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Life cycles and seasonal vertical distributions of copepods in the Iceland Sea

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Abstract

The sub-Arctic Iceland Sea is an important feeding area for the Icelandic capelin stock with copepods as a major food item. Information on the life history of copepods in the area is limited, and therefore the major aim of the present paper is to describe the population development and ontogenetic vertical migrations of dominant copepods in the area. Depth stratified samples were collected on six cruises covering all seasons of the year from 2006 to 2008. *Calanus hyperboreus* dominated the biomass (~ 45% of copepods), with *C. finmarchicus* ranking second (~ 28%) and *Metridia longa* third (~ 17%). The copepods differed in their life history strategies. *C. hyperboreus* is unique in that it has the deepest winter distribution (~ 800–1000 m), reproduces at depth in February–March in the absence of phytoplankton food, and spends relatively short time in the surface layers during summer. *C. finmarchicus* also hibernates at depth, however much shallower (~ 200-600 m), and the reproduction at the surface in May–June is timed to the productive period of phytoplankton. A 2- to 3-year life cycle is proposed for *C. hyperboreus* and a 1 year for *C. finmarchicus*. *Pseudocalanus* spp. appear to have a similar life history as *C. finmarchicus*, while occupying intermediate depths (~ 400–1000 m) during the overwintering period. The life history of the omnivorous species *M. longa* appears relatively decoupled from the phytoplankton spring bloom. The same applies to the omnivorous species *Oithona* spp. and *Oncaea* spp. The information presented adds to the comparative description and understanding of copepods in sub-Arctic areas in general.

Keywords Sub-Arctic · *Calanus* · *Metridia* · Ontogenetic migration

Introduction

The oceanic region north of Iceland, the Iceland Sea, is an important feeding area for the Icelandic capelin stock, which during its summer feeding migrations into the region mainly feeds on the rich copepod and euphausiid stocks in the area (Sigurdsson and Astthorsson 1991; Astthorsson and Gislason 1997). In the Iceland Sea, as elsewhere in the North Atlantic, the mesozooplankton is dominated by copepods (> 85% of the mesozooplankton by number), with three species, *Calanus hyperboreus*, *C. finmarchicus,* and *Metridia longa*, making up ~ 90% of the annual copepod biomass (Gislason and Silva 2012). These species are therefore in focus of this study. The smaller copepods, *Pseudocalanus* spp., *Oithona* spp., and *Oncaea* spp., are less important in

terms of biomass due to their smaller size. However, as they are numerically very important in the region, their seasonal abundance and distribution will also be examined. Despite the numerical dominance of copepods in the area and their importance as food for capelin, previous information on the population dynamics and life histories of copepods in the Iceland Sea is very limited (Gislason and Silva 2012).

This study forms a part of a larger project, the Iceland Sea Ecosystem Project, with field activity in 2006–2008, and aimed at exploring the general structure and functioning of the Iceland Sea ecosystem with the overarching aim of understanding better the factors that influence the capelin growth and feeding migrations (Palsson et al. 2012). In a previous paper, Gislason and Silva (2012) reported on the distribution, diversity, and general seasonal variability of zooplankton in the Iceland Sea using data from this project. Data collected during the project on the seasonal depth distribution of the dominant copepods in the region have, however, not been dealt with previously. Therefore, the major aim of this study is to describe the population development,

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ontogenetic vertical migration, and life cycles of the dominant copepods in the Iceland Sea, based on data collected for 3 years.

Materials and methods

Study area

The Iceland Sea is bounded by Iceland and the Iceland–Greenland Ridge in the south, Greenland in the west, the submarine ridge between Greenland and Jan Mayen in the north, and the Jan Mayen Ridge in the east (Stefansson 1962, Fig. 1). The Kolbeinsey Ridge that stretches from the middle of the north coast of Iceland towards Jan Mayen divides the Iceland Sea into two main basins.

Relatively warm and saline Atlantic water enters the area from both the southwest as a branch of the Irminger Current and the northeast from the Norwegian Sea through and over the Jan Mayen Ridge. Cold and low salinity water is brought into the Iceland Sea from the north by the East Greenland Current that flows from the Greenland Sea and into the Iceland Sea (Stefansson 1962; Valdimarsson and Malmberg 1999). In the Iceland Sea, these water masses mix, and the proportion of warm and cold water varies by region and season.

Field sampling

Sampling was conducted during seven cruises during 2006, 2007, and 2008 (Table 1, Fig. 1). The aim was to take depth stratified zooplankton samples at four fixed stations on each cruise. However, due to difficult weather and ice conditions, they could not be sampled on every cruise and/or station locations had to be adjusted slightly (Table 1). Temperature

and salinity were recorded with a CTD (Seabird Electronics SBE-9/11), but as the temporal patterns of change were generally rather similar at all stations, I present hydrography and chlorophyll data from one site only (Stns 6, 6B, Fig. 1).

The zooplankton were collected using a Multi Plankton Sampler from HydroBios (0.25 m^2 mouth area, 200 μm mesh size) that was towed from near the bottom to the surface with a speed of ~45 m min^{-1}. The Multi Plankton Sampler is equipped with five nets that can be opened and closed on command from the ship. By deploying the sampler three times, ten depth layers (50–400 m wide) were sampled from the surface to a maximum depth of 1800 m. The volume of water filtered by the net was measured with HydroBios flowmeters fitted in the mouth of each net.

Analysis

The zooplankton samples were preserved in 4% neutralized formalin until analysis in the laboratory. Except on a few occasions, the samples were subsampled with a Motoda splitter (Motoda 1959), and an aliquot containing at least ~500 copepods was analysed for species composition. Further, the copepods *C. hyperboreus* and *C. finmarchicus* were classed to copepodite stages, while *M. longa* were classed as either adult females (C6f), males (C6 m), or juveniles (C1–5).

Copepod numbers have been converted to biomass (dw) using stage-specific dry mass from various sources (Davis 1984; Norrbin et al. 1990; Longhurst and Williams 1992; Richter 1994; Auel 1999; Hirche and Kosobokova 2003). When mean individual dry weight was not available, weights of species similar in size and shape were used.

