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Structuring of zooplankton and fish larvae assemblages in a freshwater-influenced Greenlandic fjord: influence from hydrography and prey availability

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The recent increase in temperature and freshwater runoff in the Arctic will influence the functioning of the plankton ecosystem and hence the life of the fish larvae residing in these areas. Here, we studied the strength of physical–biological linkages and the adaptability of individual larval fish species to changing hydrographical and feeding environments in a sub-Arctic area in Greenland. The study was carried out along a transect covering a wide range of physical conditions from the deep ocean to the icecap in the Godthåbsfjord on the south-western Greenland coast. Along the transect, we identified a series of distinct zooplankton and larval fish assemblages which showed linkage to water mass characteristics, to the presence of frontal structures and to availability of preferred prey. Spawning site location and water circulation was also likely to influence distributional patterns of the individual larval fish species. Larvae were feeding on a variety of prey taxa and sizes; some larval species were generalists, while others were more specialized or fed on alternative prey taxa. Differences in feeding strategies might have the consequence that the species will be differently affected by changes in the plankton community. Accordingly, fish larvae that have a greater feeding flexibility and that are more adaptable to environmental variability may cope better with climate related changes.

KEYWORDS: ichthyoplankton diet; prey preferences; trophodynamics; arctic marine ecosystem

INTRODUCTION

The early stages of most fish species are planktonic and greatly influenced by physical processes associated with features such as hydrographic fronts and currents, and by biological processes linked to, for example, food availability and presence of predators (Bakun, 2006). Furthermore, as different species of fish are differently adapted to physical/biological characteristics, these factors often lead to a spatial structuring of the larval fish assemblage (Cowen *et al.*, 1993; Govoni, 2005). Recently, there has been increased focus on how physical changes affect the Arctic marine ecosystems; such as, the effect of increasing temperature and freshwater runoff on the planktonic ecosystem and early life stages of fish (e.g. Ardyna *et al.*, 2011; Swalethorp *et al.*, 2014).

Physical changes are evident in the coastal and inshore areas of West Greenland and are likely to continue (Kattsov and Källén, 2005; Holland *et al.*, 2008; Rignot *et al.*, 2010; Hansen *et al.*, 2012). Historically, the plankton and fish assemblages of West Greenland have experienced great fluctuations, which have been associated with major oceanographic changes (Pedersen and Smidt, 2000; Pedersen and Rice, 2002; Buch *et al.*, 2004). These changes have predominantly been seen in offshore areas, and were related to changes in the flow of the East Greenland Current. On the contrary, distributional patterns of fish assemblages on Greenland's continental shelf in, e.g. Disko Bay and in coastal areas off Godthåbsfjord, appear less variable (Pedersen and Smidt, 2000). However, the coastal and inshore areas are often strongly affected by freshwater outflow and, especially, the increase in melt-water from glaciers seen during recent decades is likely to change the physical conditions and potentially the ecosystems of these areas (Rysgaard *et al.*, 2003).

The Godthåbsfjord is, with its connected fjord branches, the largest fjord system on the West Greenland coast and receives $\sim 7.6 \text{ km}^3$ of glacial ice water annually (Mortensen *et al.*, 2013). This fjord and the offshore Fyllas Bank close to the fjord entrance can be considered as a model system of physical and biological variability, as this area encompasses a wide array of conditions. The system ranges from the fresh and cold waters in the innermost part of Godthåbsfjord to the Fyllas Bank area which is influenced by relatively warm and saline oceanic water. Studies on zooplankton assemblages along this gradient have shown marked zonation and they point to linkages between hydrography and assemblage composition (Arendt *et al.*, 2010; Tang *et al.*, 2011; Agersted and Nielsen, 2014). Further, historical and recent observations on larval fish abundances in the fjord indicate significant structuring of the larval fish assemblages along the hydrographic gradient

from inner to outer parts of the fjord (Smidt, 1979; Jensen and Rasch, 2008, 2010, 2011).

In the present study, we examined the structure of zooplankton and larval fish assemblages and the feeding ecology of the dominant species across this physical gradient: from the outer slope of Fyllas Bank to the ice edge at the innermost branch of Godthåbsfjord and two other branches less affected by glacial melting. We used the variability in environmental conditions to evaluate the strength of physical–biological linkages and the adaptability of individual larval fish species to different hydrographic and prey environments. Future changes in temperature and glacial melt-water runoff in this area are expected to change the distribution of species along the fjord. Hence, the study provides important baseline information on current assemblage structures for future assessment of the influence of climate change.

METHOD

Study site

Sampling was carried out from 7 June to 22 June 2010 along a 292-km transect off Fyllas Bank to the innermost part of Godthåbsfjord on the Southwest Greenland coast. Along the fjord system transect, the cruise split in three directions; (i) into the Umanap fjord branch located in the south-western part (GF4–U3), (ii) to the eastern innermost part at the glacier in the Godthåbsfjord (GF1–GF12) and (iii) to the innermost part of the fjord branch Kapisigdlit (GF9–K6, Fig. 1). Sampling was done from the research vessel RV Dana (National Institute of Aquatic Resources, Denmark) except station (St) K6 which was sampled from a zodiac. St FB3–FB1.5 were located on the shallow Fyllas Bank, St GF1 was positioned on the sill at the mouth of the fjord system, and St K5 was on a slope leading up to St K6 located within a shallow inner creek (Fig. 1).

Hydrography

Vertical profiles of temperature, salinity and density were recorded by CTD casts using a SBE SeaCat (911 plus) to $\sim 15 \text{ m}$ above the sea floor. Fluorescence profiles were recorded during the early morning using a CTD (SBE 19plus, SeaCat) and a Turner Designs fluorometer (Cyclops 7).

Mesozooplankton

Zooplankton was sampled by vertical hauls using a Hydrobios Multinet (type Mini) equipped with a flowmeter and 50- μm mesh nets. However, at St K6, a WP-2 net 50- μm mesh size equipped with a non-filtering

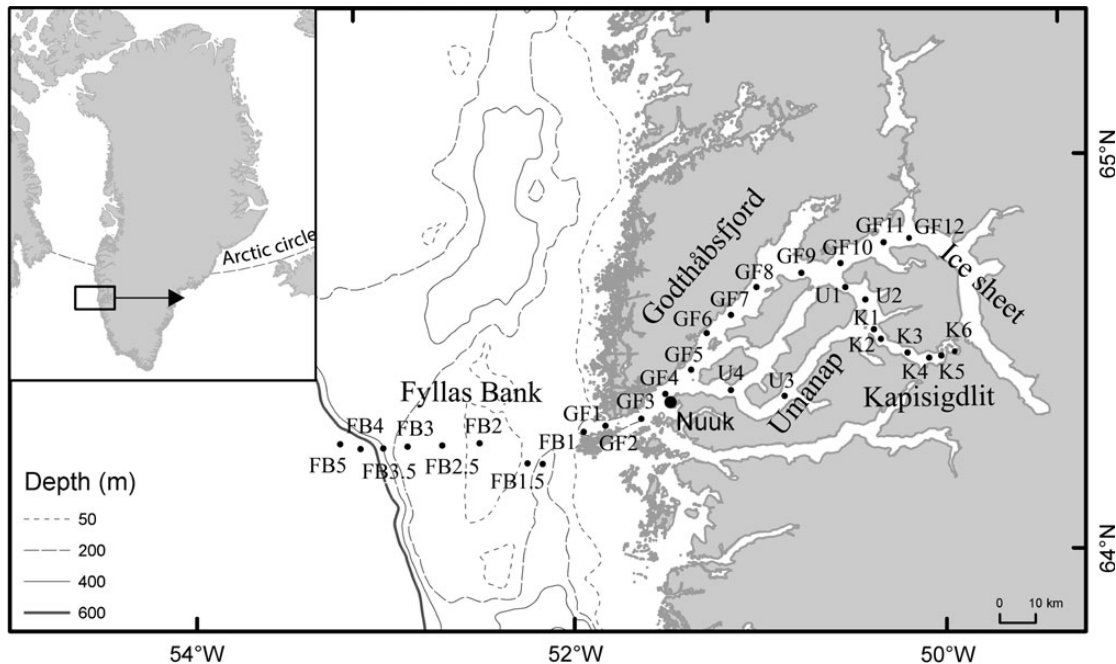


Fig. 1. Map showing the location of sampling stations within the study area.

cod-end was used instead. At St FB3.5, GF1 and K4 sampling was carried out at noon and at midnight in 25-m depth intervals, while at the remaining stations sampling was conducted at various times of day in 50-m depth intervals. The nets were hauled at a speed of $0.2\text{--}0.3\text{ m s}^{-1}$ to the surface from 100 m depth, or at shallower stations from the maximal possible depth. The content was immediately preserved in buffered formalin (4% final concentration). All samples were analysed at the Plankton Sorting and Identification Center in Szczecin, Poland (www.nmfri.gdynia.pl). Samples containing high numbers of zooplankton were split into subsamples. All copepods and other zooplankton were identified to lowest possible taxonomic level and developmental stage (~ 400 per sample). A maximum of 10 individuals of each development stage was length measured while the rest was counted. Biomass of the different zooplankton species was calculated based on length measurements (prosome length for copepodites), and carbon conversion factors from the literature (Supplementary data, Table SI). At St GF3, the 0- to 50-m sample was lost and we assumed abundance and biomass to be equal to the 50- to 100-m strata.

