (Buch *et al.*, 2004). Accordingly, the plankton communities of West Greenland are likely influenced by these long-term oceanographic shifts (Pedersen and Smidt, 2000; Swalethorp *et al.*, 2011). A possible scenario for development of plankton communities along the coast under increasing annual average temperatures would be a progressive latitudinal change, in which boreal communities will move farther to the north, replacing communities of more arctic composition (Slagstad *et al.*, 2011; Swalethorp *et al.*, 2011; Usov *et al.*, 2013). However, little is known about the responsiveness of nearshore planktonic ecosystems to climatic changes, and further insight is needed into the bio-physical linkages.

Disko Bay is situated at latitude 69°N, where West Greenland ecosystems shift from boreal to more arctic character. It is the southern limit of larval polar cod (*Boreogadus saida*) and the northern limit of larval sand eel (*Ammodytes* sp.) distributions (Pedersen and Rice, 2002), and both the boreal copepod *Calanus finmarchicus* and the more northern species *C. glacialis* and *C. hyperboreus* are found there (Nielsen and Hansen, 1995; Madsen *et al.*, 2001). The seasonal variation in the plankton composition and productivity has been studied intensively at the Qeqertarsuaq monitoring station at the entrance to the bay, and these studies emphasize the ecological importance of the *Calanus* spp., particularly their phenological ascent to surface waters that is tuned to the spring bloom of diatoms (Madsen *et al.*, 2001). However, after the descent of the late larval stages of *Calanus* spp. during mid-summer, the relative importance of smaller copepod species and protozooplankton increases. Those organisms are responsible for 90% of the carbon cycling in the late period of the productive season (Madsen *et al.*, 2008).

Further studies of zooplankton and larval fish communities off West Greenland were carried out in June 1996 (Munk *et al.*, 2003). Those studies focused on changes in plankton and fish larval communities across hydrographic fronts at offshore banks, with sampling extending across Disko Bay, Disko Bank and to offshore banks farther to the south. The abundances and compositions of copepods and fish larvae in the Disko area differed markedly from those in the more southern areas of investigation. To obtain more spatially detailed information on the plankton communities in the areas of Disko Bay and Disco Bank, that study was complemented by additional field investigations across the area in June 1997. In the light of the marked oceanographic changes in the area during recent decades, and the specific changes due to increased inflow of Atlantic water in 1996–1997 (Hansen *et al.*, 2012), we examine the findings from the 1997 study here in further detail. The main objectives are: (i) to provide baseline information regarding the structure and dynamics of the Disko Bay ecosystem prior to climate change, (ii) to ascertain the potential linkages between the plankton characteristics and oceanographic features and (iii) to investigate the hypothesis that oceanographic changes observed in 1996–1997 have led to changes in the plankton community of the bay.

METHOD

The 6000-km^2 extent and geographical position of Disko Bay are shown in Fig. 1. Bottom depth reaches 700 meters. Currents flowing north along the coast of West Greenland enter the bay in the southwestern part and leave through narrow straits in the northeast and the northwest.

Transect cruise

During the period 10–15 June 1997, hydrographic measurements and plankton sampling were carried out from the RV "Adolf Jensen" (Greenland Institute of Natural Resources, Nuuk) along four transects extending from the northern to the southern coasts of the bay (Fig. 1). The two westernmost transects crossed skerries, islets and shallow bottoms at the mouth of the bay: "Kronprinsen Ejlands," "Hunde Ejlands" and "Parry Skær" at the northeasternmost sector of Disko Bank. Sampling along these four transects was carried out sequentially, while four additional stations were added between these transects to create a fifth, east-west sampling transect from the innermost shore of the bay out to Disko Bank (Fig. 1). Distance between sampling stations varied from ∼4 to 15 km. At each station, the temperature, salinity and chlorophyll *a* concentration were profiled using a CTD
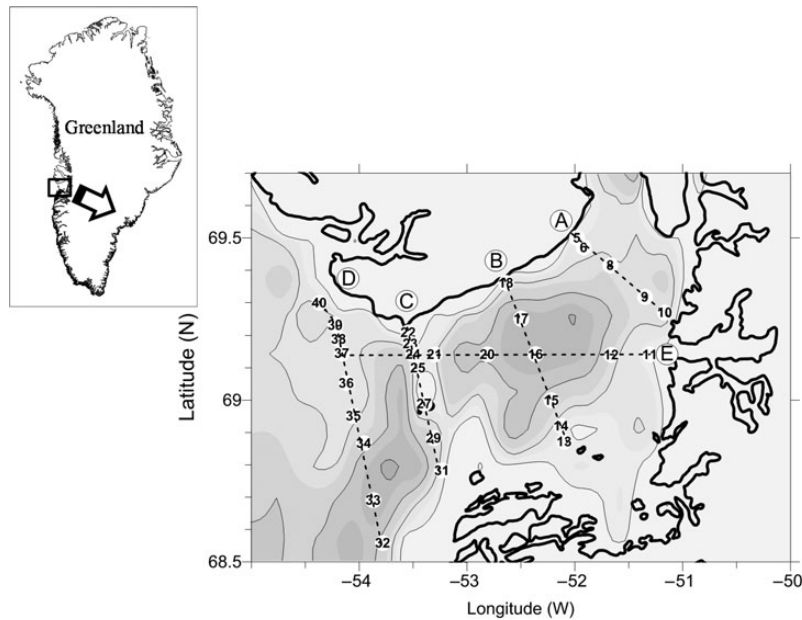
Fig. 1. Disko Bay study area, West Greenland. Bathymetry illustrated by isobaths of 50, 150 and 300 m. Stations and transects are indicated by numbers and letters, respectively. Dotted lines connect stations on the same transects.

(Seabird 25-01) with an *in situ* fluorometer. Measurements were averaged within 50 cm intervals. The depths for biological and chemical measurements were determined based on the water column structure and the fluorescence maximum.

Water was sampled using 5-L Niskin bottles equipped with Teflon-coated springs. The samples for determination of nutrient concentrations (NH_4^+, NO_2^-, NO_3^-, PO_4^{3-} and SiO_4^{3-}) were frozen immediately. Measurements were conducted following Grashoff (Grashoff, 1976) using an automatic nutrient analyzer at the National Environmental Research Institute, Roskilde, Denmark. The detection limits were 0.6, 0.03, 0.06, 0.09 and 0.12 μM for NH_4^+, NO_2^-, NO_3^-, PO_4^{3-} and SiO_4^{3-}, respectively. Duplicate samples for chlorophyll *a* measurements were placed in the dark and filtered within 1 h onto GF/F, 11, 45 and 200 μm Nitex screen filters, then extracted in 96% ethanol (Jespersen and Christoffersen, 1987) and measured using a spectrophotometer (Strickland and Parsons, 1968). A conversion factor for chl *a* to carbon of 43, determined in Disko Bay during the late summer of 1994, was applied (Nielsen and Hansen, 1999).

Mesozooplankton

Mesozooplankton were sampled at each station using a submersible pump (900 L min^{-1}, HOMA-H500) equipped with a flowmeter, a conical net of 50-μm mesh and a non-filtering cod-end. The pump was lowered to 50 m, started and retrieved slowly to the surface. Upon

retrieval, the net was washed down and the zooplankton was preserved in 4% buffered formaldehyde. In the laboratory, a minimum of 400 individuals were identified to species and stage. For each copepodite stage, the cephalothorax length was measured of up to 10 individuals. The biomass was calculated with length-to-weight regressions from the literature (Hansen *et al.*, 1999).

Live copepods (*Calanus glacialis* and *C. finmarchicus*) were collected by a WP-2 net hauled at the depth of maximal fluorescence. When available, individual ripe females of the *Calanus* species were pipetted into 600-mL polycarbonate bottles filled with surface water. The bottles were incubated on board at surface water temperature for 48 h, and the spawned eggs were isolated and counted according to the protocol by Nielsen and Hansen (Nielsen and Hansen, 1995). The prosome length of copepods was subsequently measured, and the specific egg production was calculated from estimated female weight and average egg weight as by Swalethorp *et al.* (Swalethorp *et al.*, 2011).