Data on abundance (numbers m^{-3}) were calculated for each net using the data from the flowmeters. Number per m^2 was obtained for each net by multiplying the abundance

Fig. 1 Map of the study area showing the sampling stations in the Iceland Sea. Stations 6 and 6B are the ones from where data on hydrography are presented. Inserted in the figure are the main ocean currents in the upper layers. Red arrows: Atlantic water; Blue arrows: Polar water; Green arrows: Mixed water. Currents modified from Valdimarsson and Malmberg (1999) and Blindheim and Österhus (2005)
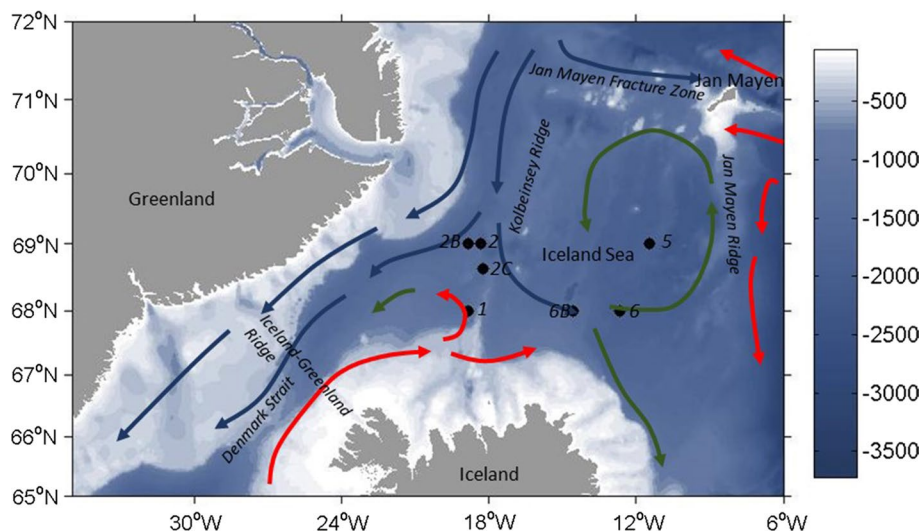
Table 1 Cruise and station identity, positions, bottom depths, dates, time of sampling, and light conditions

Cruise	Station	Position	Depth (m)	Date (d.m.y.)	Time (GMT)	Light
bs062006	1	68°00′N–18°50′W	1020	25.07.2006	15:03–16:08	D
	2B	69°00′N–18°20′W	1463	26.07.2006	14:25–15:40	D
	5	69°00′N–11°27′W	1795	27.07.2006	18:37–20:32	D
	6B	68°00′N–14°35′W	1254	25.07.2006	00:27–01:37	N
af112006	1	68°00′N–18°50′W	1020	21.11.2006	13:55–15:05	D
	6	68°00′N–12°40′W	1850	26–27.11.2006	22:00--01:00	N
bs032007	1	68°00′N–18°50′W	1020	12.02.2007	04:25–06:20	N
	2C	68°38′N–18°15′W	941	12.02.2007	12:10–13:25	D
	5	69°00′N–11°22′W	1722	13.02.2007	17:30–20:05	N
	6	68°00′N–12°40′W	1850	14.02.2007	03:38–07:22	N
bs082007	1	68°00′N–18°50′W	1020	19.05.2007	01:40–03:53	D
	6	68°00′N–12°40′W	1850	21.05.2007	19:00–22:00	D
bs112007	1	68°00′N–18°50′W	1020	13.08.2007	00:14–01:16	N
	2	69°00′N–18°50′W	1272	20.08.2007	00:12–01:23	N
	5	69°00′N–11°27′W	1795	21.08.2007	14:52–17:10	D
	6	68°00′N–12°40′W	1850	18.08.2007	03:20–05:35	N
bs062008	1	68°00′N–18°50′W	1020	01.05.2008	17:10–18:51	D
	2	69°00′N–18°50′W	1272	02.05.2008	02:35–04:40	D
	5	69°00′N–11°27′W	1795	04.05.2008	16:37–19:13	D
	6	68°00′N–12°40′W	1850	05.05.2008	06:13–08:40	D

Light conditions are designated as "D" = day, sun above horizon, "N" = night, sun below horizon. Light conditions are designated as "D" = day, sun above horizon, "N" = night, sun below horizon

(number m^{-3}) by the depth range for that net. Total water column abundances (number m^{-2}) were then calculated from the sum of the abundances (number m^{-2}) for all the nets in a vertically stratified tow.

To facilitate comparison of the depth distributions of the dominant copepods, the weighted mean depth (WMD) was calculated according to the equation:

$$\mathrm{WMD} = \sum \left(n_i d_i \right) \Big/ \sum n_i,$$

where n_i is the abundance (number m^{-3}) of copepods at depth d_i (the midpoint of each depth stratum, Bollens and Frost 1989).

Average values were calculated for the four stations, except for cruises af112006 and bs082007, when just two stations could be occupied (Table 1). Gislason and Silva (2012) reported recently on the composition and seasonal variability of total mesozooplankton in the Iceland Sea, using partly the same material as dealt with here. They found that while total numbers and biomass of copepods were around 1.5 times higher on the east side of the Kolbeinsey Ridge than west of it, the seasonal variability in total numbers and biomass was similar on both sides, with relatively low winter values and one main peak in July and August. I, therefore, feel justified in combining data from stations occupied on both sides.

Due to logistical reasons, the stations could not be sampled at the same time of day during the cruises. As some of the animals of the present study are known to be active diel migrators with different depth distributions during day and night, combining the data in this way may be questioned. The extent to which the results may have been influenced by this fact was explored in some detail during the analysis (see "Discussion" section). Note also that to examine seasonal patterns, the data were organized in the temporal sequence 12–14 February 2007, 1–5 May 2008, 19–27 May 2007, 17–30 July 2006, 11–26 August 2007, and 21–26 November 2006, although the data were not sampled chronologically. Although it would obviously have been desirable to survey the area chronologically, this was not possible for logistical and practical reasons. It should be borne in mind that some smaller zooplankton components will inevitably escape through the 200-μm mesh nets of the Multi Plankton Sampler. It has been pointed out that the breadth of the zooplankters determines their retainment by plankton nets (Colton et al. 1980; Nichols and Thompson 1991) and, therefore, the zooplankters, whose breadth is less than the mesh size (200 μm), will be underrepresented in the samples. Accordingly, the younger stages of some copepods caught in the present investigation (*Pseudocalanus* spp., *Scolecithricella minor,* and *Spinocalanus* spp.) have been undersampled. For the smallest copepods (*Oithona* spp., *Oncaea* spp., and

Microcalanus spp.), it is likely that adults were also underestimated. Despite the above-mentioned limitations, I nevertheless believe that the present material demonstrates the main seasonal dynamics of the copepods in the Iceland Sea.

Results

Hydrography and phytoplankton

Depth profiles of temperature and salinity showed low salinity surface layer at all sampling occasions reflecting the influence of low salinity Polar or Arctic Water (Fig. 2). The temperature in this water was ~0 °C in February till early May, started to increase in late May, and had reached ~5–6 °C in July and August. Thereafter the surface layers cooled to ~1–2 °C in November. Below ~200 m depth, temperatures ranged between ~−0.8 and 0 °C and salinities were close to ~34.9 throughout the study period (Fig. 2). This water is the Arctic Bottom Water (Stefansson 1962).

Abundance and composition of copepod community

Total integrated average biomass fluctuated rather irregularly through the study period, while being lowest in February (5.4 ± 2.1 (mean ± SD) g dw m^{-2}) and highest in August (13.3 ± 5.1 (mean ± SD) g dw m^{-2}) (Fig. 3a). Similarly, total numbers of copepods, integrated for the whole water column, were generally lowest in February (~30,000 ind m^{-2}), started to increase in May, and had reached maximum in July and August (~330,000 ind m^{-2}) (Fig. 3b).

Calanus hyperboreus dominated the annual copepod biomass (~45%), with *C. finmarchicus* ranking second (~28%) and *M. longa* third (~17%) (Fig. 3c). In terms of numbers, *Oithona* spp. dominated (~36% of all copepods), with *C. finmarchicus* ranking second (~18%) and *Pseudocalanus*

spp. third (~16%) (Fig. 3d). *Oncaea* spp. made up less than 1% of the biomass but ranked fourth in numbers (~12%).