Fish larvae

Larvae were collected using a Bongo net (two circular rings of 60 cm diameter with mounted nets of 300- and 500- μm mesh size) and two different ring nets of 2 m

diameter with 14-m long nets. One ring was equipped with a 600- μm mesh size white net (MIK1) and the other with a $\sim 1500\text{-}\mu\text{m}$ mesh size black net (MIK2). This was done to optimize our abundance estimates as Munk and Nielsen (Munk and Nielsen 1994) documented a higher catch efficiency of small larvae by the Bongo and of large larvae by the MIK. All three net types were fitted with a flowmeter and a CTD (MicroCat SBE 25 SM) to record flow of water into the net together with the haul profiles. They were towed at a ship speed of 2.5 knots. Oblique net tows with Bongo and MIK1 were carried out down to 110 m depth and with the MIK2 down to 140 m or at shallower stations down the maximal possible depth. On St K6 sampling was done by vertical tows using a WP-2 net (200- μm mesh size). Within 2 h of capture, all larvae, with the exception of the very small capelin larvae (*Mallotus villosus*), were sorted out and preserved in 96% ethanol. The whole samples from the Bongo nets and a subsample from the two MIK nets were then preserved in buffered formalin (4% final concentration). As capelin were difficult to sort out on the ship due to their small size, they were sorted later from the Bongo samples under a dissecting microscope. All larvae were identified to genus or species level and all or a maximum of 40 individuals from each sample were length measured (standard length) to the nearest 20–170 μm , depending on larval size. This was done for each taxon in each sample. Fish larvae were soaked in freshwater for ~ 2 min. before measurement to minimize larval bending due to preservation. In total,

2426 larvae were length measured out of 5927 larvae caught. Standard lengths were corrected for shrinkage due to handling and preservation using the following equation from Theilacker (Theilacker 1980):

$$\ln(L) = \ln X_1 + 0.289 e^{-0.434X_1X_2^{-0.68}}, \quad (1)$$

where L is the standard length (mm) prior to handling and preservation, X_1 is the standard length of the preserved larvae and X_2 is the time from death to fixation, which was set to 20 min. in the present study.

The maximum gape of the mouth was calculated using the following equation from Shirota (Shirota 1970):

$$\text{Max.gape} = \sqrt{\text{LJ}^2 + \text{UJ}^2}, \quad (2)$$

where LJ is the lower jaw and UJ the upper jaw length.

The larval fish abundances were calculated as an average between the three types of gear (Bongo, MIK1 and MIK2) and between deployments (at selected stations where nets were deployed multiple times), after applying a gear correction factor. The correction factor was calculated as the ratio between (i) the average abundance of larvae caught by each gear type and (ii) the gear type with the highest abundance, assuming this to represent the true abundance (Table I). To maximize the number of larvae caught by the smaller Bongo, the catches from both nets (300- and 500- μm) were pooled. This was done

Table I: Larval fish catch efficiency of three types of nets

Larval size interval (mm)	Bongo 300 and 500 μm	MIK1 600 μm	MIK2 (black) $\sim 1500 \mu\text{m}$
2-3	1.00 (3)	0.04 (2)	0.00 (0)
4-5	1.00 (18)	0.17 (13)	0.01 (3)
6-7	1.00 (19)	0.16 (20)	0.02 (9)
8-9	1.00 (18)	0.27 (26)	0.05 (12)
10-11	1.00 (18)	0.15 (26)	0.03 (12)
12-13	1.00 (13)	0.17 (20)	0.07 (17)
14-15	0.78 (3)	1.00 (17)	0.42 (17)
16-17	1.00 (9)	0.23 (20)	0.16 (23)
18-19	1.00 (9)	0.21 (20)	0.19 (17)
20-21	1.00 (10)	0.21 (23)	0.16 (26)
22-23	1.00 (10)	0.28 (25)	0.20 (22)
24-25	1.00 (6)	0.26 (12)	0.22 (20)
26-27		0.97 (5)	1.00 (10)
28-29		1.00 (3)	0.97 (5)
30-31		0.86 (5)	1.00 (6)
32-33		0.87 (3)	1.00 (7)
34-35		1.00 (6)	0.27 (4)
36-37		1.00 (2)	0.11 (1)
38-39			1.00 (2)

Values are calculated for every 2-mm larval length interval and expressed as the relative catch efficiency of each net, compared to that with the highest catch. In brackets is the number of larvae caught by each net within each size interval.

for every 2-mm larval length interval independent of species. An average could not be calculated for capelin larvae as they were only sorted from the Bongo nets, and likewise for St K6 samples, as larvae were only caught by WP-2 net.

Gut content analysis

Stomachs were dissected out and the content removed with fine needles under a dissecting microscope from the 10 most abundant larval/post-larval species: redbfish (*Sebastes* spp.), American plaice (*Hippoglossoides platessoides*), sand eel (*Ammodytes* spp.), Atlantic cod (*Gadus morhua*), shorthorn sculpin (*Myoxocephalus scorpius*), Arctic shanny (*Stichaeus punctatus*), daubed shanny (*Leptoclinus maculatus*), alligatorfish (*Aspidophoroides monoptyerygius*), snake blenny (*Lumpenus lampretaeformis*) and capelin (*M. villosus*). The prey were length and width measured and identified to lowest possible taxonomic level. Some prey were partially digested. Here, identification was done based on size, shape and other morphological characteristics. A maximum of 20 individuals per taxon and development stages (e.g. nauplii or copepodite) were measured and the rest counted.

The prey carbon weight was calculated using length-carbon conversion factors from the literature listed in Supplementary data, Table SI. Calanoid nauplii and copepodites were converted using the conversion factor from Hygum *et al.* (Hygum *et al.* 2000) and Breteler *et al.* (Breteler *et al.* 1982) for *Pseudocalanus* spp., respectively. For prey with part of the main body missing (for copepodites only prosome), carbon weight was calculated as the average of other individuals of the same taxa found in the larval gut. In the few cases where no other individuals of the same taxa were present, the length of the remains was used in calculating carbon weight.

Prey size preference model

The prey size preference was determined for nine dominant larval species using the Chesson (Chesson 1978) α -selectivity index in the following equation:

$$\infty_i = \frac{d_i/z_i}{\sum (d_j/z_j)} \text{ for } j = 1, \dots, N, \quad (3)$$

where d_i and z_i are the abundance of prey item i in the gut and environment, respectively, and N is the number of prey length classes considered. We chose logarithmic size intervals based on the theory that biomass should remain constant within equal logarithmic size intervals (Sheldon *et al.*, 1972). Thus, theoretically the larval fish should be presented with an equal number of feeding opportunities within each prey size class (see Pearre, 1986)

which would improve the fit of the model. All prey taxa were therefore divided into 16 logarithmic length classes with the following midpoints: 55, 65, 77, 92, 119, 168, 237, 335, 473, 668, 994, 1334, 1884, 2661, 3758 and 5309 μm , based on total length (although prosome length for all copepodites except *Microsetella* spp.). Prey taxa included were all arthropods positively identified to class or order, depending on the organism, and bivalves, gastropods, polychaetes, rotifers and eggs.

To describe the larval prey size spectra, a Gaussian distribution function was fitted to the relative preferences for each prey length relative to larval length, for each larval species considered. The relative prey length of maximum preference (prey_{max}) and the width of spectra (b) were determined by nonlinear fit to the data. We assumed the frequency distribution of α to be normal over the prey length classes. The relative preference (p) for the i th relative prey length was then estimated from the following equation:

$$p_i = q_i / \sum_{j=1}^N q_j \text{ for } j = 1, \dots, N, \quad (4)$$

where $q_i = \exp\left(-0.5 \times \frac{\log(i) - \log(\text{prey}_{\text{max}})}{b}\right)^2$,

and where i is the prey length/larval length ratio and N is the number of relative prey length classes considered.

Prey availability ($\text{prey}_{\text{available}}$) could then be calculated based on the relative prey length preference of the fish larvae, relative to their own length, for each length class of zooplankton (expressed as biomass) in the environment (z) using the following equation:

$$\text{prey}_{\text{available}} = \sum_{j=1}^N p_{jk} \times z_j, \text{ for } j = 1, \dots, N, \quad (5)$$

where p_{jk} is the relative preference for the i th prey length interval by the k th 2-mm fish larval size group (Simonsen et al., 2006). We assumed that prey length/larval length and niche width remained constant for all larval size groups.

Data analysis

Correlation of larval fish abundance estimates from the three types of gear was tested using the Pearson's Product Moment correlation in SigmaPlot v. 11. Larval abundances were log transformed to meet the assumptions of the test. Analysis of similarities in zooplankton and larval fish species composition between different geographical regions was done on fourth root transformed abundance m^{-2} data, using ANOSIM followed by pair-wise testing in the PRIMER v. 6 statistical software package. Based on the Bray Curtis similarity index, comparison of zooplankton and larval fish assemblage composition

between different stations was done by multidimensional scaling. Comparison between taxonomic composition of prey in the diet and the environment was done using resemblance analysis. Relationship between prey length relative to larval length preferences and larval length was tested by linear regression analysis in SYSTAT v. 13. Differences in prey availability were tested on log transformed biomass data using one-way ANOVA, followed by Tukey's HSD *post hoc* test. Assumptions of normality and homogeneity of variance were tested using Shapiro–Wilks and Levene's test, respectively.