Fish larvae

Larger plankton were sampled with a ring-net of 2 m diameter equipped with black netting of 1-mm mesh size. The haul was oblique from surface to 90 m depth and back to the surface; at shallower depths the maximum depth was 10 m above bottom. All fish larvae were immediately sorted and preserved in 96% ethanol, while a subsample of 5–10% of the remaining plankton was preserved in 4% formaldehyde. The fish larvae from this

sampling were identified to species, and their standard lengths were measured to $+0.5$ mm. Fifteen to 20 larvae of polar cod from each station were used for growth analysis by microstructure examination of their otoliths. The lapilla were dissected with fine needles under a stereo microscope and transferred to thermoplastic resin on microscope slides. They were then ground with 1-μm lapping film, and their ring structure was investigated using a light microscope ($\times$63 objective) with connected camera and image analysis system. The ring pattern was counted from the prominent inner ring (the hatch check) toward the periphery. Two counts were made on otoliths from each side, and the average of the four counts was used as an estimate of ring number. We assume that the alternating concentration of calcium carbonate, which is visible as the ring pattern, is laid down in a daily rhythm (Bouchard and Fortier, 2011). Growth of larvae was estimated using a nonlinear fit (least squares) to the Laird-Gompertz growth equation. This describes exponential growth at rates that decay exponentially with age (Laird, 1969): $L_t = L_0 \times \exp\{b \times [1 - \exp(-a \times t)]\}$; where L_t is length (mm) at age t (in days), L_0 is length (mm) at first feeding (set as 6 mm; from Fortier *et al.*, 1995), and a and b are model parameters. Based on estimated model parameters, the daily growth rate at a given larval length, GRL$_f$, was estimated as described by Munk (Munk, 1993), and the specific daily growth rate in weight was found from SGRW$_f$ = 3.1 $\times$ (GRL$_f$/L_f) where 3.1 is the exponent in the length–weight relationship (Ponomarenko, 2000).

Diurnal investigation

After the main cruise from 10 to 15 June, an investigation of the diurnal variation in distribution of mesozooplankton and fish larvae was conducted from 20 to 21 June on board the research vessel R.V. Porsild of the Arctic Station at Qeqertarsuaq (Copenhagen University). The station selected for the investigation was at 69°12′ N, 53°32′ W over 250-m bottom depth. Operations were initiated by a CTD cast, followed by mesozooplankton sampling starting at 18.00, 0.00, 6.00, 12.00 and 18.00 (local time). Larval fish sampling started 2 h after the zooplankton sampling and lasted for ∼2 h. Zooplankton was sampled using the pump described above in a sequence of depth strata (m): 0–15, 15–25, 25–40, 40–60, 60–85, 85–150, 150–200. Fish larvae were sampled using a 60-cm diameter Bongo net with nets of 500- or 330-μm mesh. The Bongo net was lowered within a few minutes to 5, 10, 25, 30–40, 60 or 85 m depth, hauled at a speed of 1 m s^{-1} for 15–20 min and then retrieved rapidly. There was no sampling of fish larvae during the second 18.00 sequence. Two depths were only sampled twice: 5 m (at 18:00 and 12:00) and 85 m (at 24:00 and 6:00). The volumes filtered by the

bongo were estimated with a flowmeter in the net opening. We expected low catchability of the gear during launch (the gear was just dropping though the water column) and retrieval (the fast retrieval speed would lead to a standing wave in front of gear), so most larvae were assumed to have been taken from the nominal towing depth. Samples of zooplankton and fish larvae were treated as described for the standard sampling above. The peak depth of the vertical distribution of a given copepod species is described by the center of mass:

CM = ($\Sigma a_j \times b_j$)/Σb_j, $j = 1, \ldots, n$, where a_j is the mean depth of sampling interval j, and b_j is abundance within sampling intervals, j.

Prey preference estimation

Following the cruise for vertical studies, a subsample of 38 polar cod larvae from the 12.00 series was investigated for stomach contents. The stomachs were opened with fine needles, and the contents (which were only copepods) were staged to eggs, nauplii or copepodites, and lengths measured. The log-scale size distribution of all stomach contents for all larvae was compared with the log-scale size distribution of copepods from the corresponding 0–15 m zooplankton sample, and the Chesson size preference index (Chesson, 1978) was calculated according to:

$$\text{Preference} = \frac{(d/p)}{\sum(dj/pj)} \quad j = 1, \ldots, n$$

where d is number of prey items, and p the number of copepods sampled in the respective size intervals, j.

The peak and width of this log-scaled size-preference spectrum were calculated as the mean and SD of the indices. The prey availability at each station was estimated by comparing the preference spectrum and the zooplankton size spectrum. Zooplankton biomass in a given size interval was multiplied by the relative prey preference in that interval, and these weighted biomasses were summed for all size classes covered by the spectrum. This sum expresses the availability to the larvae of preferred zooplankton biomass.

A cluster analysis was carried out using the programme "Cluster" in SAS (SAS Institute®). The result of the cluster analysis is illustrated as a tree with height representing semi-partial r^2, SP-RSQ, values.

RESULTS

Hydrography

The hydrography of Disko Bay varied significantly both vertically and horizontally (Fig. 2). In the north–south vertical sections across the bay, a colder water mass was
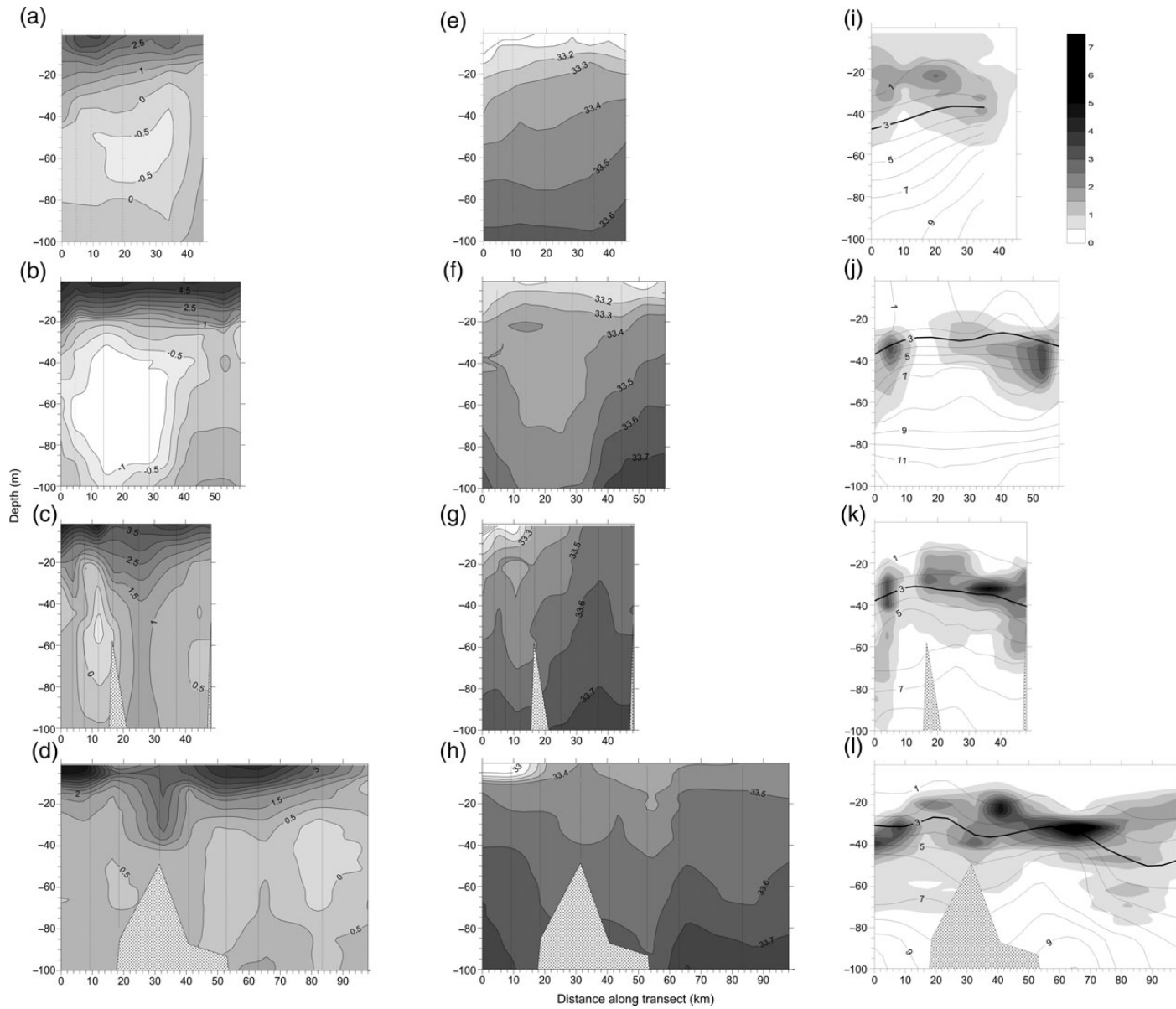
Fig. 2. Vertical sections of hydrography. Columns (a)-(d): temperature (°C), (e)-(h) : salinity, (i)-(l) : nutrients, $NO^2 + NO^3$, (contour lines, kg m^{-3}) and chlorophyll a (shading, mg m^{-3}). Rows (a)-(e)-(i) : Transect A, (b)-(f)-(j) : Transect B, (c)-(g)-(k) : Transect C and (d)-(h)-(l) : Transect D. North is to the left of the transect plots.