Calanus hyperboreus

During winter (February), the population stayed deep in the water column, the highest concentrations being observed from ~800 to 1000 m at sub-zero temperatures (Figs. 2, 4). Ascent to the upper layers started sometime between February and early May, when concentrations were highest in the 0–100 m depth layer. By late May, nearly the whole population was confined to the uppermost depth layer (0–50 m). Concentrations remained high in the surface layer (0–100 m) in July (Fig. 4). The return migration to the deeper overwintering layers appeared to take place mainly after July and be completed by November when abundance was again highest in the 800–1000 depth layer (Fig. 4).

During winter and spring (February–May), depth integrated total numbers fluctuated between ~2000 and ~5000 individuals m^{-2}, but after May, numbers increased dramatically to ~11,000 individuals m^{-2} in July. Thereafter numbers decreased to ~6000 individuals m^{-2} in November.

All stages were found in the winter samples (February), while stages C4 and adult females were relatively most abundant (~29% and 31%, respectively) (Fig. 5). Females were present at all sampling times, while males were extremely rare (0–0.4%), except during winter and fall (~13% and ~4% in February and November, respectively) (Fig. 5) below 400 m depth (Fig. 4). The youngest copepodite stages (C1) were seen in greatest abundance during the first half of May (~160 individuals m^{-2}, ~3%).

Calanus finmarchicus

The animals overwintered mainly from ~200 m to ~600 m depth (February, Fig. 6). As for *C. hyperboreus*, the ascent
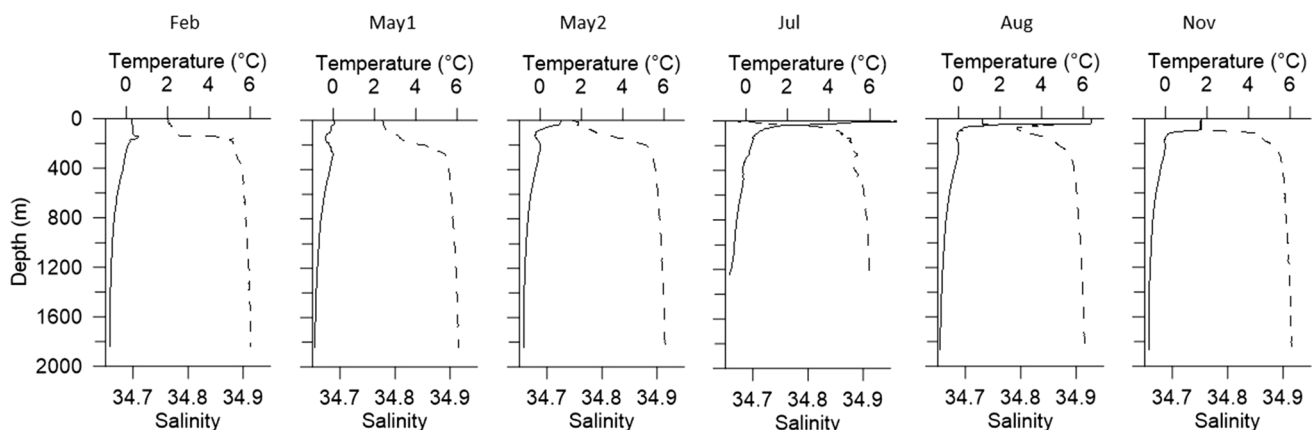

Fig. 2 Vertical profiles of temperature (solid line) and salinity (dashed line) in the Iceland Sea from February to November. The plot shows a composite of data collected in 2006–2008. For location of stations see Fig. 1
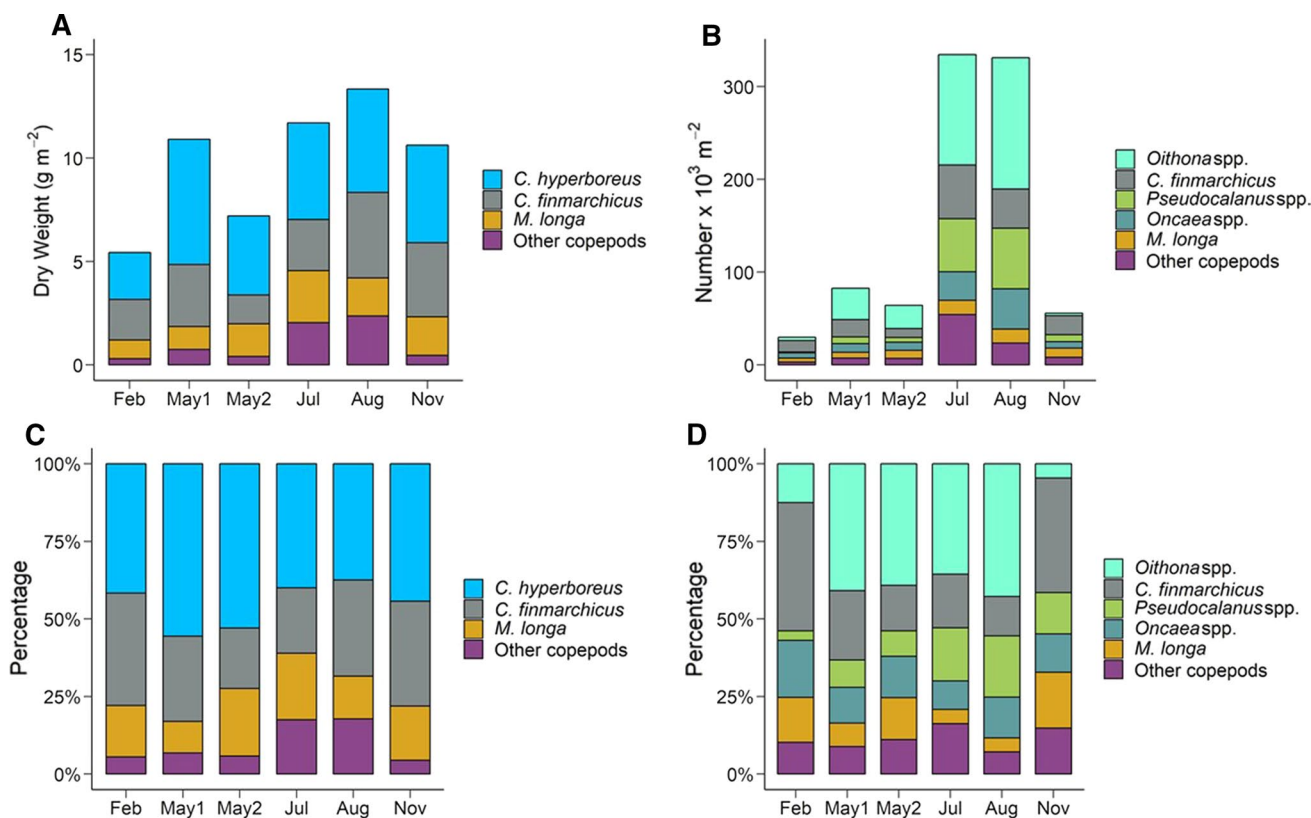
Fig. 3 Total depth integrated (0–1800 m) biomass (**a**), number (**b**), relative biomass (**c**), and relative number of copepods (**d**) at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite of data collected during 2006, 2007, and 2008 (Table 1)
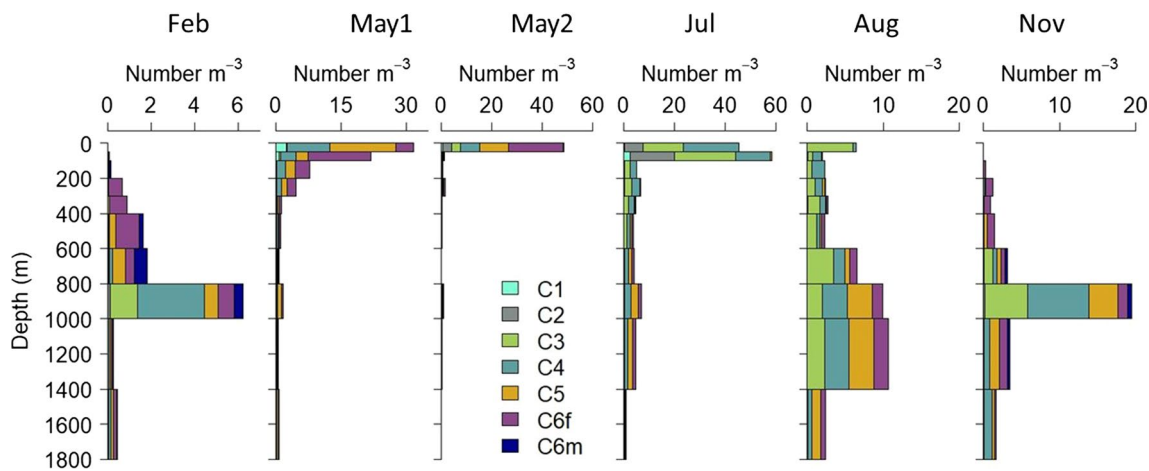