RESULTS

Hydrography and chlorophyll *a*

A cold and fresh surface layer originated from the inland Ice sheet and Kapisigdlit river and covered the area between St GF5 and K6 (Fig. 2a and b). The pycnocline was located at around 20 m depth and became less prominent the further the distance from the inner fjord. At the sill around the mouth of the fjord, strong mixing was apparent (St FB1–GF5). Fronts were established on either side of Fyllas Bank, in the central Godthåbsfjord, at the mouth of the fjord branch Kapisigdlit and south-western Umanap. Surface water temperatures (0–20 m) were higher within Kapisigdlit (5.5–6.8°C) and south-western Umanap (St U4–U3, 5.4–6.4°C), compared with most of the remaining study area. Temperatures were, however, higher in the central Godthåbsfjord (St GF5–GF8), and on both sides of Fyllas Bank (Fig. 2a). Midwater temperatures (20–100 m) were lowest around the bank and near the Ice sheet (1.5–1.9°C), and highest furthest offshore (3.3°C), in the central Godthåbsfjord (GF5, 2.7°C) and in south-western Umanap (2.9°C). Fluorescence, as a proxy for chlorophyll *a*, was highest offshore and close to the glacier and lowest in the central Godthåbsfjord and Kapisigdlit (Fig. 2c).

Zooplankton distribution

The copepod assemblages differed between the different regions of the study area (Fig. 3). *Calanus* spp. and the cyclopoid *Oithona similis* were mainly found offshore around Fyllas Bank, in the coastal area at the fjord entrance and in Kapisigdlit (Fig. 3). *Oithona similis* was also found in Umanap. *Metridia longa*, *Pseudocalanus* spp. and the poecilostomatoid *Oncaea* spp. (which included the genus *Triconia*) had a different distribution and were restricted to the inner fjord. The harpacticoid *Microsetella norvegica* was restricted to the fjord branches Umanap and Kapisigdlit (Fig. 3). Calanoids were almost absent in

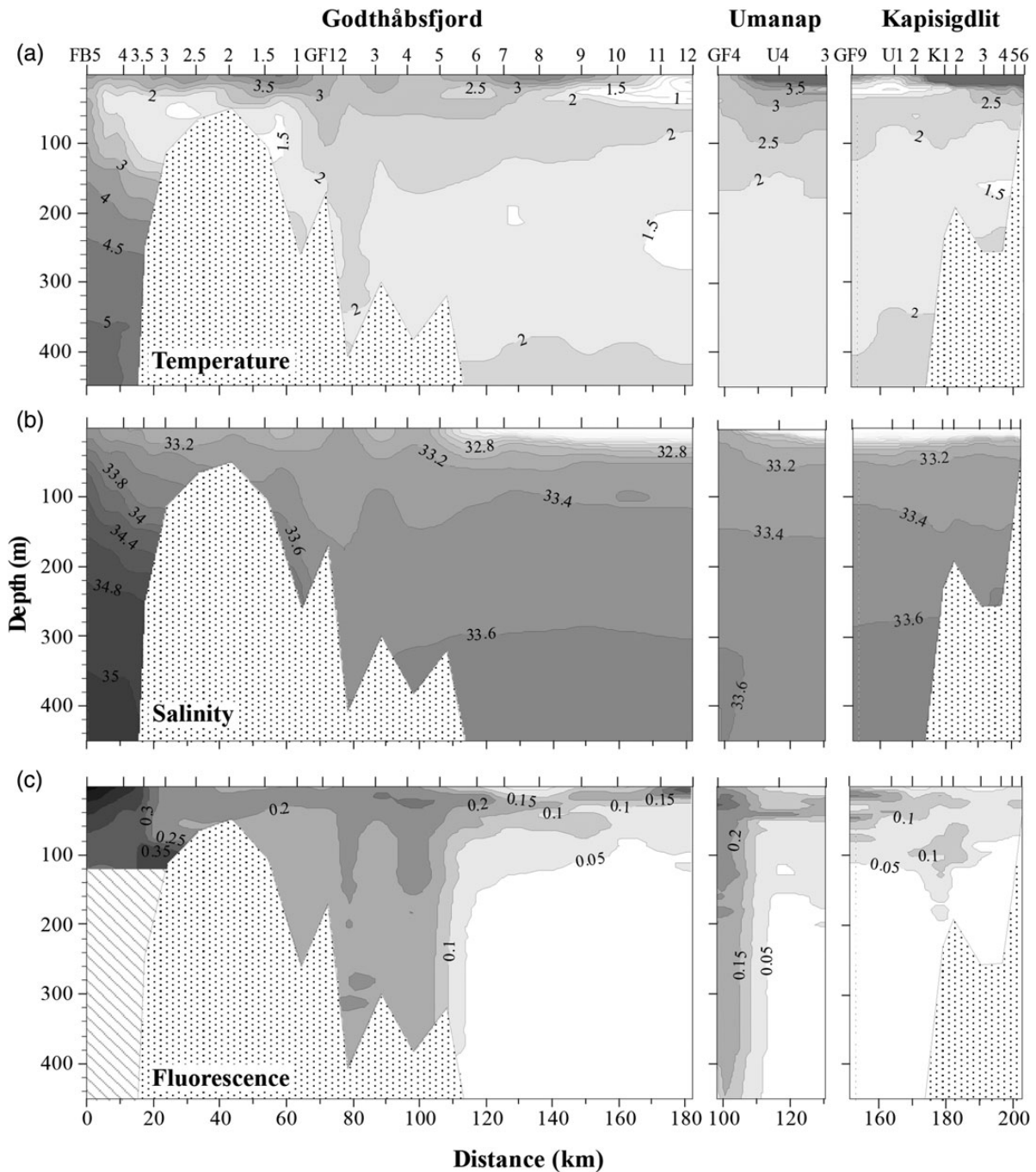


Fig. 2. Vertical distribution of temperature, salinity and fluorescence. (a) Temperature isolines in 0.5°C intervals, (b) Salinity in 0.2 intervals and (c) fluorescence in 0.05 intervals. Distances along transects are for Godthåbsfjord from station FB5, for Umanap from station GF4 and for Kapisigdlit from GF9.

south-western Umanap. In terms of abundance, *O. similis* was the most abundant copepod outside the fjord, while *M. norvegica* dominated inside the fjord (data not shown). Other copepod species not displayed in Fig. 3 only accounted for 0.5% of the total copepod abundance in these areas. Most copepodites, with the exception of

M. norvegica and *Oncaea* spp., had a deeper distribution in Umanap and Kapisigdlit (Supplementary data, Table SII). Nauplii, with exception of *M. longa* and *Oncaea* spp., had a shallower distribution.

Distribution of other zooplankton taxa found in the fish larvae diet is shown in Fig. 4. Interestingly, the cladocerans