apparent at $40-80$ m depth that could be followed from section to section. This water mass, which is below $0°C$ at its core in the central part of the bay (Fig. 2b), was surrounded by warmer surface-, bottom- and coastal- water masses. Measurements at the entrance indicated a divergence of this coldest water mass into two branches on each side of Kronprinsens Ejlands/Disko Bank (Fig. 2c and d). The variation in salinity was not as prominent, but specific patterns were apparent (Fig. 2e−h). A surface layer of relatively low salinity was present over the innermost part of the bay and along the northern coast ($\sim$33.1 in the upper 5 m there), while cold water of intermediate salinity ($33.35-33.45$) occupied a mid-column layer. Below that layer the salinity increased to $\sim$33.7 at 100 m, with a tendency to be more saline in the southern part of the area. The salinity rose to 34.4 at the bottom of our deepest casts (not shown) that extended to 430 m depth.

Nutrients, illustrated by the $NO^2 + NO^3$ content in Fig. 2i−l, were nearly depleted in the surface to $\sim$20 m, and below that we found a broad nutricline from 20 to 40 m. Chlorophyll *a* was most abundant from 20 to 60 m, peaking at $30-35$ m in the central nutricline. Low concentrations were seen at the surface of the innermost part of the bay (Fig. 2i). The nutricline declined somewhat in frontal areas toward the coast and close to the skerries, where we found the greatest vertically integrated chlorophyll *a* concentrations.
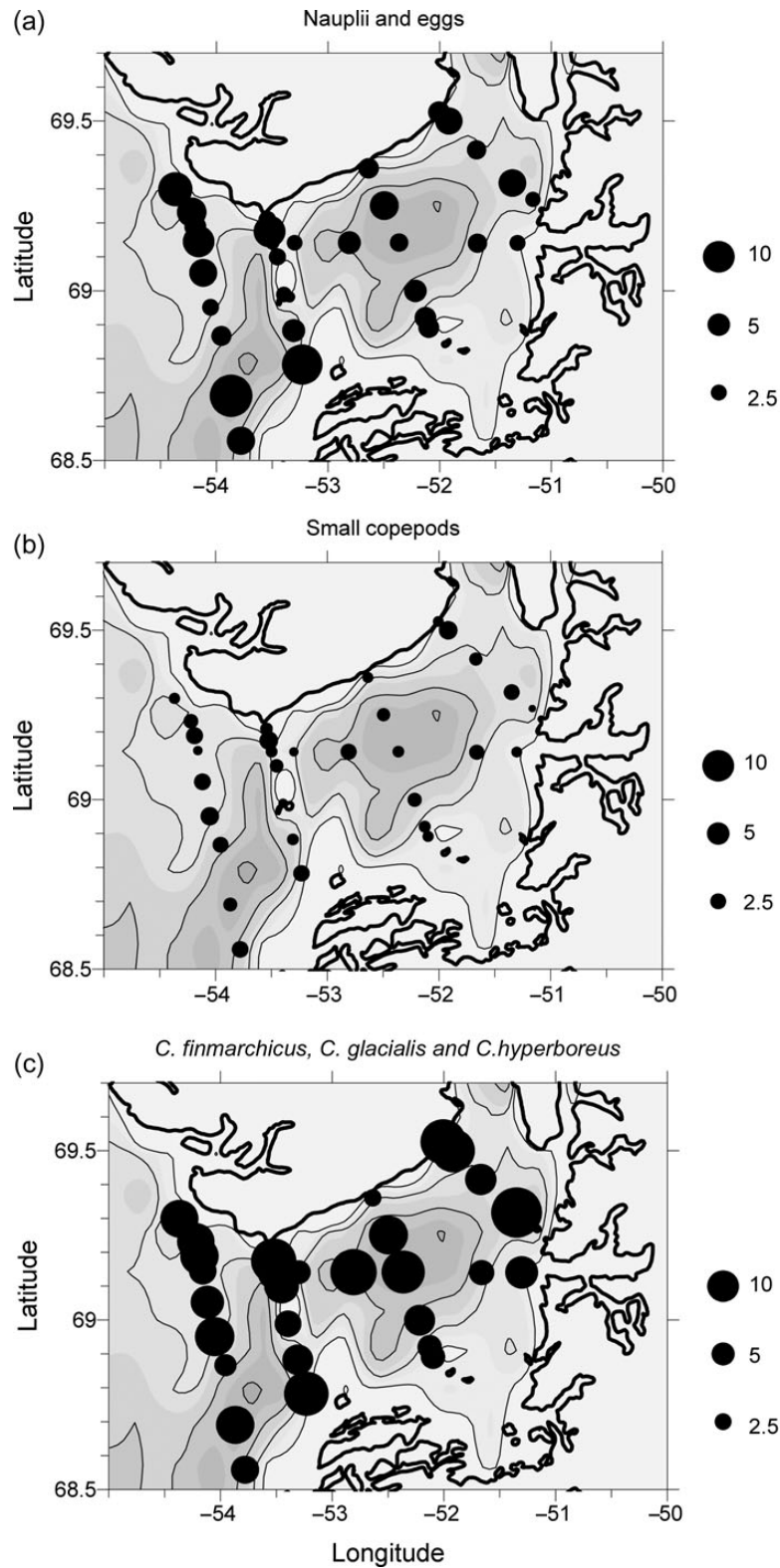
Copepods

Throughout the investigation area, copepods, in all stages, were the most numerous mesozooplankton group (Supplementary Tables SI and SIII), and by far the dominant in biomass (Supplementary Table SII). Among the species of copepods, the overall abundances of the copepodite stages of the *Calanus* spp., *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* were half to a third of the summed abundances of the smaller copepod species (*Oithona* spp., *Pseudocalanus* spp., *Oncaea* sp., *Microcalanus* spp., *Metridia* spp., *Acartia* spp. and *Microsetella* sp.). However, because of their relatively larger sizes, their biomass was five to six times that of the smaller species. The copepod eggs and nauplii ranged in size from $60-200$ and $150-500$ μm, respectively. Due to the relatively large sizes of the majority, they likely belonged to the three *Calanus* species. The egg and naupliar stages were very numerous, and their biomass could reach the level of the respective copepodite biomass (Supplementary Table SII). Accordingly, the copepod biomass is bi-modally distributed across a logarithmic spectrum of sizes. The lower mode was primarily *Calanus* eggs and nauplii, and the upper mode was *Calanus* copepodites (Fig. 3). The other copepod species, of which *Pseudocalanus* spp. had the largest biomass, contributed to the middle part of the spectrum ($0.5-1.0$ mm), but their biomass did not fill the gap between the modes.