Fig. 4 *Calanus hyperboreus*. Vertical distribution at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite of data collected during 2006, 2007, and 2008 (Table 1). Note the change in abundance scales for the various months

to the surface layers occurred sometimes between February and May, when the highest concentrations were found between the surface and 50 m depth. The animals resided in the surface layers at least until August. Thereafter, the animals descended to the deeper layers and by November they were again mainly found at the overwintering depths (~200–600 m) (Fig. 6).
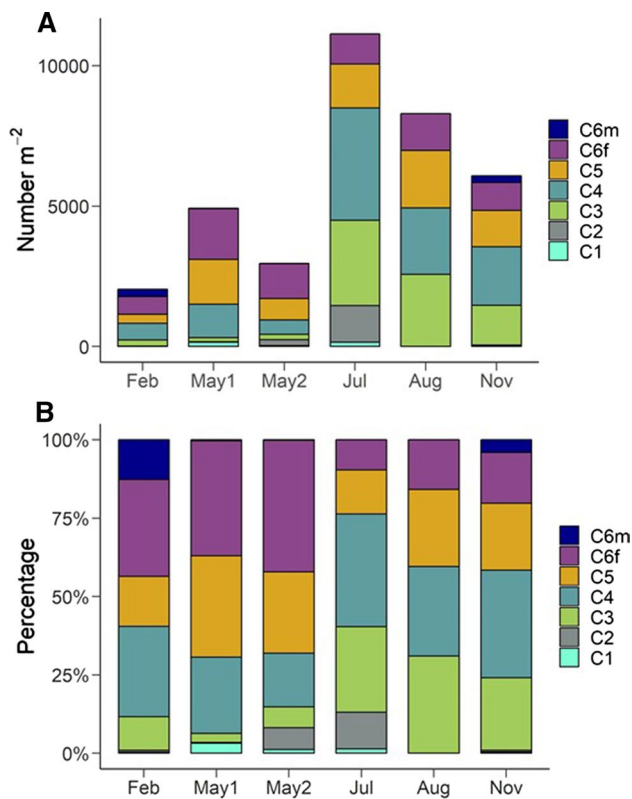
Fig. 5 *Calanus hyperboreus*. Total depth integrated (0–1800 m) number (**a**) and relative number (**b**) of copepodite stages at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite of data collected during 2006, 2007, and 2008 (Table 1)

During winter and spring (February–May), depth integrated numbers were relatively low, fluctuating between ~ 14,000 and ~ 19,000 individuals m^{-2} (Fig. 7). In July,

numbers had increased dramatically (to ~ 58,000 individuals m^{-2}). In August, numbers were much lower (~ 42,000 individuals m^{-2}), and in November low winter values were again observed (~ 21,000 individuals m^{-2}) (Fig. 7).

During the winter (February), the stocks consisted mainly of animals of stages C4 (~ 32%) and C5 (~ 60%) (Fig. 7). A small proportion of the overwintering stocks were adults (~ 7%). In May, adults were most prominent in the samples, both females (~ 30%) and males (~ 3%) (Fig. 7). The abundance of juveniles (C1) of the new spring generation was highest in July (~ 20,000 individuals m^{-2}, ~ 33%). In August, the proportion of C1s and C2s decreased with a parallel increase in proportion of C3s, C4s, and C5s, reflecting the development of the stock to the more advanced overwintering stages (C4–5). By November, when the stocks had returned to overwintering depths, they consisted mainly of stages C4 (~ 17%) and C5 (~ 77%).

Metridia longa

The seasonal depth distribution is shown in Fig. 8. In February, the animals were rather evenly distributed between 100 and 1000 m depth. In early May, a small part of the population had surfaced to the shallowest depth layer (0–50 m), while the main part still stayed relatively deep (~ 100–600 m). In late May, the main part of the population occupied the shallower layers with the concentrations of animals being by far the highest above 50 m depth. In July, the population had shifted to greater depths, while still being abundant in the surface layers (Fig. 8). In August, a bimodal depth distribution was observed, with the highest concentrations of animals being observed in the 0–100 m and 300–600 m depth layers. In November, the depth distribution remained bimodal, with two modes one at the
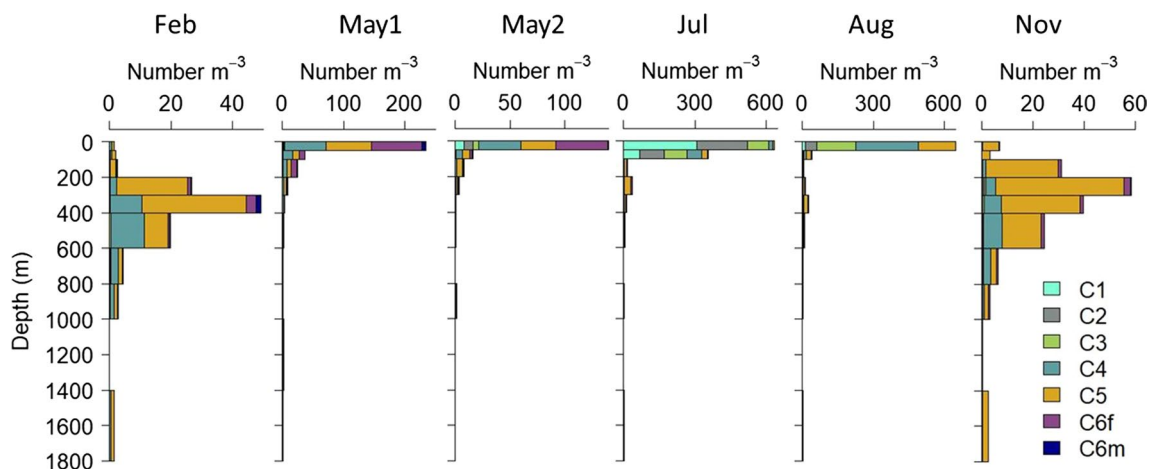