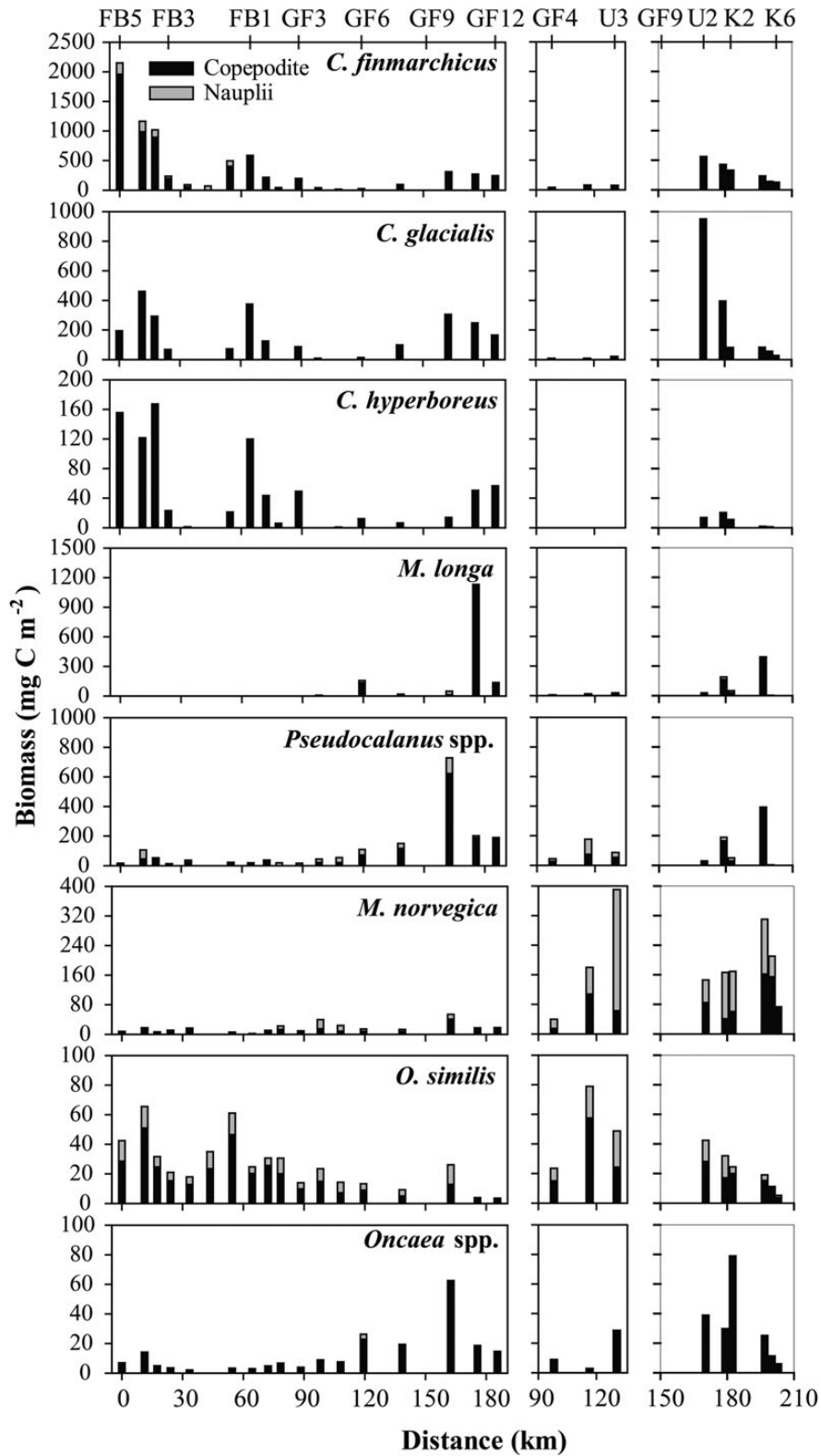


Fig. 3. Biomass distribution of eight dominating taxa of copepods from Fyllas Bank to the Ice sheet (St FB5–GF12), from the central Godthåbsfjord to south-western Umanap (St GF4–U3) and from the Godthåbsfjord to the end of Kapisigdlit (St GF9–K6). *Calanus* spp. nauplii could not be assigned to species and are displayed on the graph of *C. finmarchicus*. Note different scales on y-axis.

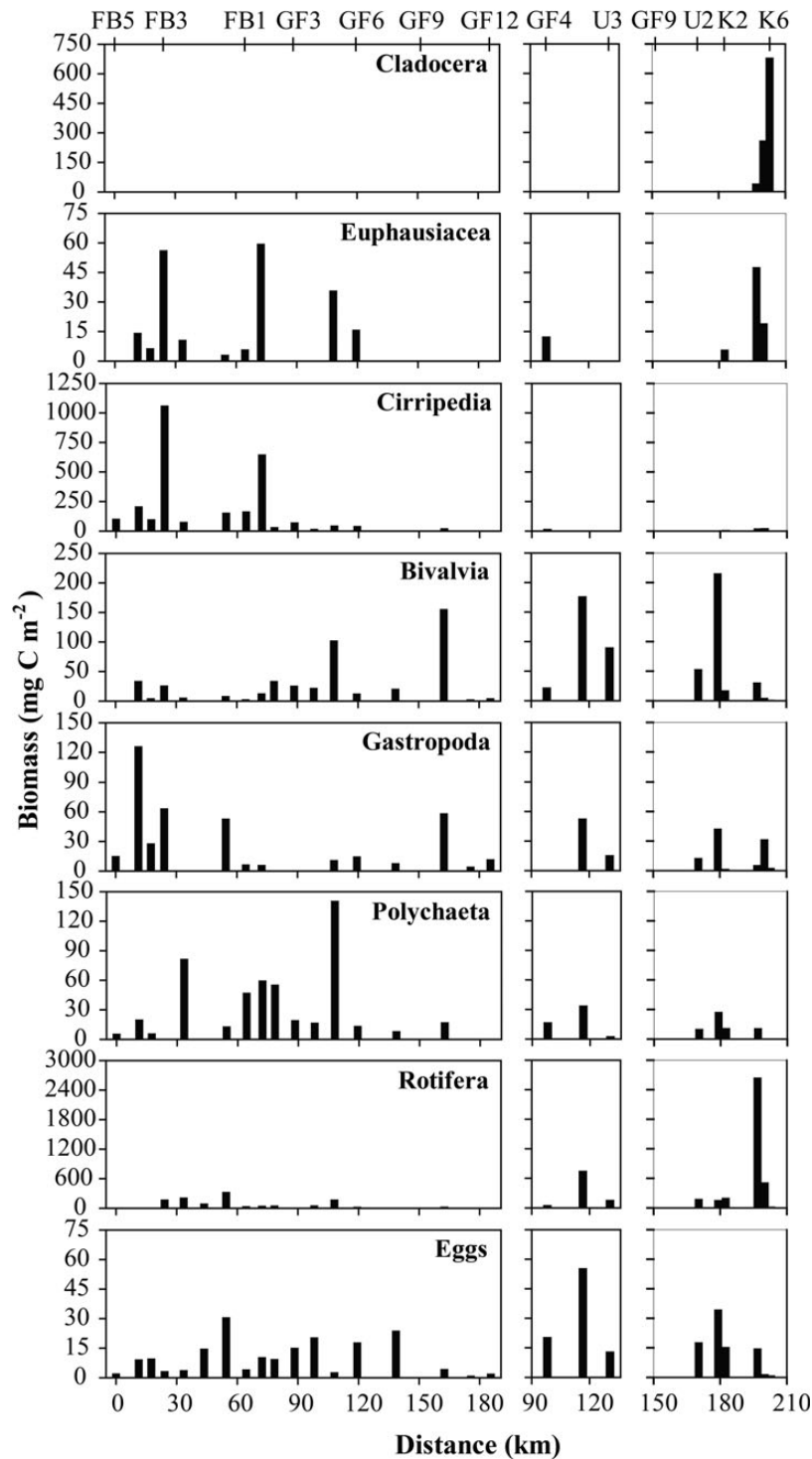


Fig. 4. Biomass distribution of seven dominant non-copepod groups of zooplankton and free spawned eggs from mainly euphausiids and copepods along the three transects. Euphausiacea includes nauplii and calyptopis, but not furcilia as they were not sampled quantitatively by the net. Cirripedia includes nauplii and cypris development stages. Note different scales on y-axis.

(*Podon* spp. and *Evadne* spp.) were only found in the innermost part of Kapisigdlit, which was affected by river outflow. Cirripedia and polychaeta were mainly located

around Fyllas Bank and in the outer fjord, while bivalvia and rotifera were centred on the inner fjord and distributed shallower (Fig. 4, Supplementary data, Table SII).

Larval fish distribution

Larval fish abundances were estimated using three different types of nets. The correlation between the three estimates was positive and significant ($P < 0.002$); however, the nets differed in catch efficiency (Table I). Abundance estimates of larvae in the length range 2–25 mm were on average 26 and 13% for the MIK1 and MIK2, respectively, compared with those from the Bongo net. The estimates from all three nets were therefore corrected for reduced catch efficiency in each 2-mm larval length interval using the correction factors listed in Table I.

Variation in the distribution of the 10 most abundant larval species were observed. Redfish (*Sebastes* spp.), short-horn sculpin (*M. scorpius*) and capelin (*M. villosus*) were restricted to Fyllas Bank, the outer Godthåbsfjord and Kapisigdlit/south-western Umanap, respectively (Fig. 5). The remaining seven species were mainly found within the fjord system but still differed in their distributions (Fig. 5). Less abundant species included snailfish (*Liparis* spp.), Greenland halibut (*Reinhardtius hippoglossoides*), goitre blacksmelt (*Bathylagus euryops*), rock gunnel (*Pholis gunnellus*), Atlantic wolffish (*Anarhichas lupus*) and spotted wolffish (*Anarhichas minor*). Snailfish were widely distributed, while the other species were mainly found between Fyllas Bank and the central Godthåbsfjord (St FB5–GF8). Few species were present and in low abundances in the inner part of Godthåbsfjord close to the Ice sheet.

The length frequency distribution differed among the larval species (Fig. 6). American plaice (*H. platessoides*) larvae were generally the smallest while snake blenny (*L. lampraeformis*) was the largest. Larval length generally increased with distance from Fyllas bank for redfish, and with distance from Fyllas Bank and Godthåbsfjord for Atlantic cod (*G. morhua*), American plaice, Arctic shanny (*S. punctatus*) and alligatorfish (*A. monopterygius*) (data not shown). Capelin, sand eel (*Ammodytes* spp.) and daubed shanny (*L. maculatus*) were longest in Godthåbsfjord and shortest at Fyllas bank and in Kapisigdlit.