The abundance of all copepod taxa was quite variable; however, there were some trends in the distribution of major groups. The nauplii and eggs were most abundant at the entrance to the bay, and they tended to increase in the coastal areas (Fig. 4a). The smaller copepods were more evenly distributed across the area sampled, with a weak tendency toward enhanced abundance closer to the coast (Fig. 4b). All of the *Calanus* species were more abundant at the entrance to the bay than in the bay itself
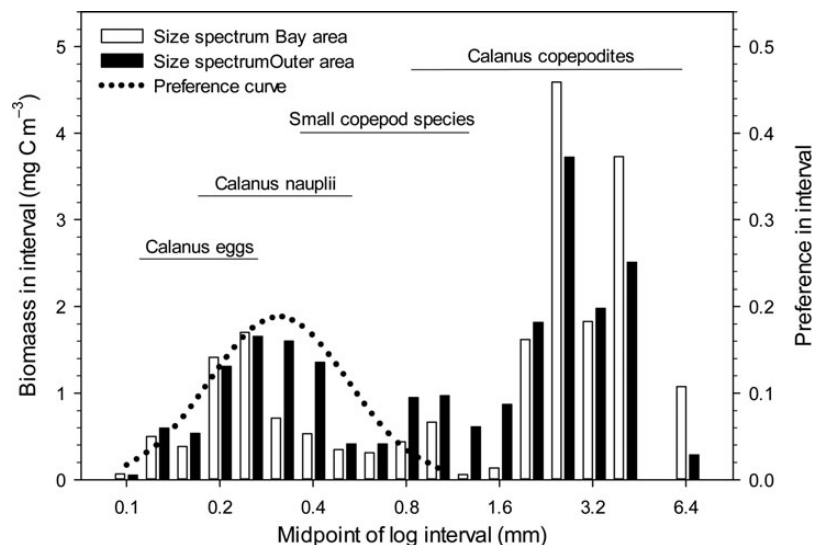
Fig. 3. Log-scaled spectrum of copepod biomasses. Biomass (in mg C m^{-3}) of copepods from inner and outer bay areas accumulated in log-scaled size (cephalothorax length) intervals. Size-ranges of major copepod groups are indicated. Dotted line illustrates the prey-preference spectrum of polar cod larvae as described in the text.
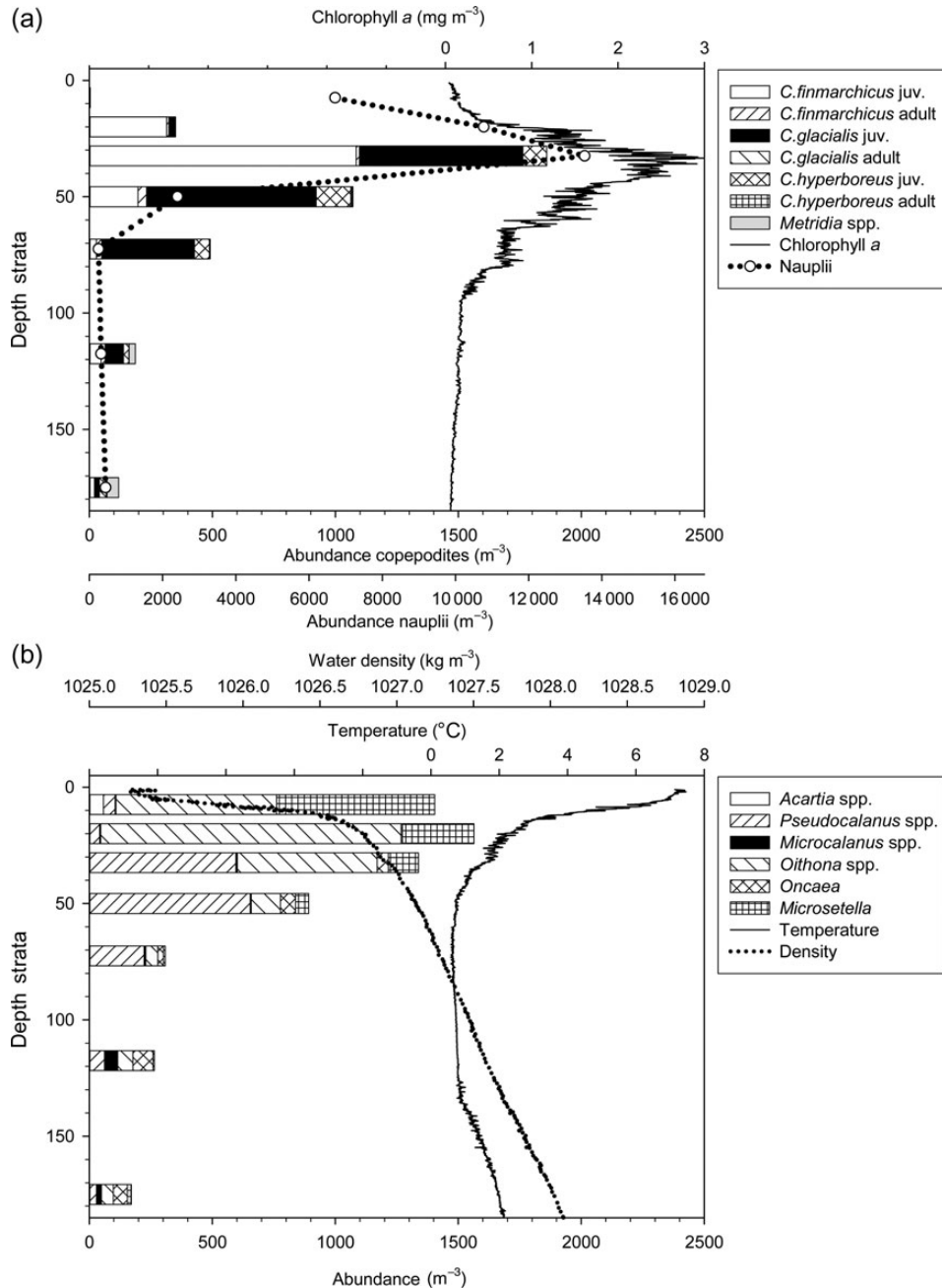
Fig. 4. Biomass distributions of major copepod groups. Biomass in mg C m^{-3} illustrated by area of circles as indicated by example values to the right of figures. (a) nauplii and eggs of all species, (b) copepodite stages of all non- *Calanus* species, (c) copepodite stages of the three *Calanus* species.

(Fig. 4c); this tendency was prominent for *C. finmarchicus* and C. *glacialis*, whereas *C. hyperboreus* was also relatively abundant at the innermost stations (Supplementary Table SI)

The copepod species showed marked differences in their patterns of vertical distribution (Fig. 5). The nauplii of *Calanus* spp. were most concentrated in the 25–40 m stratum, which included the peak in chlorophyll *a* at 30 m

depth. The overall majority of nauplii was found above 40 m. Among the *Calanus* species juveniles, *C. finmarchicus* also peaked in the 25–40 m stratum, while the two other species were most abundant in the 40–60 m stratum and were generally more widely distributed with depth (Fig. 5a). Adult stages of all the *Calanus* species were found deeper than the respective juvenile stages (Fig. 5a and 6a). Among the other copepod species, *Acartia* spp. showed the


Fig. 5. Vertical distributions of major copepod groups. Abundances illustrated by stacked bars (adults and copepodites) and dotted line (nauplii). (a) *Calanus* species and *Metridia*, (b) smaller copepod species. The vertical profiles of fluorescence and water density/temperature are shown in (a) and (b), respectively.

shallowest distribution; almost all specimens were collected in the $0-15$ m stratum. *Microsetella* sp. was also collected at shallow depths, but its distribution extended into the adjacent deeper strata. Farther down the water column we observed abundances of *Oithona* spp., *Pseudocalanus* spp., *Oncaea* spp., *Microcalanus* spp. and *Metridia* spp. peaking in that downward order (Fig. 5 and 6a). These differences in depth distribution of copepod species were generally consistent throughout the diurnal cycle (Fig. 6a). There was only slight overlap of their distributions, and it was apparent that the species were separated into different water masses, as expressed here by the density of the water (Fig. 6b). Our observations indicate very little diurnal migration. There was a tendency for the copepods to concentrate in the centers of their layers during daytime observations ($\sim$6:00 and 12:00), i.e. the individuals at shallower levels moved down, and those deeper moved upward. The vertical migrations of each species took place within a narrow range of water density, $\sim$0.5 kg m^3 (Fig. 6b).