Fig. 6 *Calanus finmarchicus*. Vertical distribution at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite

of data collected during 2006, 2007, and 2008 (Table 1). Note the change in abundance scales for the various months
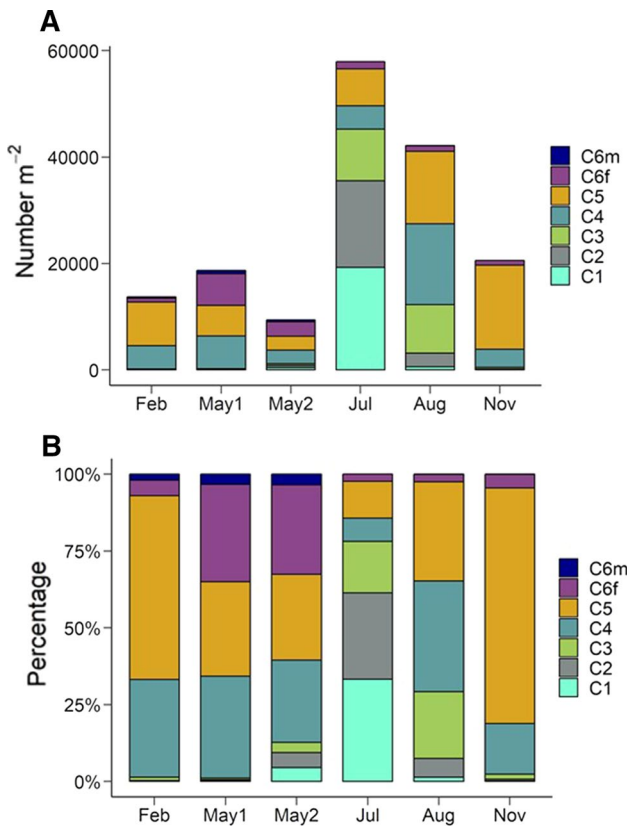
Fig. 7 *Calanus finmarchicus*. Total depth integrated (0–1800 m) number (**a**) and relative number (**b**) of copepodite stages at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite of data collected during 2006, 2007, and 2008 (Table 1)

surface (0–100 m) and the other at depth (maximum at 800–1000 m).

The numbers of *M. longa*, integrated over the depth range of the samples, increased from low winter values in February (~ 4000 individuals m^{-2}) to high summer values in July and August (~ 15,000 individuals m^{-2}). Numbers decreased after August and by November relatively low values were observed again (~ 10,000 individuals m^{-2}) (Fig. 9).

Adults of both sexes were present on all sampling occasions: females generally constituted ~ 20–50% of the stocks while males ~ 5–20% (Fig. 9). The younger copepodite stages (C1–5) constituted ~ 25–70%, with the highest incidence in August.

Pseudocalanus spp.

The morphological differences between the different species of the genus *Pseudocalanus* are small and they are difficult to separate. Hence, we have not attempted to classify the genus to the species level. Frost (1989) revised the genus, and according to his distribution maps, the animals probably belonged to either *P. minutus* or *P. acuspes*, or where a mixture of both species.

The seasonal depth distribution of *Pseudocalanus* spp. is shown in Fig. 10a. In February, the animals were mainly found from 400 to 1000 m depth. In early May, the population had shifted to shallower depths with the highest numbers caught in the 100–200 m depth layer. From late May and until August, the animals occupied mainly the shallowest depth layer (0–50 m). The return migration to depth occurred after August and by November the population was again mainly found at 400–1000 m depth.

During winter and spring (February—May), the depth integrated numbers fluctuated between ~ 1000 and ~ 7000
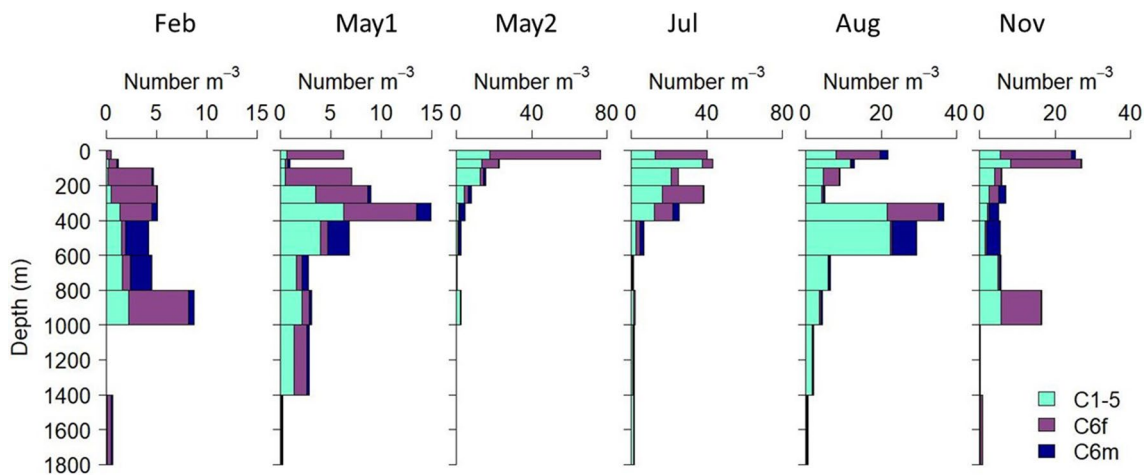