Fish larvae diet and prey size preference

Differences in stomach content were observed between the different larval species. In terms of numbers, eggs, bivalve larvae, copepod nauplii and copepodites generally accounted for most of the diet (Fig. 7a). In terms of biomass, calanoid nauplii, copepodites, euphausiid calyp-topsis/furcilia and cladocerans were the most important prey (Fig. 7b). Calanoid nauplii contributed most to the diet in the smaller larval species, while calanoid copepodites contributed most in the larger species (Fig. 6 and 7b). Alligatorfish, daubed shanny and shorthorn sculpin

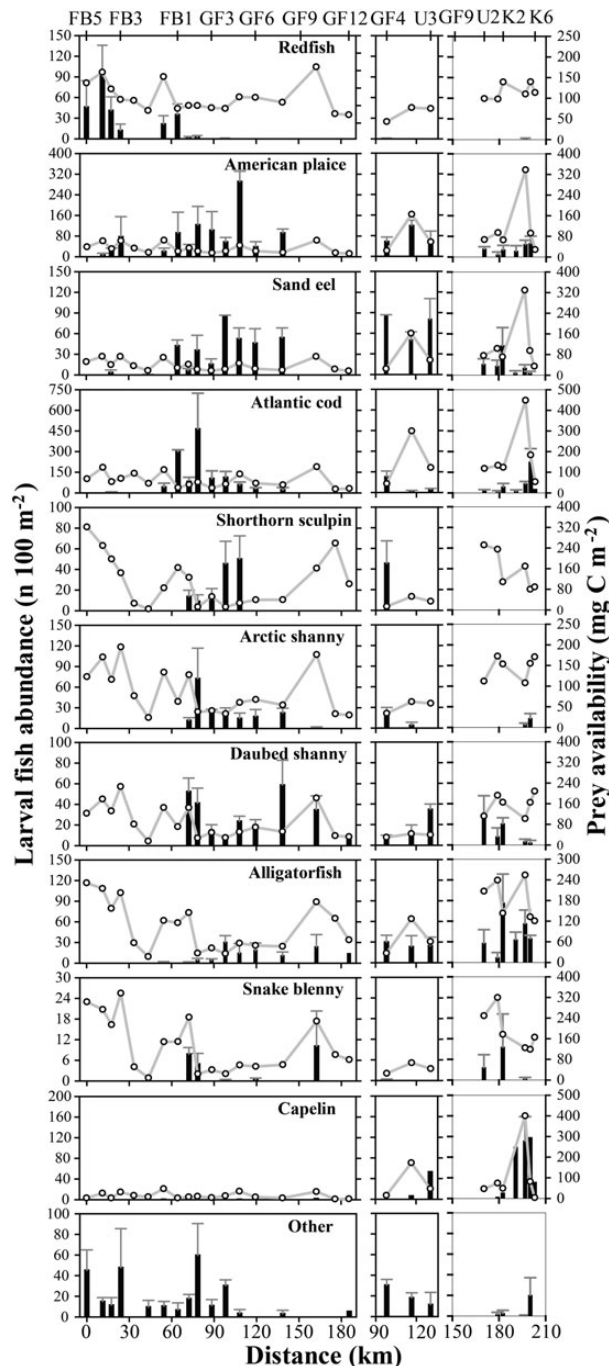


Fig. 5. Abundances per 100 m² of the 10 most abundant species of larval fish (bars) along three transects within the study area (\pm SE). “Other” is the sum of 12 minority species. Lines display the prey availability (mg carbon m⁻²) to each of 10 larval species, calculated from their specific prey size spectrum. Note different scales on y-axis.

differed most from the other larval species in terms of diet, with bivalves, gastropods, polychaetes and/or euphausiids being important prey (Fig. 7b).

Resemblance analysis revealed no significant correlation between prey species composition in the diet and the

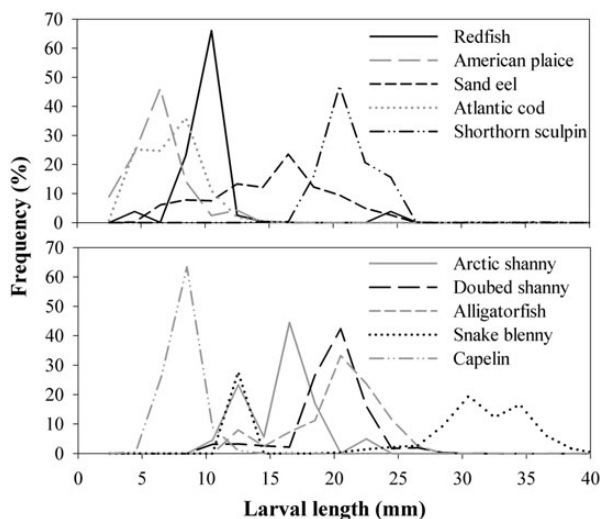


Fig. 6. Length-frequency distribution of 10 dominating larval species based on 2-mm length intervals (standard length).

environment for Atlantic cod, daubed shanny and snake blenny (Table II). However, there was a significant resemblance for all other species where the species composition in the environment explained 19–49% of that found in the diet (not including capelin). This relationship was also supported by the intraregional diet comparisons for most larval species (Fig. 7). For instance the diet of daubed shanny was very similar between regions, while American plaice, sand eel, Atlantic cod, Arctic shanny and alligatorfish differed substantially (Fig. 7b). For species preferring larger prey, the regional difference in diet was mainly due to a high contribution of cladocerans to the diet in Kapisigdlit, where these were very abundant (Figs 4 and 7b). Interestingly, daubed shanny did not exploit the abundant cladocerans. The contribution of euphausiacea also accounted for much of the regional differences. Biomass of polychaetes in the diet is underestimated as most found seemed large based on body width, but were too degraded to length measure.

Clear differences were observed in preferred prey length relative to larval length between the different species. Redfish, Atlantic cod and shorthorn sculpin preferred relatively larger prey, and American plaice, sand eel and snake blenny preferred relatively smaller (Fig. 8; Table II). The width of the prey size spectrum was much greater for American plaice, sand eel, shorthorn sculpin and alligatorfish, compared with the other species (Fig. 8). The preferred prey length for shorthorn sculpin may be slightly overestimated due to difficulties quantifying large zooplankton *in situ* due to use of a small plankton net. Too few prey items were found in capelin to obtain a fit, and we assumed equal preferences across the prey length classes found in their stomachs (0.1–3.3% of

larval length, data not shown). The species-specific differences in preferred prey length corresponded to differences in mouth size relative to larval length (Table II). Furthermore, sand eel and snake blenny were ingesting narrower prey relative to mouth gape. Generally, the relationship between prey width and mouth gape did not change with larval length, but for redfish, Atlantic cod and Arctic shanny, the relative mouth size did increase with larval length (data not shown).

Prey availability

For each larval species the prey availability was calculated from the preference for each relative prey length class. This was done for each 2-mm size group and a population average was estimated for each station, assuming that the overall length frequency distribution displayed in Fig. 6 was representative for each station. Our assumptions of constant prey length relative to larval length preference and niche width (calculated as the standard deviation) across different larval size groups, were generally supported by a linear regression analysis. The analysis showed no significant relationship between the preferred prey length/larval length. This was true for all species except sand eel and Atlantic cod which did not meet the assumptions of the test ($P > 0.05$). The analysis on niche width showed no significant relationships either ($P > 0.05$) with the exception of alligatorfish that widened its feeding niche with increasing larval length ($P = 0.03$). Arctic shanny and sand eel did not meet the assumptions of the test. Inspection of data from species that did not meet the assumptions revealed no changes in preferred prey size or niche width with increasing larval length.

For larval species preferring larger prey, availability of prey was highest in the frontal zones around Fyllas Bank, close to the inland Ice sheet (inner part of Godthåbsfjord) and in Kapisigdlit (Figs 5 and 2, Table III). For larval species preferring small prey, availability was highest in Kapisigdlit and Umanap. Differences in prey availability were tested between five geographic regions of the study area: Fyllas Bank (St FB5–FB1), Godthåbsfjord (St GF1–GF8), Ice sheet (St GF10–GF12) close to the glacier, Umanap (St U2–U4) and Kapisigdlit (St K1–K6). Significant regional differences in prey availability were found for American plaice, sand eel, Atlantic cod and alligatorfish (Table III).

Zooplankton and larval fish assemblages

The study area contained different zooplankton and larval fish assemblages, revealed by dissimilarities in species abundances (Fig. 9). For zooplankton St FB2 and K6 differed substantially from all other stations. Lower