Meroplankton and non-copepod holoplankton

The distribution of non-copepod zooplankton showed no apparent tendencies, but noteworthy high abundances were seen at some stations (Supplementary Table SIII). This was the case for coastal stations 5 and 6, which had relatively large abundances of bivalve and gastropod larvae and particularly of rotifers. The more offshore, northerly stations 17 and 21 had exceptionally high larval abundances ($\sim$100.000 bivalve larvae m^{-3}, Supplementary Table SIII), and Station 21 had $>$2100 polychaete larvae m^{-3}. The southerly stations 29 and 31 exhibited very large abundances of benthic invertebrate larvae and of rotifers. Station 31 had a very high abundance of balanoid larvae ($\sim$3000 m^{-3}). Along transect D at Disko Bank beyond the bay, relatively lower abundances of non-copepod zooplankton were generally observed. However, balanoid larvae and rotifers were abundant at Station 33, and larval bivalve abundance
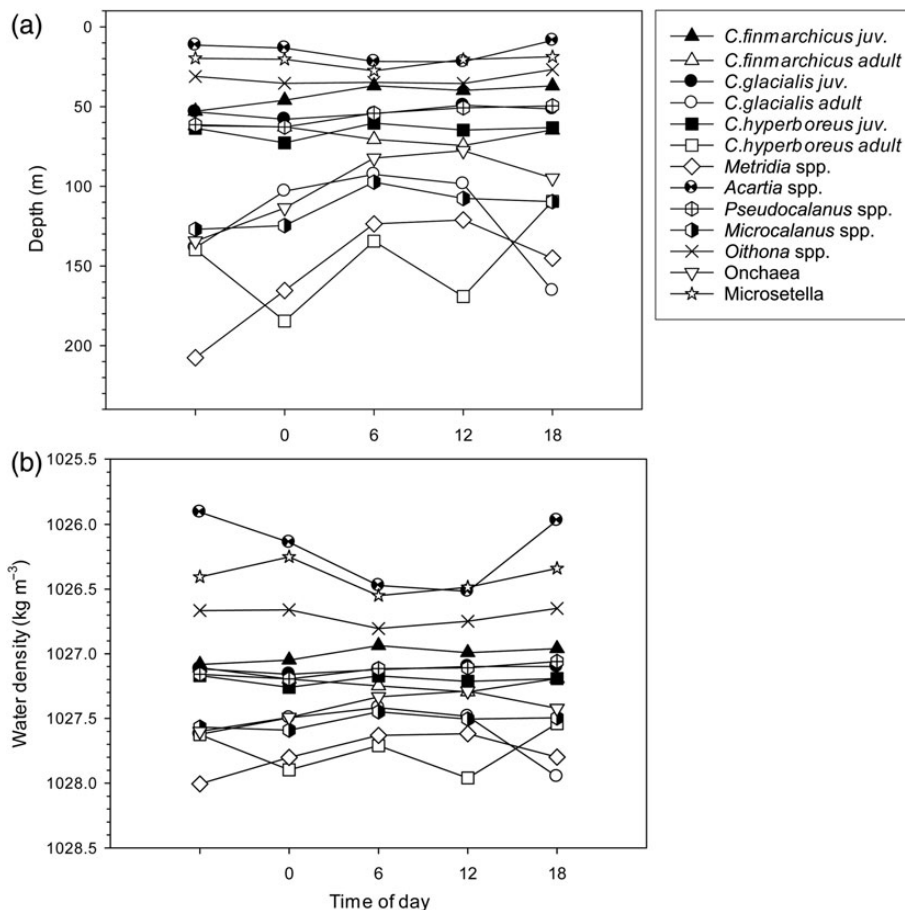
Fig. 6. Centres of mass for major copepod species/stages. (a) centre of mass in the water column (depth in m below surface), (b) centre of mass related to density of water (kg m^{-3}).

was as high as $3041\,m^{-3}$. Most of the non-copepod mesozooplankton were concentrated in the upper 50 m with abundances peaking around the pycnocline (data not shown). This was the case for the dominant groups, i.e. bivalve, polychaete and echinoderm larvae, abundances of which peaked in the $15–25\,m$ stratum. Gastropod larvae and balanoid nauplii peaked deeper, between 25 and 60 m, and appendicularians were predominantly found below 85 m.

Fish larvae

Nine species of fish larvae were caught, of which polar cod (*Boreogadus saida*) and sandeel (*Ammodytes* sp.) were most abundant (Supplementary Table SIV). All fish larvae showed quite wide size distributions with means around 15 mm (Supplementary Table SIV). The spatial distributions differed markedly among species. Some were predominantly distributed in central areas of the bay, e.g. polar cod (Fig. 7a) and Atlantic poacher (*Leptagonus decagonus*) (Supplementary Table SIV), some were more widely distributed, e.g. arctic shanny (*Stichaeus punctatus*) (Supplementary Table SIV), and others were predominantly found in shallow, coastal areas or around the Kronprinsens Ejland, e.g. snakeblenny (*Lumpenus lampretaeformis*) (Fig. 7b), shorthorn sculpin (*Myoxocephalus scorpius*) and daubed shanny (*Leptoclinus maculatus*) (Supplementary Table SIV). Sandeel larvae showed a distinctive distribution highly concentrated at three stations in the southern entrance to the bay (Fig. 7c).

Larvae of five species were sufficiently abundant to allow descriptions of their vertical distribution (Fig. 8). However, sample abundances were insufficient to describe possible diurnal changes, so samples have been averaged for the four sequences. All five species of larvae preferred the part of the water column above the pycnocline (Fig. 8). Sandeel and Atlantic poacher peaked in the 5 m samples, while polar cod were abundant in both 5 and 10 m samples. Arctic shanny was most abundant at 10 m, while snake blenny was mostly caught at 25 and 30–40 m. We tried to avoid contamination of the deeper hauls by surface catches during launch and retrieval, but we cannot exclude the possibility that the few larvae in the 65 and 85 m hauls came from occasional catches nearer the surface.

Distribution of plankton communities

The distributional differences among both copepod species and larval fish species point to differences in plankton communities across Disko Bank and Disko Bay. We analyzed community patterns by a cluster analysis combining the abundance estimates for copepods and larval fish. We included estimates for species shown in Supplementary Tables SI and SIII, except for the least abundant copepod species: *Metridia longa*, *Microcalanus* spp. and *Acartia* spp. The output of the cluster analysis is a tree with branch lengths as semi-partial r^2 values, SP-RSQ (Fig. 9). The first branching at SP-RSQ = 0.24 separates more coastal stations from those more centrally located in the bay and over the bank. The coastal branch separates into the southern bay entrance, the northern bay entrance and the northeastern area. The more offshore stations separate into predominantly eastern versus predominantly western parts of the central area. Beyond that level the subclusters do not show any spatial pattern.

Production and growth of key species (Calanus spp. and polar cod larvae)

The productivity of *C. finmarchicus* and *C. glacialis* was measured by the egg production of females. The prey (phytoplankton) sizes preferred by these species were assumed to be larger than 10 μm (*sensu* Nielsen and Hansen, 1995). The estimates for the two species were significantly correlated across stations ($n = 26$; $r^2 = 0.39$; $P < 0.001$), and their productivity was insignificantly (*C. finmarchicus*: $n = 27$; $r^2 = 0.06$; $P = 0.21$, *C. glacialis*: $n = 26$; $r^2 = 0.04$; $P = 0.31$), related to the abundance of phytoplankton >10 μm (Fig. 10b and d). The egg production estimates showed pronounced spatial variation: the productivity of *C. finmarchicus* was high in the innermost parts of the bay and near the northernmost coast; that of *C. glacialis* was low at all stations outside Disko Bay with an even more pronounced increase toward the innermost stations (Fig. 10a and c).