Fig. 8 *Metridia longa*. Vertical distribution at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite of data collected during 2006, 2007, and 2008 (Table 1). Note the change in abundance scales for the various months
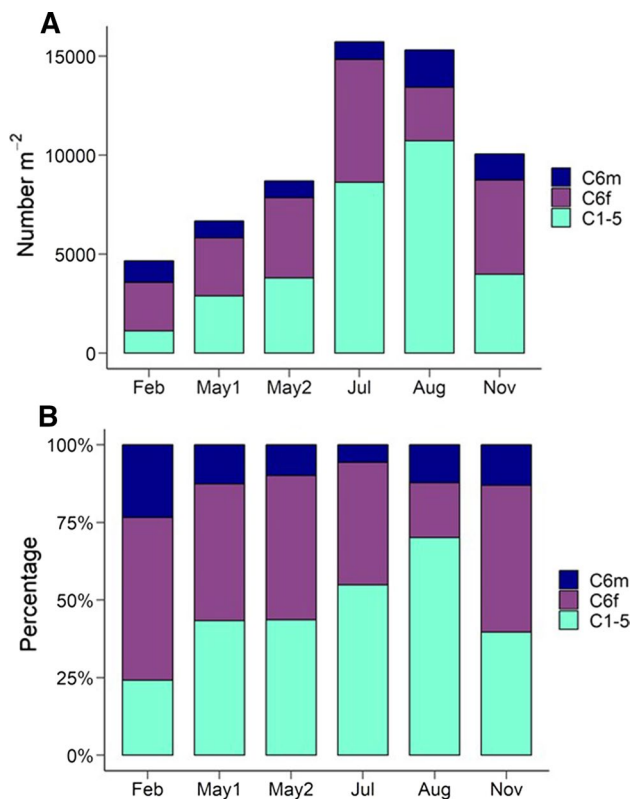
Fig. 9 *Metridia longa*. Total depth integrated (0–1800 m) number (**a**) and relative number (**b**) of copepodite stages at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite of data collected during 2006, 2007, and 2008 (Table 1)

individuals m^{-2} (Fig. 3b). After May, the numbers increased markedly to a maximum in July and August (~ 60,000 individuals m^{-2}). In November, relatively small numbers were again observed (~ 7000 individuals m^{-2}).

Oithona spp.

The genus *Oithona* was represented by two species, *O. similis* and *O. spinirostris*. However, as they were usually counted as belonging to one group, they are treated together in the present analysis.

In February, while concentrations were highest in the uppermost depth layer (0–50 m), more than half of the stock was caught below 100 m (Fig. 10b). The population shifted to shallower depths in May and from then on and until August, the depth distribution was rather similar, with concentrations generally being highest in the uppermost depth layer and only a very small part of the stock staying below 100 m. In November, most of the stock was observed at 400–1000 m depth.

The numbers of *Oithona* spp. integrated over the depth range of the samples was low in February (~ 4000

individuals m^{-2}) and fluctuated from ~ 25,000 to ~ 34,000 individuals m^{-2} in May (Fig. 3b). In July, numbers had increased markedly (~ 120,000 individuals m^{-2}) and in August a maximum was observed (~ 140,000 individuals m^{-2}). In November, low winter values (~ 3000 individuals m^{-2}) were again observed.

Oncaea spp.

During winter (February), the animals resided deep in the water column (~ 600–1000 m) (Fig. 10c). In early May, the population had shifted to shallower depths (100–400 m) and thus appeared to be in the process of ascending to the surface. In late May and in July, the population was mainly found relatively shallow in the water column (0–200 m), whereas already by August, the animals had returned to the deeper layers (400–1000 m).

Integrated numbers were low in February and May, fluctuating between ~ 5000 and ~ 9000 individuals m^{-2} (Fig. 3B). Numbers had increased by July (~ 30,000 individuals m^{-2}) to a maximum in August (~ 43,000 individuals m^{-2}). In November, numbers had decreased again to low winter values (~ 7000 individuals m^{-2}).

Other copepods

Several other copepods were found in the samples, but only in relatively low numbers. These rarer copepods are listed in Gislason and Silva (2012). Of these relatively rare copepods, copepods of the genus *Euchaeta* represented considerable biomass (~ 5%), while being very rare numerically. In the Iceland Sea, the genus is represented by four species (*E. glacialis, E. norvegica, E. barbata*, and *E. hanseni*) and they will be dealt with in a separate paper.

Discussion

The seasonal dynamics of nutrient concentrations and phytoplankton development during the study are described in Palsson et al. (2012). In the central Iceland Sea, phytoplankton spring growth began in April and culminated in late May, reflecting stratification of the water column due to warming of surface waters in spring. After the main bloom event, significant phytoplankton growth continued until end of August. The increase in primary production during spring and summer was associated with a rapid and simultaneous decrease in the concentrations of nitrate (Palsson et al. 2012). Similarly, in the southeastern parts of the Iceland Sea, the main growth season of the phytoplankton is confined to the four-month period of May–August (Astthorsson and Gislason 2003).
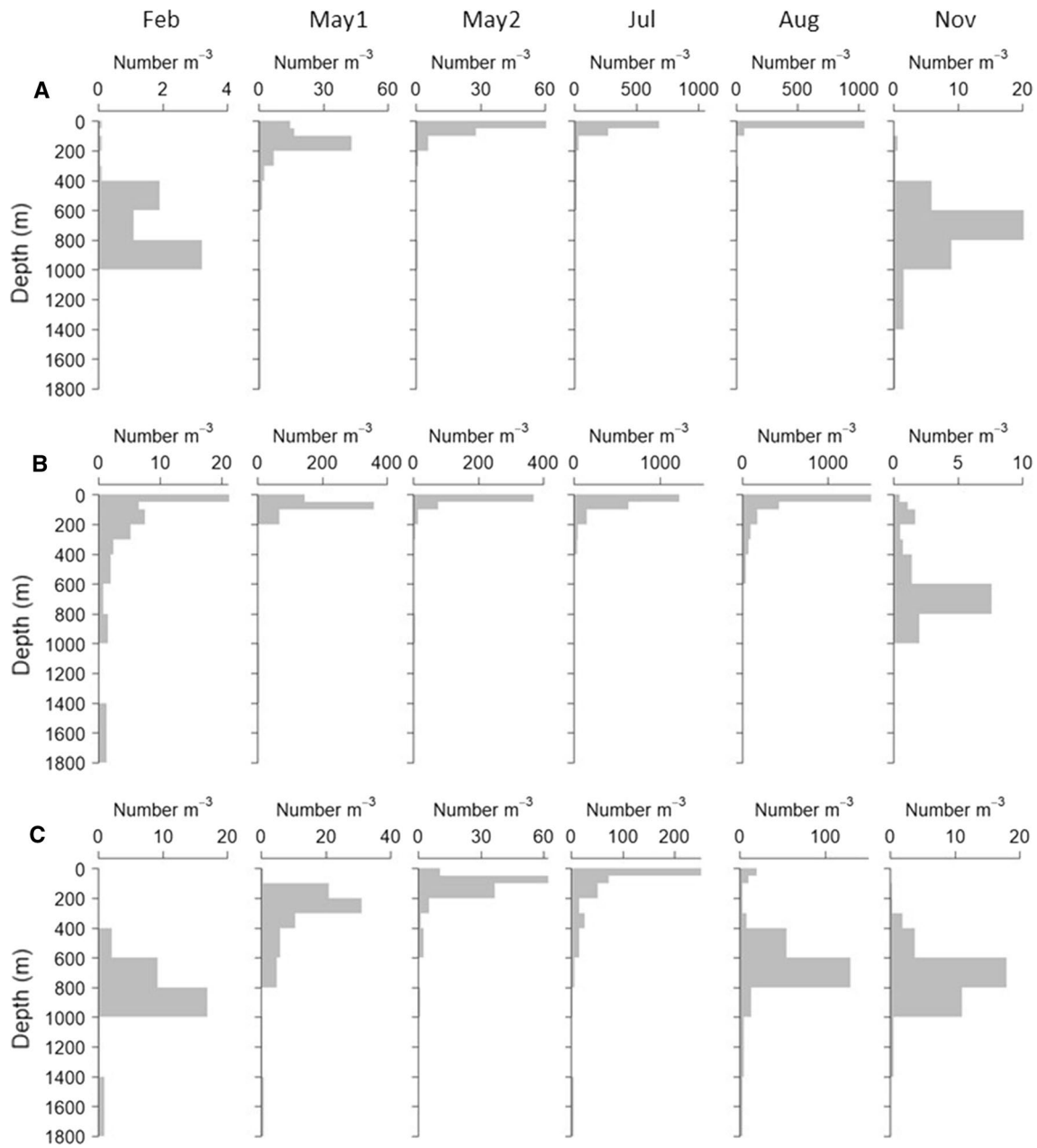
Fig. 10 Vertical distribution of *Pseudocalanus* spp. (**a**), *Oithona* spp. (**b**), and *Oncaea* spp. (**c**) at sampling stations in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. Composite of data collected during 2006, 2007, and 2008 (Table 1). Note the change in abundance scales for the various months