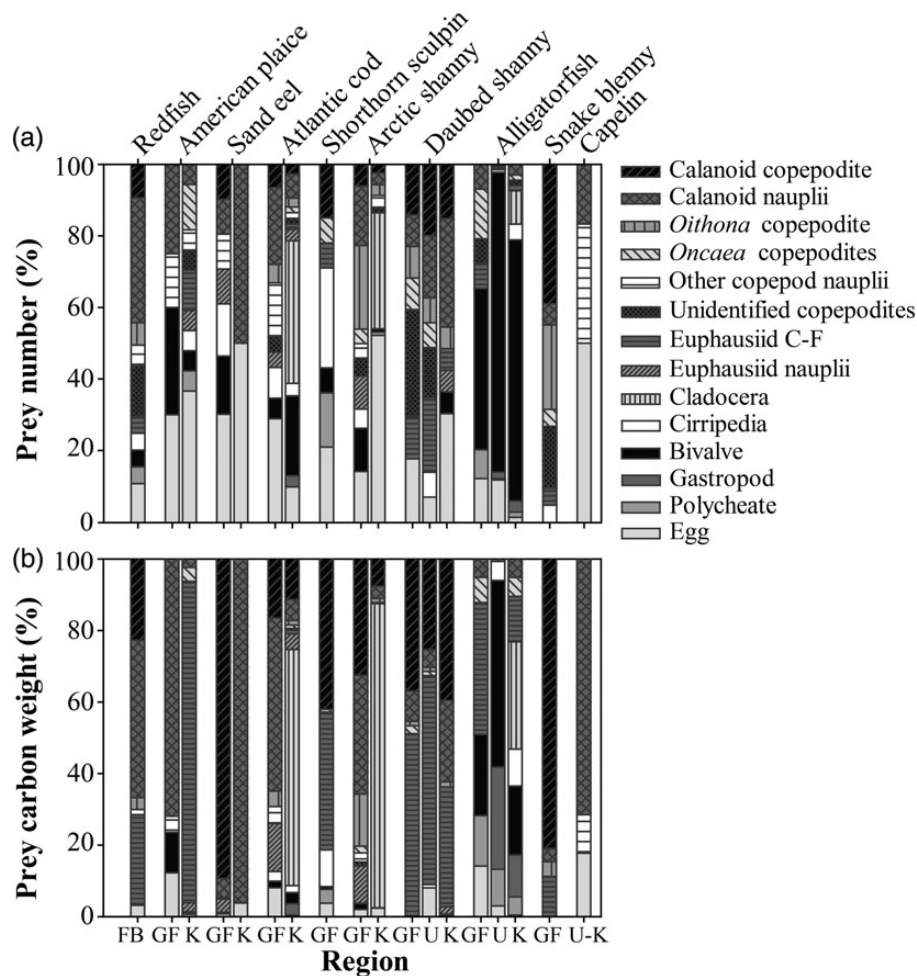


Fig. 7. Relative composition of diet in 10 larval fish in terms of (a) numbers, and (b) biomass. Six of the species were widely distributed and the diet was determined for different geographic regions; FB is Fyllas Bank, GF is Godthåbsfjord, U is Umanap and K is Kapisigdlit. Only few prey were found in stomachs of capelin, and therefore Umanap and Kapisigdlit are combined for this species.

abundances per m^2 due to shallower station depth could only explain part of this difference (Fig. 9a). Within the region of Fyllas Bank, large dissimilarities in fish larvae assemblages were observed between stations, whereas considerable similarity was found between several stations in Umanap, Kapisigdlit and Godthåbsfjord (Fig. 9b). The MDS (multidimensional scaling) plots shows changes in zooplankton and larval fish assemblages moving from Fyllas Bank through the Godthåbsfjord towards Umanap and Kapisigdlit or towards the inland Ice sheet (Fig. 9). Assemblages differed significantly between the five geographic regions within the study area for zooplankton (Global $R = 0.56$, $P = 0.001$) and fish larvae (Global $R = 0.47$, $P = 0.001$). Fish larvae assemblages in Umanap were similar to Godthåbsfjord ($P = 0.09$) and both zooplankton and fish larvae assemblages in Umanap were similar to Kapisigdlit and the Ice sheet regions ($P > 0.1$), while all other regional comparisons were significantly different ($P < 0.05$).

DISCUSSION

This study presents new information on physical and biological linkages in sub-Arctic fjord and coastal systems. We identified zooplankton and larval fish assemblages specific to environmental conditions. Zooplankton assemblages were mostly determined by physical conditions of the water masses. Larval fish assemblages also appeared to be influenced by frontal zones, and furthermore by the proximity to the Ice sheet and availability and species composition of prey.

Hydrographic regimes

Physical conditions differed between different regions of the fjord and coastal system. We observed a hydrographical gradient, from the offshore Fyllas Bank, affected by the northward flowing West Greenland current, towards the glacially affected inner Godthåbsfjord, as previously

Table II: Fish larvae sizes, stomach content and preferred prey sizes relative to body length

Larval fish species	Redfish	American plaice	Sand eel	Atlantic cod	Shorthorn sculpin	Arctic shanny	Daubed shanny	Alligatorfish	Snake blenny	Capelin
Larvae analysed for stomach content										
No. of larvae (empty gut)	13 (1)	32 (14)	33 (12)	44 (3)	10 (0)	17 (2)	29 (9)	24 (0)	14 (4)	13 (8)
Larval length range (mm)	8-17	5-15	11-23	5-17	22-24	13-24	11-27	16-28	22-47	8-14
No. of prey items found	103	86	106	874	67	413	110	2241	120	11
Stomach content										
Mean no. of prey per larvae	8.6 ± 7.1	5.1 ± 3.9	5.0 ± 3.5	21.9 ± 25.9	6.7 ± 4.4	27.5 ± 25.7	5.5 ± 4.1	93.4 ± 232.6	12.0 ± 13.8	2.2 ± 2.7
Mean prey weight per larvae (µg C)	7.6 ± 5.2	4.5 ± 10.8	2.9 ± 6.7	25.5 ± 54.9	204.8 ± 248.7	44.2 ± 70.0	15.8 ± 15.4	29.7 ± 59.4	51.6 ± 74.1	0.8 ± 0.2
Resemblance										
Diet and environment										
P	0.046	0.038	0.039	0.265	0.017	0.001	0.189	0.003	0.385	-
Rho	0.274	0.186	0.334	0.032	0.364	0.488	0.112	0.224	0.074	-
Prey and larval dimensions										
Max. mouth gape/larval length (%)	14 ± 3	9 ± 2	8 ± 1	13 ± 2	17 ± 2	10 ± 1	9 ± 1	8 ± 1	8 ± 0	6 ± 1
Prey width/max. mouth gape (%)	11 ± 3	13 ± 3	8 ± 3	13 ± 5	15 ± 6	12 ± 3	12 ± 4	13 ± 8	10 ± 1	-
Pref. prey length/larval length (%)	5.4	1.7	0.7	4.5	17.1	3.7	3.3	3.5	2.4	-

Calculated is the average prey weight in carbon (of identifiable prey), numbers of prey per larvae, max. mouth gape relative to larval length and ingested prey width relative to max. mouth gape (± SD). Preferred prey length relative to larval length is derived from Fig. 8.

described (Arendt *et al.*, 2010; Mortensen *et al.*, 2011; Tang *et al.*, 2011). Across the length of the gradient, we observed several frontal structures formed by the convergence of water masses. Frontal zones were present on both sides of Fyllas Bank, where coastal waters meet Atlantic water to the West and mixed sill water to the East (Mortensen *et al.*, 2011; Tang *et al.*, 2011). Frontal zones also occurred further inside the Godthåbsfjord where sill region water and surface water from Kapisigdlit and Umanap meet the sub-glacial water emanating from the inland Ice sheet. The thermal conditions within Kapisigdlit and Umanap differed substantially from those in the Godthåbsfjord due to the larger distance from the cold glacial plume. It is possible that runoff from melting snow in these two fjords facilitated surface heating by exporting heat from land. A previous study by Mortensen *et al.* (Mortensen *et al.* 2011) described an estuarine circulation mode that develops during summer, with freshened water flowing out at the surface and saline oceanic water flowing in below. A similar circulation pattern was also observed within Kapisigdlit in a concurrent study (R. Swalethorp, unpublished data).

Zooplankton distribution and environment linkages

Zooplankton assemblages were linked to physical conditions of the water masses. The North Atlantic and Arctic *Calanus* spp. dominated outside of the fjord in correspondence with an influence from Atlantic inflow. Through the fjord towards the glacier, the relative contribution of *M. longa*, *Pseudocalanus* spp. and *M. norvegica* increased, as observed in earlier studies (e.g. Arendt *et al.*, 2010; Tang *et al.*, 2011). In the inner fjord regions (Kapisigdlit, Umanap and close to the Ice sheet), we observed high abundances of the particle-associated copepod *M. norvegica* (Koski *et al.*, 2005) and the omnivorous *O. similis*, *Oncaea* spp. and *M. longa* (Turner, 2004, and references therein; Kjellerup and Kiørboe, 2012). Their high abundances were probably due to the high biomass of protozoans, rotifers and nauplii found in the inner fjord regions (Calbet *et al.*, 2011; Riisgaard *et al.*, 2014; present study) which offer good feeding conditions for omnivorous copepods. The presence of *M. norvegica* may also explain the lower vertical carbon fluxes previously reported for Godthåbsfjord (Arendt *et al.*, 2010) due to its capacity to degrade aggregates (Koski *et al.*, 2005). Glacially derived suspended sediments (Arendt *et al.*, 2011) and thermal conditions may also be key factors in shaping the zooplankton assemblages.