Prey-size preferences were estimated for polar cod, the dominant larval fish species, based on the investigation of 38 specimens of 18 mm mean size (range 14.5–22.5 mm) sampled at 06:00 ($n = 11$), 12:00 ($n = 16$) and 18:00 ($n = 11$). Most of the prey items were copepod eggs and nauplii, but smaller copepodite stages were also found. A total of 2600 prey items were found in those 38 larvae, the average stomach contents were 75, 55 and 82 items for the groups of larvae sampled at 06:00, 12:00 and 18:00, respectively. Within the size range investigated, the average prey size was not significantly related to larval size, so a common prey-size preference spectrum was calculated for the entire size range. This spectrum peaked at 0.42 mm, which is 2.3% of average larval length. The width of the spectrum (Fig. 3), described by the SD of log-scaled prey sizes, was 0.19. The spectrum was used to estimate prey available in preferred sizes at stations by weighting copepod biomass in size intervals by the relative prey preference in intervals.
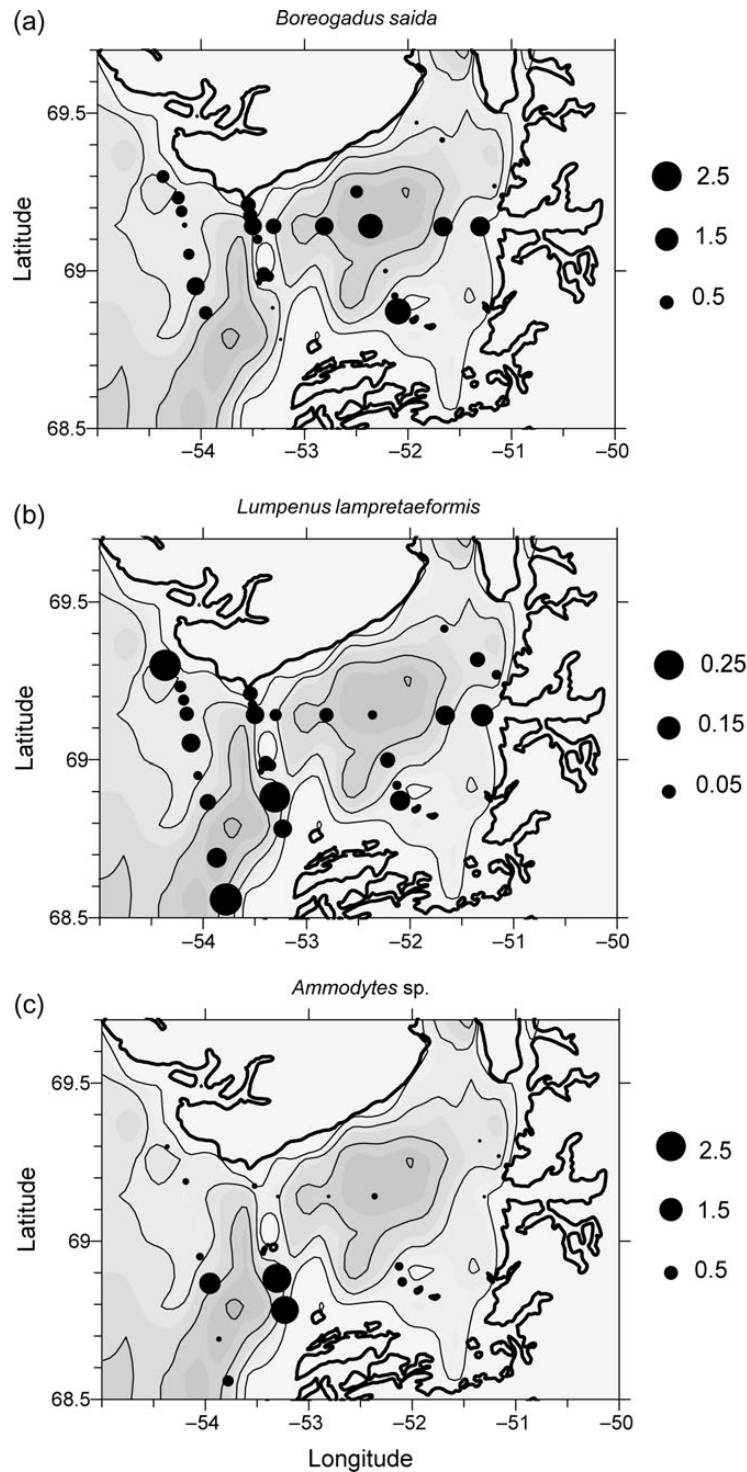
Fig. 7. Horizontal distributions of three larval fish species. (a) polar cod (*Boreogadus saida*), (b) snake blenny (*Lumpenus lampretaeformis*) and (c) sandeel (*Ammodytes* sp.). Area of circles illustrates abundances in no. m^{-2}, as indicated for three values to the right of graphs.

The analysis of growth rates of polar cod was based on the investigation of 330 larvae of a mean size of 10.8 mm and a range of 7.8–17.2 mm. Larval age averaged 15 days, ranging from 7 to 21 days. The growth rate estimates varied markedly among stations, from 13.8% weight increase per day (SGRW) off Kronprinsens Ejland to 8.8% in the western part of the bay (Fig. 11a). The average of growth estimates from the two western
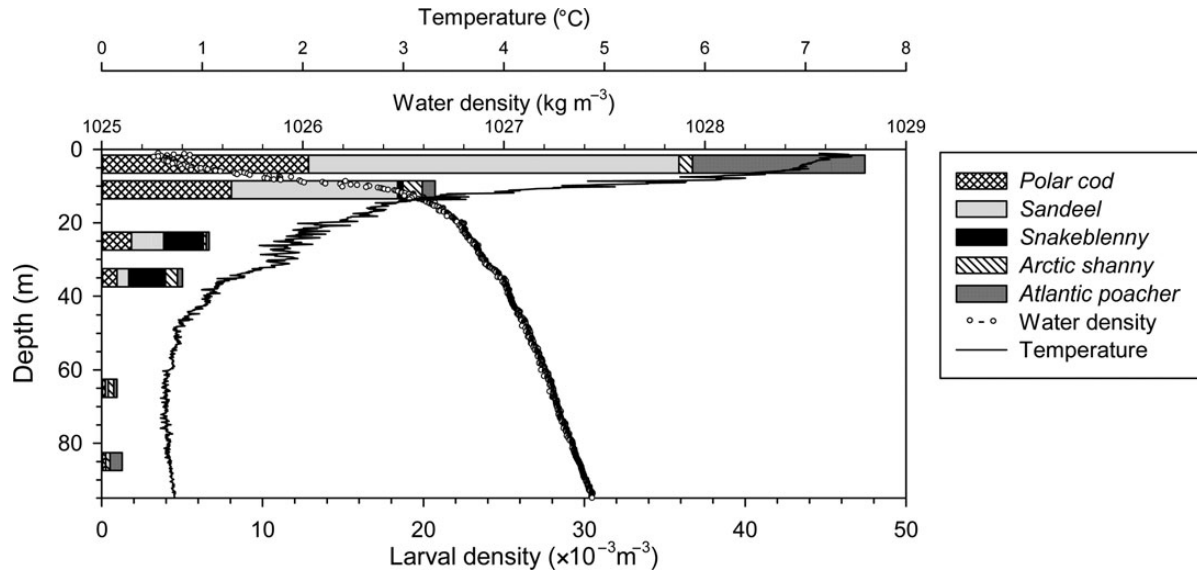
Fig. 8. Vertical distributions of five larval fish species. Abundances illustrated in numbers x 10^{-3} m^{-3} by stacked bars; differences in shading are given in the inserted legend. Water density (in kg m^{-3}) illustrated by a solid line.
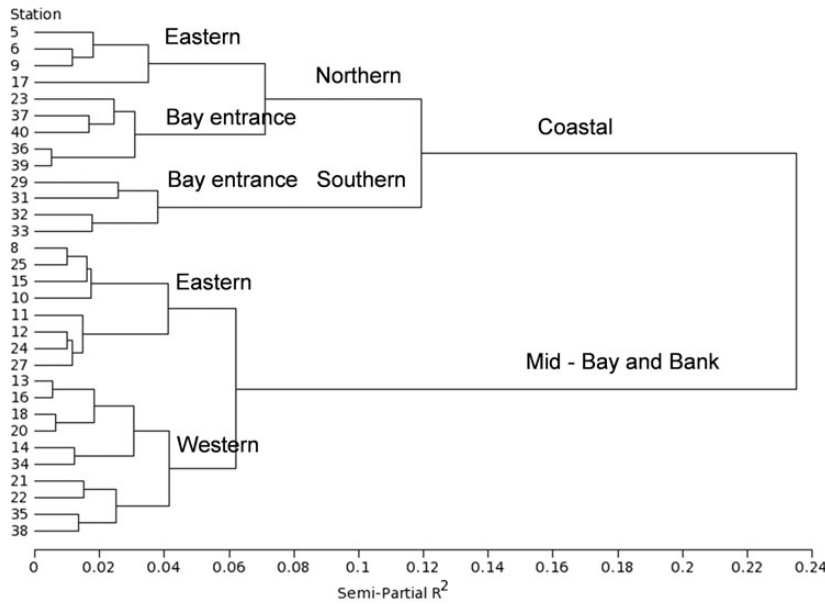

Fig. 9. Distribution of plankton communities. Cluster tree of sampling stations where height is given by the semi-partial r-square values. Interpretations of major branches are indicated (see text).

transects, at the entrance and on the bank was significantly greater (12%) than estimates for the stations in the bay ($n = 20$; $F = 5.7$; $P < 0.05$). Specific growth rates were not correlated to temperature at water depth ~10 m, where larvae were most abundant and temperature ranged from 1.0 to 5.5°C ($n = 19$; $r^2 = 0.04$; $P = 0.39$). Growth rate estimates also did not correlate to prey availability estimated by the weighted copepod prey biomass across the stations ($n = 19$; $r^2 = 0.01$; $P = 0.69$) (Fig. 11b).