Composition

In general, the copepod species reported here are also reported among the most abundant ones in other Arctic and sub-Arctic seas, with dominance of *C. hyperboreus*, *C. finmarchicus*, and *M. longa* in terms of biomass and *Oithona* spp. in numbers (Hassel 1986; Richter 1994; Kosobokova and Hirche 2000; Head et al. 2003; Hopcroft et al. 2005).

Life cycle strategies

In the Iceland Sea, the studied copepods exhibited clear similarities and differences in seasonal abundance, vertical distribution, and age structure, reflecting differences in the life history of these species. All the species stayed relatively deep during winter and shallow during spring and summer. However, the extent of ontogenetic vertical migration varied among species. For all species, the main increase in numbers

was observed during late summer, but the time spent in surface waters during the summer growing season differed among species.

Calanus hyperboreus

The presence of juvenile and adult stages in the winter samples, as we have found (Fig. 5), indicates a multiyear life cycle (Conover 1988). As stated in the results section, females were present at all sampling times, while males only during winter and fall (February, November) (Fig. 5) below 400 m depth (Fig. 4). Thus, the males most likely fertilize the females during winter deep in the water column and die thereafter. The offspring from the winter spawning (C1s) were seen in greatest abundance during the first half of May (Fig. 5). From this and the mean temperatures in the water below 100 m depth in March–April (~ 0 °C), peak spawning may be estimated by back-calculations using Belehradek equations (Corkett et al. 1986), to have occurred around February–March. The C1s appeared to develop into C4s during the summer in the surface layers as evidenced by an increase in the incidence of C2s, C3s, and C4s from the latter half of May till July in the surface layers (Figs. 4, 5). Mating and release of eggs at depth during winter is in line with previous reports that egg production in this species is independent of the algal bloom, being fuelled by internal body reserves (Conover 1988; Hirche and Niehoff 1996; Melle and Skjoldal 1998; Ashjian et al. 2003). During the summer, adult females made up a significant part of the population (Fig. 5); however, they were probably not reproductively active as males were hardly recorded in the population at that time. During autumn (August), when most of the stock had returned to deep waters for overwintering (Fig. 4), the population consisted mainly of stages C3–5 (Fig. 5). The C3s and C4s were probably derived from previous winter's spawning, whereas the C5s were likely more than 1 year old, possibly 2 years old. The incidence of C5s decreased from August to November, whereas that of adults increased. This indicates that the C5s were moulting into adult males and females during autumn and winter. Moulting of C5 into adults during winter accords with what Hirche (1997) proposed for the populations in the Greenland Sea and Madsen et al. (2001) for the population in Disco Bay. The adult females and males that were found in November constitute the part of the population that would spawn in late winter to produce a new generation. If the above interpretation of the seasonal stage composition holds, the life cycle of *C. hyperboreus* in the Iceland Sea takes 2 years to be completed, with development into C4s the first year and into adults the second year. If, however, during the first year the offspring from the winter spawning only develop to stage C3, then the life cycle probably takes 3 years to be completed (into C3 the first year, into C5 the second year, and to adults the

third year). Model studies indicate that C3 *C. hyperboreus* have accumulated enough storage lipids to survive the winter (Falk-Petersen et al. 2009) and thus it is quite possible that the animals only develop to C3 the first summer in their lives. The stage structure, with an increase in incidence of C4s from May to July (Fig. 5), does, however, indicate that at least a part of the population grows to C4 the first summer, so I feel a 2-year life cycle is more likely than a 3-year one. Similarly, Astthorsson and Gislason (2003) interpreted the seasonal stage composition of *C. hyperboreus* along a cross shelf transect northeast of Iceland as at least biannual.

In Arctic and sub-Arctic regions, *C. hyperboreus* generally has a 2–4-year life cycle (Conover 1988; Richter 1994; Hirche 1997; Madsen et al. 2001; Ashjian et al. 2003), whereas in the southern regions and in fjords in Norway and Svalbard the species is reported as annual (Digby 1954; Matthews et al. 1978; Smith and Schnack-Schiel 1990; Arnkværn et al. 2005). The long life span in Arctic environments is generally considered an adaption to the variable food supply at high latitudes (Conover 1988; Falk-Petersen et al. 2009).

The stocks of C. *hyperboreus* in the Iceland Sea rise to the surface probably mainly during March and April. They stay in the surface layers (mostly above 100 m depth) from May to July, and the return migration is completed by August. Thus, the growing period of the population in the surface waters appears to be confined to the three-month period of May–July (Fig. 4). This is in line with observations from the southeastern fringes of the Iceland Sea (Astthorsson and Gislason 2003) and the neighbouring Greenland Sea (Hirche 1997). The relatively short growing period in the surface waters is consistent with the multi-annual life cycle of this species.

Calanus finmarchicus

The abundance of C1s was by far the greatest on 25–27 July both in relative and absolute terms (Fig. 7), and from this and the surface temperatures in May (~ 0–1 °C, Fig. 2), peak spawning may be estimated by back-calculating, using temperature functions for stage duration (Corkett et al. 1986; Campbell et al. 2001), to have occurred in May–June, i.e. approximately coinciding with the spring bloom maximum (Palsson et al. 2012). The growth of the new generation then mainly takes place in the surface layers (0–50 m) from May to August. In the southern and eastern fringes of the Iceland Sea, the main spawning of *C. finmarchicus* is reported to take place somewhat earlier (April and May), likely reflecting an earlier development of the bloom in these areas (Gislason and Astthorsson 1998; Astthorsson and Gislason 2003). The close association between the spawning of *C. finmarchicus* and phytoplankton growth has previously been shown by many workers (see Melle et al. 2014 for a review).

The vertical distribution by stages in February (Fig. 6), with relatively high abundance of males deep in the water column, suggests that mating may take place at depth while the animals are ascending to the surface after the overwintering period. This is a similar pattern as found in the waters to the south and west of Iceland (Gislason and Astthorsson 2000).