A unique zooplankton assemblage was observed in the inner part of Kapisigdlit where the biomass of the cladocerans *Podon* spp. and *Evadne* spp. was high. Although previously found in the Godthåbsfjord (Tang *et al.*, 2011),

Table III: Prey availability calculated from the prey size spectrum

Larval fish species	Fyllas Bank (n = 8)	Godthåbsfjord (n = 7)	Ice sheet (n = 3)	Umanap (n = 3)	Kapisigdlit (n = 5)
Redfish	87 ± 41	56 ± 13	70 ± 78	83 ± 14	120 ± 19
American plaice	41 ± 19	25 ± 10 ^A	30 ± 29 ^{AB}	95 ± 59 ^{BC}	123 ± 123 ^C
Sand eel	47 ± 21	27 ± 11 ^A	36 ± 30	97 ± 55 ^B	126 ± 116 ^B
Atlantic cod	74 ± 34	48 ± 21 ^A	55 ± 62 ^{AB}	179 ± 103 ^{BC}	188 ± 152 ^C
Shorthorn sculpin	152 ± 109	47 ± 39	177 ± 80	113 ± 120	136 ± 65
Arctic shanny	115 ± 57	63 ± 32	82 ± 84	78 ± 29	152 ± 26
Daubed shanny	124 ± 66	62 ± 40	86 ± 85	66 ± 40	166 ± 41
Alligatorfish	141 ± 77	58 ± 41 ^A	125 ± 55	132 ± 73	178 ± 63 ^B
Snake blenny	189 ± 118	75 ± 77	139 ± 81	121 ± 111	181 ± 81
Capelin	22 ± 17	17 ± 11	15 ± 20	91 ± 74	121 ± 159

Values are expressed in mg carbon per m², averaged between stations within five geographic regions of the study area (± SD), and letters indicate regions that differs significantly ($P < 0.05$).

these species are most abundant in Kapisigdlit (Smidt, 1979). Cladoceran abundance at St K4 was significantly higher in 2010 (max. 64 000 ind m⁻², Swalethorp *et al.*, 2014) than recorded earlier (743 ind m⁻² in the period 1955–1963, with a 120- μ m mesh size net, Smidt, 1979). This may be due to high surface temperature in 2010 ($\sim 3.5^{\circ}\text{C}$ higher in the top 20 m than the highest mean temperature between 1953 and 1966, Smidt, 1979, R. Swalethorp, unpublished data), favouring the cladocerans (Johns *et al.*, 2005), and possibly explains their absence in Godthåbsfjord where surface temperatures were lower.

Larval fish distribution and environmental linkages

The larval fish assemblages found appeared to be structured in relation to the different water masses. The structuring may stem from species-specific differences in the location of spawning sites within the area. Regional differences in glacial melt-water outflow, circulation patterns and converging water masses forming frontal zones could direct fish spawning and further impact larval drift and aggregation. This was indicated by the distinct differences in assemblage composition between Fyllas Bank, Godthåbsfjord, Kapisigdlit and the Ice sheet region, and by the enhanced abundance of larvae in the vicinity of frontal zones. The segregation of redfish, shorthorn sculpin and capelin was particularly clear. Redfish were associated with Atlantic water and concentrated in the frontal zones bordering Fyllas Bank. This species spawns in the southern part of Greenland and its offspring are transported North with the West Greenlandic Current and are often associated with strong stratification (Pedersen and Rice, 2002). The concentration of fish larvae in frontal areas is attributed to spawning strategies, aggregation processes due to water flow convergence and an increased plankton productivity and therefore, a higher biomass of prey available

(e.g. Fortier *et al.*, 1992; Munk *et al.*, 1995, 2003). Shorthorn sculpin was associated with the colder frontal areas within the Godthåbsfjord, where the mixed sill water meets sub-glacial melt water (Tang *et al.*, 2011). American plaice and sand eel were also abundant here, while Atlantic cod, Arctic shanny and snake blenny seemed to concentrate on the opposite side of the mixed sill area, influenced by coastal water. Considering the estuarine circulation during summer (Mortensen *et al.*, 2011) and the low occurrence of fish larvae close to the glacier, much of the spawning of these species may have taken place in the coastal areas or from around the sill at the fjord entrance. Capelin was found in the warmer Kapisigdlit and Umanap regions, where spawning takes place in shallow water close to shore (R. Hedeholm, personal communication). Although a weak estuarine circulation was observed in Kapisigdlit, most larval species found in this area were likely spawned there as well, as eggs and small larvae were found in higher abundance in the central and inner part of the fjord during spring (R. Swalethorp, unpublished data). Sand eel were, however, only found in the outermost part of Kapisigdlit. The earlier increase in surface temperature within Kapisigdlit, compared with other branches of the fjord system, would facilitate faster larval growth and improve survival chances (Chambers and Leggett, 1987; Houde, 1989; Kjesbu, 1994; Carscadden *et al.*, 1997). This may explain the relatively high number of species spawning here.

In large parts of the study area, we observed an overlap in the distribution of larvae and the estimated availability of the preferred prey sizes. Biomass of prey taxa that were important in the diet, also overlapped with the distribution of several larval species. A linkage between larvae and preferred prey was further supported by the significant resemblance between diet and environmental composition of prey organisms in six of the larval species. Fish may spawn in areas where zooplankton production is high or from where the progeny will drift to such areas (e.g. Bergstad

et al., 1987). Comparison between regions of our study area showed that Kapisigdlit generally contained the highest availability of prey to all larval species found there, and in general had a high biomass of calanoid nauplii and copepodites. This richness was likely fuelled by the relatively high primary production found in this area (Arendt *et al.*, 2010; Calbet *et al.*, 2011; Riisgaard *et al.*, 2014). Calanoid copepods were important in the diet and are preferred by most species of fish larvae (Monteleone and Peterson, 1986; Anderson, 1994; Pepin and Penney, 1997; Heath and Lough, 2007; Pedersen and Fossheim, 2008; Demontigny *et al.*, 2012). The productive frontal zone along Fyllas Bank (Arendt *et al.*, 2010), where many larval species were located, also supported a high biomass of prey. Conversely, prey availability and biomass of prey taxa important in the diet was low in the less productive inner part of the Godthåbsfjord (GF4–GF8). This low zooplankton biomass may be due to the small cells dominating the phytoplankton assemblage here (Arendt *et al.*, 2010). Predation could also lower zooplankton abundance. Although estimated larval predation impact is often limited (e.g. Nielsen and Munk, 1998; Pepin and Penney, 2000) and rarely exceeds zooplankton production, the combined grazing pressure of carnivorous invertebrates, larval fish and planktivorous fish could reduce the zooplankton standing stock (Fortier and Harris, 1989; Munk and Nielsen, 1994).

The estimates of prey availability may be biased towards larvae within the length range that was analysed for stomach content. These analyses were only carried out on a limited range of larval sizes and changes may occur outside this range. However, the relative prey length preferences were relatively constant for any of the species. Only alligatorfish significantly widened its feeding niche with increasing size. Moreover, our examination of the stomach contents could not account for the contribution of unicellular protozoans which are degraded rapidly post ingestion (De Figueiredo *et al.*, 2005).

Species-specific differences in feeding

We found dietary differences between larval species that in part resulted from differences in their morphology, behavioural flexibility and distribution. The differences in prey size preference largely corresponded to differences in mouth size relative to body length, i.e. large mouthed Atlantic cod, redbfish and shorthorn sculpin preferred relatively larger prey, while small mouthed American plaice, sand eel and snake blenny preferred smaller prey. Such prey size differences related to relative mouth sizes have been shown in other species comparisons as well (Pepin and Penney, 1997; Sabatés and Saiz, 2000; Østergaard *et al.*, 2005). The observed regional

differences in diet indicated that some species were more flexible in their feeding. For instance larvae of daubed shanny did not modify their diet in response to changes in the prey assemblage, nor did they predate on the highly catchable cladocerans (Verity and Smetacek, 1996). This finding was supported by resemblance analysis between the diet and environment, which found no resemblance for daubed shanny, Atlantic cod and snake blenny. This suggests a more specialized feeding in agreement with other studies (Robert *et al.*, 2011; Demontigny *et al.*, 2012). Other species such as Arctic shanny and alligatorfish were more generalists, based on the regional dietary changes and the resemblance of diet to the environmental composition. Alligatorfish, in particular, also exploited an alternative feeding opportunity by having a high contribution of bivalve larvae.

Of note, the fish larvae which overlapped in distribution in most cases ingested different sizes or types of prey. Species-specific differences in feeding niche, or a general diversity in prey size and type, may reduce competition for food (e.g. Pedersen and Fossheim, 2008; Demontigny *et al.*, 2012). Especially in Kapisigdlit, we observed that larvae residing here ingested different sizes and types of prey. Such difference in diet was less evident for the main Godthåbsfjord area where non-calanoid copepods, which typically are less preferred by fish larvae (Pepin and Penney, 1997; Heath and Lough, 2007; Demontigny *et al.*, 2012), contributed more to the diet.

A comparison between available information on zooplankton and ichthyoplankton assemblages from the area, reveals some inter-annual variability (Jensen and Rasch, 2009, 2010, 2011; Arendt *et al.*, 2011; Tang *et al.*, 2011; Jensen, 2012; present study). Daubed shanny and sand eel are apparently species that show marked variability in their distribution and abundance between years, while much less variation is seen in the distributions of, e.g. Arctic shanny larvae. A wide distribution across years is seen for, e.g. daubed shanny and alligatorfish. These species were also found in close proximity to the inland ice sheet. This may indicate that these larvae are more robust to changes in salinity and temperature. Observations indicate that some species could be more resilient towards future biological–physical changes in their environment.