DISCUSSION

Hydrography and plankton distribution

The hydrography of Disko Bay was characterized by a cold (<0°C), central water mass and a warm, high-salinity bottom water mass. Hydrographic patterns are strongly influenced by the inflow of West Greenland water, which fluctuates greatly with varying winds and tides (Andersen, 1981). Tidal amplitude is up to 2.8 m, and the spring/neap variations in tidal currents
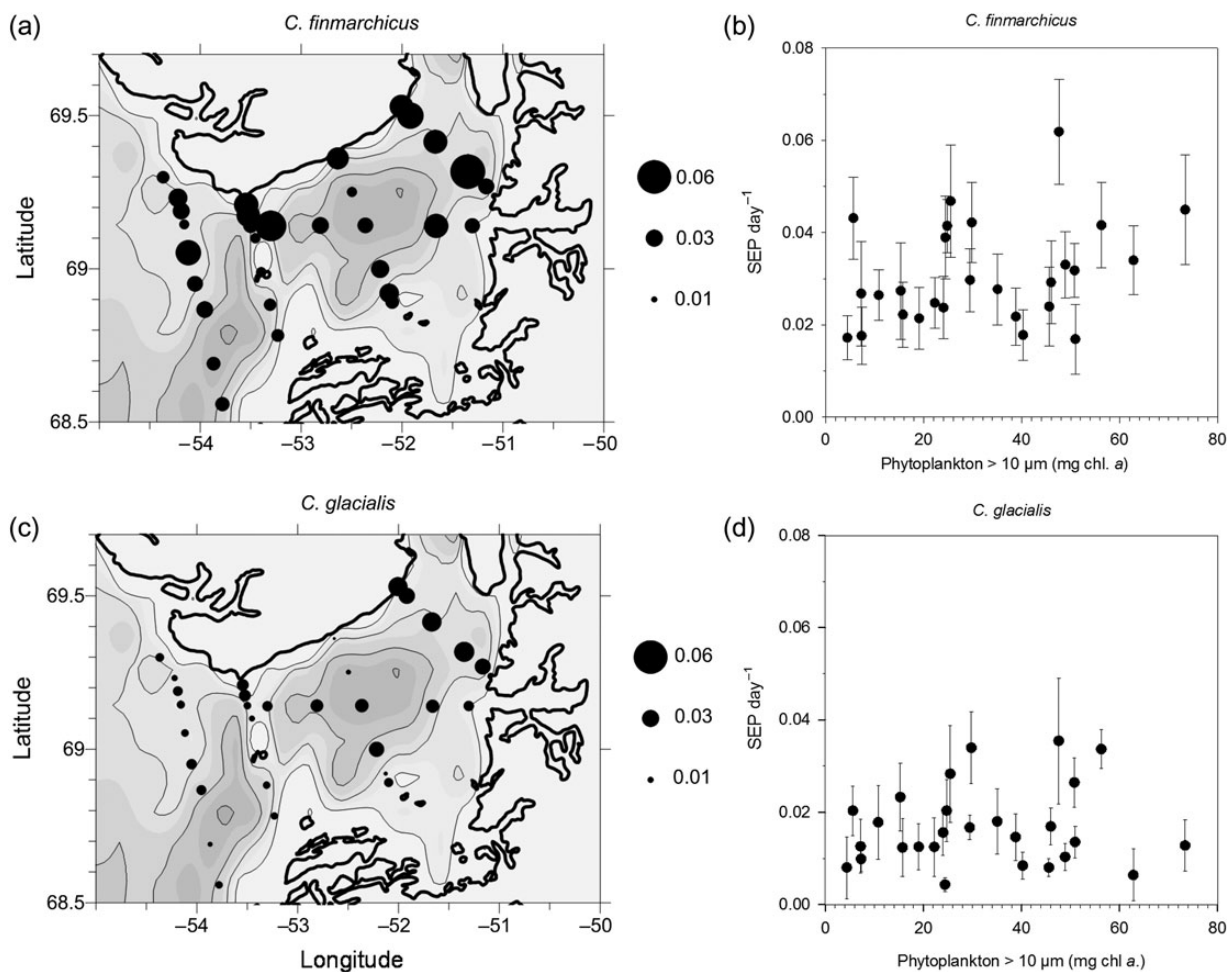
Fig. 10. Productivity of key species of copepods. (a)-(b): *C. finmarchicus*, (c)-(d): *C. glacialis*. (a)-(c): Spatial distribution in estimates of specific production of eggs by weight (SEP, d^{-1}), illustrated by diameter of circles as indicated by example values. (b)-(d): SEP related to chlorophyll *a* of algae larger than 10μm..

contribute to the very variable hydrography where the West Greenland current meets the less saline surface water of the bay (Andersen, 1981). The annual variability of the inflow has been analyzed by Hansen *et al.* (Hansen *et al.*, 2012). Their study showed a major shift in April 1997 when the contribution from the warmer West Greenland Current increased, and they further indicated that this enhanced influx continued to recent times. In accordance, our 1997 measures of salinity and temperature are markedly higher than those from the summer season of 1996 (Munk *et al.*, 2003; Hansen *et al.*, 2012), both for the deep water masses and for the upper strata.

In our planning of sampling positions, we aimed to resolve possible hydrographic fronts in the bay. Frontogenesis could be expected close to the bay's coast (due to coastal currents and tidal mixing) and, therefore, we used relatively shorter station distances (3−5 km) in those areas. We did find frontal characteristics in the coastal areas and in vicinity of the skerries, specifically seen as inclined isotherms and isohalines. However, while plankton at higher trophic levels are often concentrated in frontal zones, (Le Fèvre, 1987), the Disko Bay plankton community showed neither marked enhancement in species abundance nor increased productivity/growth of key species at the near-coastal stations. This could be due to our inability to sufficiently resolve the biological gradients close to the coast, where our hydrographic observations indicated that significant changes could take place within a few kilometers. The oceanography of the bay and its surroundings is, however, very dynamic, and the enhanced primary productivity related to fronts and tidal mixing processes are likely to be dispersed across wider areas of the bay. Hence, food availability to secondary consumers could be consistent across most of the area. Possibly, also, food organisms may be quickly dispersed by currents, benefitting fish larvae across the whole of the bay.
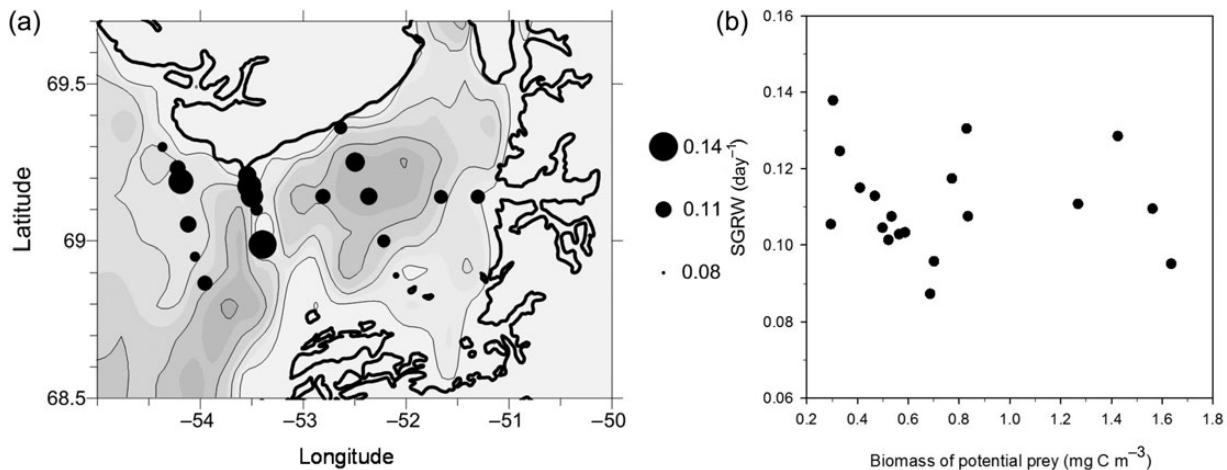
Fig. 11. Growth rate of polar cod, *Boreogadus saida*. (a): Spatial distribution in estimates of specific growth in weight (SGRW, d^{-1}) illustrated by diameter of circles as indicated by example values. (b): SGRW related to estimates of available prey biomass (mg C m^{-3}).

In general, the temporal variability could influence our evaluation of linkages between spatial patterns in physics and biology. Beside the progression of patterns due to dispersion and drift of plankton, potential asynchrony in the trophodynamic aspects could obscure linkages. Hence, when sampling at a given site, the effect of a changed productivity/abundance at one level might not yet be visible at the subsequent trophic level. We cannot resolve this potential influence in the present study; however, historical studies of seasonal development in physics and plankton communities in an area of the bay showed reasonable temporal consistency in measures of plankton productivity or abundance at a given site (Nielsen and Hansen, 1995; Madsen *et al.*, 2008). In these studies, the physical, chemical and biological characteristics were followed by frequent sampling at one site over several months, and while there was an obvious succession in all parameters investigated during the study periods, the findings also suggest reasonably steady conditions for a period of time.