CONCLUDING REMARKS

The present study provides a baseline for evaluation of the zooplankton and larval fish assemblages, and for an evaluation of the impact of future environmental changes on the West Greenlandic marine ecosystem. Both the zooplankton and the fish larvae showed great variability in

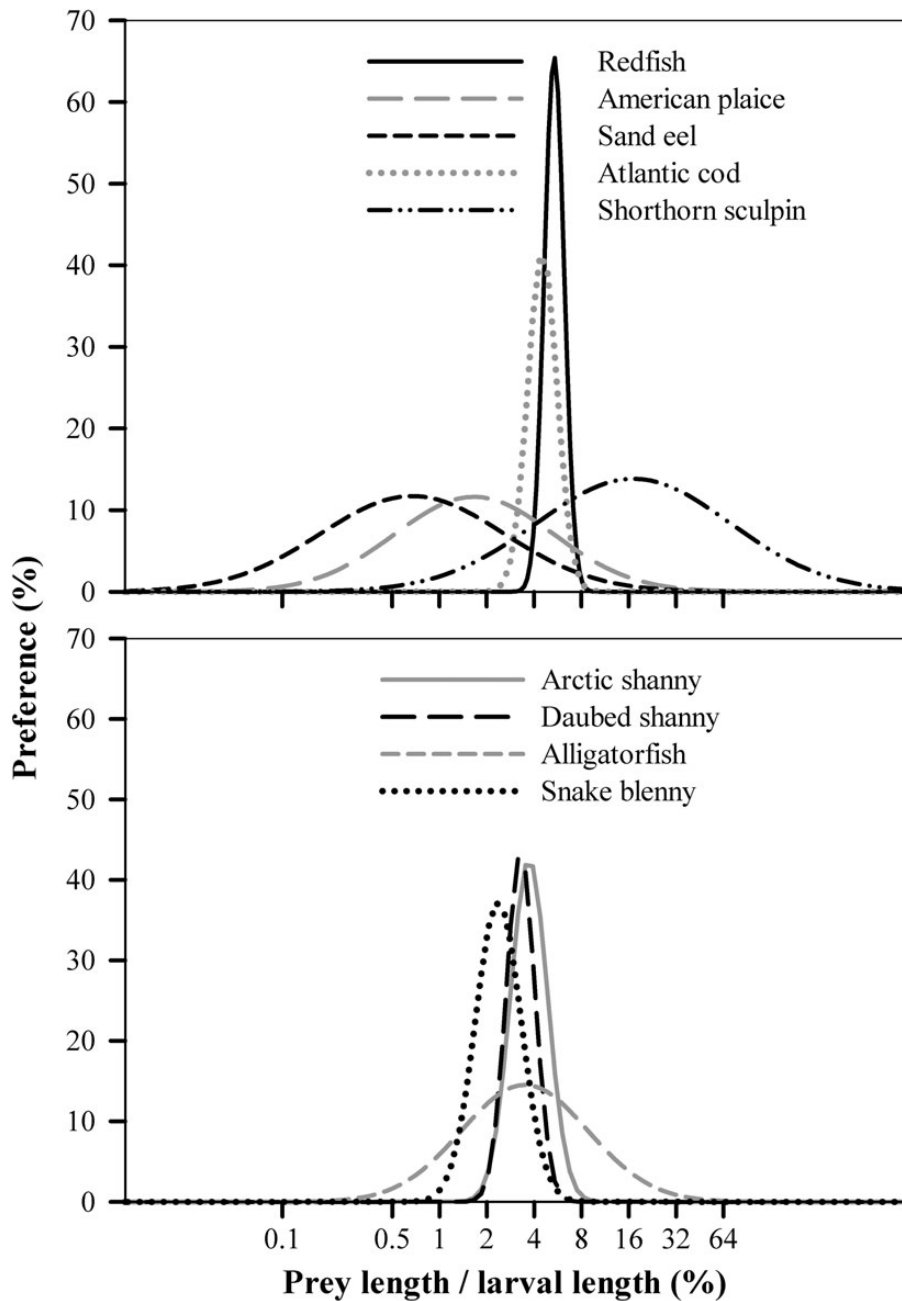


Fig. 8. Theoretical prey length preference spectra as percentage of larval length in nine larval species. Coefficients are found in Supplementary data, Table SIII.

abundance across the range of environmental conditions within the study area. Species-specific patterns of distribution were shown for the zooplankton and fish larvae, and appeared to be linked to specific water masses, presence of frontal zones and to the availability of their preferred prey. Fish larvae were differently adapted to the physical and biological environment and it is likely that they will be differently affected by changing environmental conditions. The climate of West Greenland is changing, as shown by

increasing temperatures, alterations in Atlantic water inflow and intensified glacial melting and runoff from land (Kattsov and Källén, 2005; Holland *et al.*, 2008; Rignot *et al.*, 2010). An increase in outflow of cold glacial meltwater into the fjords may directly impact the distribution, growth and survival of many species of larval fish. The influence from climatic changes might also take effect as a bottom-up cascade from phytoplankton to fish larvae. Predicted increases in temperature and stratification of the

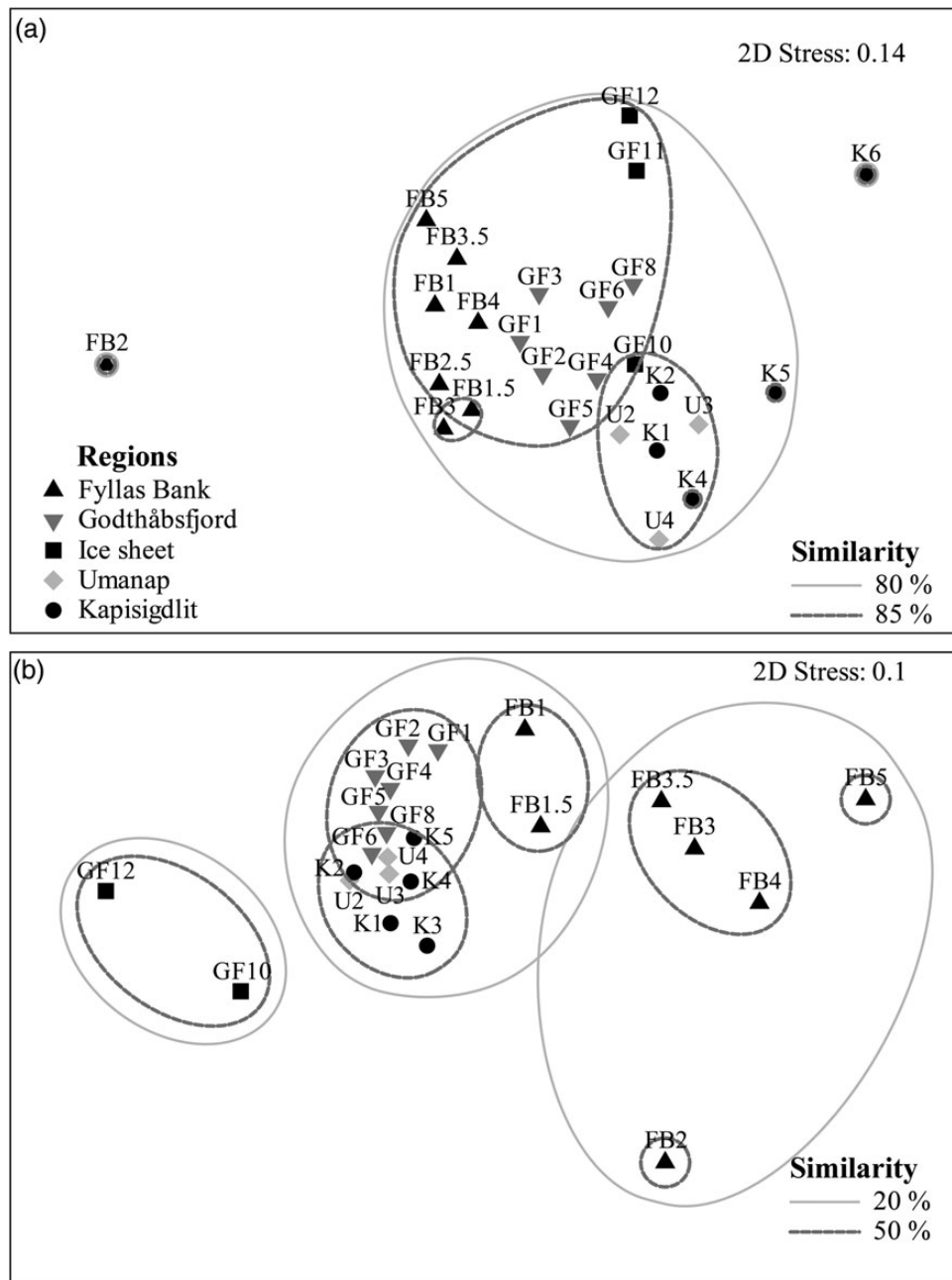


Fig. 9. Similarities (%) in (a) zooplankton and (b) larval fish community composition between different sampling stations, using the Bray Curtis similarity index. Station symbols identify in which geographic region they are located. Note that some stations were only sampled for zooplankton or fish larvae.

water column will reduce phytoplankton cell size (Ardyna *et al.*, 2011). This will favour protozoan grazers, which in turn will favour omnivorous copepods (Riisgaard *et al.*, 2014) over the large lipid rich suspension feeding copepods, which are important in the diet of most fish larvae species. Therefore, such changes in oceanographic conditions and prey availability could negatively affect the growth and survival of fish larvae and hence change the

fish communities in the area. Species that are more flexible in their feeding and more adaptable to environmental variability may cope better with climate related changes.

SUPPLEMENTARY DATA

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

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