Contrasting with the broad horizontal dispersal of plankton organisms, we found all were strongly aggregated in the vertical dimension. Most of the biomass at all trophic levels was found in the $0-50$ m stratum above the cold water mass. Our observations of shallow distributions of copepods, with limited diurnal vertical migration, agree with those of Sameoto (Sameoto, 1984) in Melville Bay, off Greenland, some 700 km north of the present study area. In his study, only *Metridia longa* and *Pseudocalanus minutus* females were distributed significantly deeper and, as in the present study, he found different vertical stratification of species and stages within the shallow layer. Further observations of shallow distributions and limited diurnal migration of arctic zooplankton were made by Blachowiak-Samolyk *et al.* (Blachowiak-Samolyk *et al.*, 2006), who concluded that changes observed over time were merely a result of habitat changes in water mass distribution and water depth, as well as random patchiness. Our sampling of ichthyoplankton vertical distributions showed a particularly shallow distribution, with dominant species such as polar cod, sandeel and Atlantic poacher predominantly living in the upper 5 m of the water column. Very few other studies of vertical distribution of fish larvae have been carried out in polar areas. In an antarctic fjord in South Georgia, North and Murray (North and Murray, 1992) found fish larvae predominantly in the upper water column ($<140-200$ m), during summer, often very near the surface (<2 m), and a study by Ponton and Fortier (Ponton and Fortier, 1992) of polar cod and sand lance distributions under ice cover in Hudson Bay showed high abundance of larvae throughout the upper 20 m stratum, with insignificant differences in distribution among species and between night and day observations.

Species characteristics

Plankton species community composition varied across the investigated area, primarily due to differences between inshore and offshore and between the inner bay and the skerries and bank areas. Further, the larval fish component showed both boreal and arctic influences: arctic species like polar cod and arctic shanny were found in the central and north, whereas boreal species like sandeel and snake blenny were found more to the south and around the skerries at the bay opening.

Polar cod larvae showed their highest abundance and shortest lengths in the central bay, which indicates that

spawning occurred in this area. Our estimations of larval ages (range 6–23 days, mean 15 days) indicate that hatching of larvae was in late May. Other studies have also found indications of peak polar cod hatching in late May (Fortier et al., 1995: Hudson Bay, Canada; Michaud et al., 1996: Northeast Polynya Greenland Sea; Ponomarenko, 2000: Barents Sea). Sandeel larvae have historically been found in large numbers in the bay, predominantly in the southern part, and their distribution extends as far south as the Fyllas Bank off Nuuk (Petersen and Smidt, 2000). Peak abundances have been found in May–June in the Fyllas Bank area, whereas larval emergence in Disko Bay peaked June–July (Petersen and Smidt, 2000).

Productivity of the area

The observed chlorophyll a values and plankton abundances in the bay were generally high, both when compared with other high latitude areas and to productive temperate areas. A series of high arctic measures of chlorophyll a compiled by Sabbao Rao and Platt (Sabba Rao and Platt, 1984), showed maximal values of 5–8 mg m^{-3} (and a single observation of 40 mg m^{-3}). That is comparable with our measures of up to 8 mg m^{-3} in frontal areas. Our estimates also matched chlorophyll a values in temperate areas well known for high productivity, e.g. the North Sea (e.g. Nielsen and Munk, 1998). The abundances of copepodite stages were of the same order as observed in high arctic waters [Beaufort Sea: Walkutz et al. (Walkusz et al., 2011), Northeast Baffin Bay: Sameoto (Sameoto, 1984)]. Egg production rates measured for the Calanus species during the present study (up to 40 eggs female^{-1} day^{-1}) were within the range of estimates made by Hirche and Kosobokova (Hirche and Kosobokova, 2007) for the high arctic Nansen Basin and the boreal Barents Sea (5–70 eggs female^{-1} day^{-1}). Those authors attributed differences to temperature and chlorophyll a variations. We were not able to show similar correlations in our study.

Our estimates of the growth rates of polar cod (9–14% weight-increase per day) were at the high end compared with other findings for polar cod, i.e. a range of 6–9% day^{-1} for 8–10 mm larvae estimated by Fortier et al. (Fortier et al., 2006) from an age-at-length regression. Though we could not see an influence of temperature on our growth estimates, the surface temperatures experienced by the larvae analyzed by Fortier et al. (Fortier et al., 2006) were much lower than in our study (−1 to 3°C vs. 1 to 5°C), so temperature might explain some of the difference. Another contrast with the study by Fortier et al. (Fortier et al., 2006) is their more offshore sampling site compared with ours. We found significantly enhanced growth rates along our sampling transects in vicinity of

the skerry entrance to Disko Bay. As we could not trace this enhancement to higher abundance of available prey, the conditions there apparently have other beneficial characteristics. The spatial variability in growth rates in the vicinity of the skerries, for example of a 40% increase in attained growth rate (from 10 to 14% day^{-1}) within distances of only 15 km, implies that the frontal hydrography close to the skerries (and the coastal areas in general) could result in strong gradients in biological parameters. The spatial variation in growth rates could be reflected in larval survival probabilities. For example, findings and modeling of Meekan and Fortier (Meekan and Fortier, 1996) and Thanassekos and Fortier (Thanassekos and Fortier, 2012) indicate that a growth rate variation of the observed magnitude can potentially lead to a 3-fold difference in survival. Thus, the magnitude of estimated spatial growth rate variability of polar cod larvae points to strong environmental influence on fish recruitment processes in Disko Bay.

Annual variability

Because the dominant Calanus species spend their diapause in deep water, a change in the temperature of deep water masses for a prolonged period of years would likely influence the general biology of the species and the relative proportions of these species in the plankton community of the bay. Higher temperatures might influence the metabolic rate and lead to changes in diapause durations of the respective species (Saumweber and Durbin, 2006). Further, a change in the salinity profile will change the relative density difference between planktonic organisms and their surroundings, and hence could change their depth of neutral buoyancy. The present estimates for July 1997 showed a 50% lower biomass of Calanus spp. across the central bay than was measured in June 1996 (Munk et al., 2003). However, there were differences in the sampling procedures used in the two studies, and the 1997 sampling occurred closer to the time of the descent by Calanus spp. into near-bottom waters. Hence, this comparison should be taken with caution. Nevertheless, the indication of a significant decline in biomass of Calanus spp., from 1996 to 1997 is supported by findings of Madsen et al. (Madsen et al., 2001) during a seasonal study at a single station (close to our Station 22). In that study, the same sampling procedures were carried out at monthly intervals through 1996 and 1997, and the estimated 1997 abundances of Calanus spp. were 30–40% of those for comparable weeks in 1996 (Madsen et al., 2001).

Differences in larval fish abundances between 1996 and 1997 can also be evaluated from a comparison between the present study and that by Munk et al. (Munk et al.,

2003). The present sampling at stations along 69.15°N (Fig. 1, transect E) coincides with a sampling transect from the 1996 study, and the gear and procedures for fish larvae sampling were the same. The comparison showed approximately the same total abundance of larvae at stations along the transects, but great differences in relative abundance of species. Among the more prominent differences between the years were a 2–5-fold 1997 increase in polar cod and a decline of sandeel to only a fraction of the 1996 abundances. Also, abundances of arctic shanny declined, while snake blenny increased. Other species had approximately the same abundances. The 14-day difference in sampling times between the two investigations cannot explain the marked differences, so it is likely that the larval fish community in the area changed from 1996 to 1997. A potential relative increase in boreal species at the expense of artic species is not evident from this comparison, given the increase in polar cod and the decline in sandeel abundances.

Overall, our observations of generally high, but variable, plankton abundances at all trophic levels and high dynamic rates of key species, point to Disko Bay and especially the skerries at its opening being very dynamic and productive areas. Such richness of plankton is consistent with the high abundances of post-larval fish and the importance of the fishery in the bay. The 1997 investigation was at the beginning of a new era for the bay, an era of generally warmer waters and shorter periods of winter ice cover. More recent observations of the planktonic ecosystem do not indicate dramatic changes in the plankton ecosystem during the period since 1997. However, changes in seasonal appearance of key species have been observed (Madsen *et al.*, 2001; Swalethorp *et al.*, 2011), and it is apparent that the resilience of this important arctic ecosystem is challenged by effects of climate change.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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