Worth noting is the relatively high proportion of C4s among the overwintering animals (~ 20–30%, Fig. 7). This is much higher than in the warmer waters off the south and west coasts of Iceland (~ 12–14%, Gislason and Astthorsson 2000). The relatively high proportion of C4s is not unique for the waters around Iceland and has been observed in several other regions (see Melle et al. 2014 for a review). As pointed out by Melle et al. (2014), it is unlikely that the C4s would be able to moult to C5s without feeding as they are much smaller. It is therefore most likely that they would develop further (to C5s and adults) during the summer after having ascended to the productive surface layers. The data presented here, with one main peak in abundance of C1–3 recruits, clearly point to a 1-year life cycle of *C. finmarchicus* in the sub-Arctic waters north of Iceland as also found in the earlier studies from the southern parts of the Iceland Sea (Gislason and Astthorsson 1998; Astthorsson and Gislason 2003).

In the Iceland Sea, *C. finmarchicus* overwintered at ~ 200–600 m depth, the major part, i.e. those staying below 300 m, at sub-zero temperatures (Figs. 2, 6). This is a very different overwintering environment than in the Irminger and the Iceland Basins southwest and south of Iceland, where the overwintered animals are distributed from ~ 400 to ~ 1500 m depth at temperatures between 3 and 5 °C (Gislason and Astthorsson 2000). The depth at which *C. finmarchicus* overwinters varies greatly throughout its distributional range, from ~ 100 to ~ 400 m in the Gulf of Maine Channel, the Laurentian Channel, and Eastern Scotian Slope waters to ~ 400–1500 m in the basins southwest of Iceland (Melle et al. 2014). The widely different depth and temperature regimes experienced by *C. finmarchicus* in the different overwintering habitats are suggestive for the broad plasticity in this species with respect to the physical environment. While a detailed discussion of the possible reasons for these differences is beyond the scope of this paper, it seems unlikely that local populations in the North Atlantic have different depth and/or temperature preferences. More likely the choice of overwintering depth is governed by either predation pressure (Kaartvedt 1996) or seawater-copepod density contrast (Visser and Jonasdottir 1999). We did not measure the density of the copepods, and information on the predatory field during the cruises is limited. In the basins south and southwest of Iceland, significant parts of the overwintering population reside below the potential predation pressure represented by mesopelagic predators of sound scattering layers (mainly mesopelagic fish, Gislason et al. 2007). Similarly, Dale et al. (1999) found overwintering *C. finmarchicus* to be centred below the sound scattering layers in the Norwegian Sea, with the depth distribution becoming shallower as the sound scattering layers became shallower and weaker. During the winter cruises in the Iceland Sea, comparable deep scattering layers were not observed (Petursdottir 2012), indicating the paucity of mesopelagic fish in the Iceland Sea. The rareness of planktivorous mesopelagic fish in the Iceland Sea may thus be a factor in explaining the shallower distribution of *C. finmarchicus* in the Iceland Sea compared to the deep basins in southwest and south of Iceland.

Calanus finmarchicus is the biomass dominant copepod in the North Atlantic, and the present study is the first one to describe its seasonal abundance in the sub-Arctic Iceland Sea, based on sampling from the whole water column thus providing an estimate of total stock abundance. Abundance and distribution of overwintering animals that resupply shelf waters in spring are of paramount importance for biological productivity on the shelf. Comparison of winter abundance estimates from the present study with those from other areas is therefore of interest. The winter abundance of *C. finmarchicus* in the Iceland Sea as observed in the present investigation (~ 14,000–20,000 individuals m^{-2}, Fig. 7) is similar to that observed in the Labrador Sea (~ 15,000–20,000 individuals m^{-2}), the Irminger Sea (~ 10,000–15,000 individuals m^{-2}), and the Iceland Basin (~ 15,000–20,000 individuals m^{-2}) (Gislason and Astthorsson 2000; Heath et al. 2004; Head and Pepin 2008). In the Norwegian Sea, the winter abundance of *C. finmarchicus* appears higher (~ 15,000–40,000 individuals m^{-2}), while of the same order of magnitude (Dale et al. 1999; Heath et al. 2004). Therefore, the abundance of overwintering animals in the sub-Arctic Iceland Sea is comparable to those observed in the Labrador/Irminger Seas and the Southern Norwegian Sea, the two major overwintering areas of the species, underlining the importance of the Iceland Sea as overwintering site of *C. finmarchicus*.

Metridia longa

As the juvenile stages were lumped together in the present study, the data cannot be used to elucidate precisely the life cycle of *M. longa*. However, the fact that adults of both sexes were relatively abundant at all seasons is indicative of some reproduction activity throughout the year. From the increase in numbers of juveniles from winter to July–August, it is likely that reproduction took place mainly during spring and summer. In Balsfjorden, Northern Norway, the species has an annual life cycle with spawning occurring from early to mid-May (Tande and Grönvik 1983; Grönvik and Hopkins 1984), while from the Greenland Sea, Richter (1994)

reported the recruitment of the youngest copepodites as taking place in late summer.

A considerable fraction of the *M. longa* population stayed near the surface at all sampling times, with males being present at all sampling occasions. They are omnivorous (Haq 1967) species that do not rely strongly on internal energy reserves (Hagen and Auel 2001). This, together with the relatively shallow depth distribution, indicates that the animals were active at all times. This is in accordance with reports from other areas (e.g. ; Grönvik and Hopkins 1984; Diel 1991; Ashjian et al. 2003). Information on the seasonal depth distribution of this species in other areas of the North Atlantic is limited, but data from the western Arctic ocean (Ashjian et al. 2003) show greatest abundances at mid-depths during winter, like we found here (Fig. 8). Males appeared generally to have a deeper depth distribution than the females (Fig. 8), which could indicate mating at depth and/or different feeding capabilities of the males compared to the females (Gislason 2008). The vertical distribution appeared bimodal in fall and early winter, which may reflect diurnal migration activity (Pearre 2003). This interpretation

is supported by a plot of the weighted mean depths of *M. longa* by day and night, showing that the weighted mean depths were shallower during night than day on all cruises when differences in sunlight between day and night were evident (Fig. 11c). This is an indication of the activity of these animals throughout the year. *M. longa* is known to perform extensive diel vertical migrations (Grondahl and Hernroth 1986; Diel 1991; Mumm 1993; Falkenhaug et al. 1997; Daase et al. 2008), and the seasonal depth distribution observed here is likely to be obscured by this fact.

Pseudocalanus spp.

As the developmental stages of *Pseudocalanus* spp. were not separated, it is difficult to evaluate to what extent the increase after May reflects reproduction of the animals. However, since the seasonal pattern is very clear, with low values during winter and spring and one main increase from May to July–August (Figs. 3b, 10a), it is considered most likely that the main breeding activity occurred sometime between May and July. As judge by the vertical distribution

Fig. 11 Weighted mean depths of *Calanus hyperboreus* (**a**), *Calanus finmarchicus* (**b**), *Metridia longa* (**c**), *Pseudocalanus* spp. (**d**), *Oithona* spp. (**e**), and *Oncaea* spp. (**f**) in the Iceland Sea from February to November. May 1 and May 2 denote the first and second half of May, respectively. White circles: Animals sampled during daylight; black circles: Animals sampled during darkness
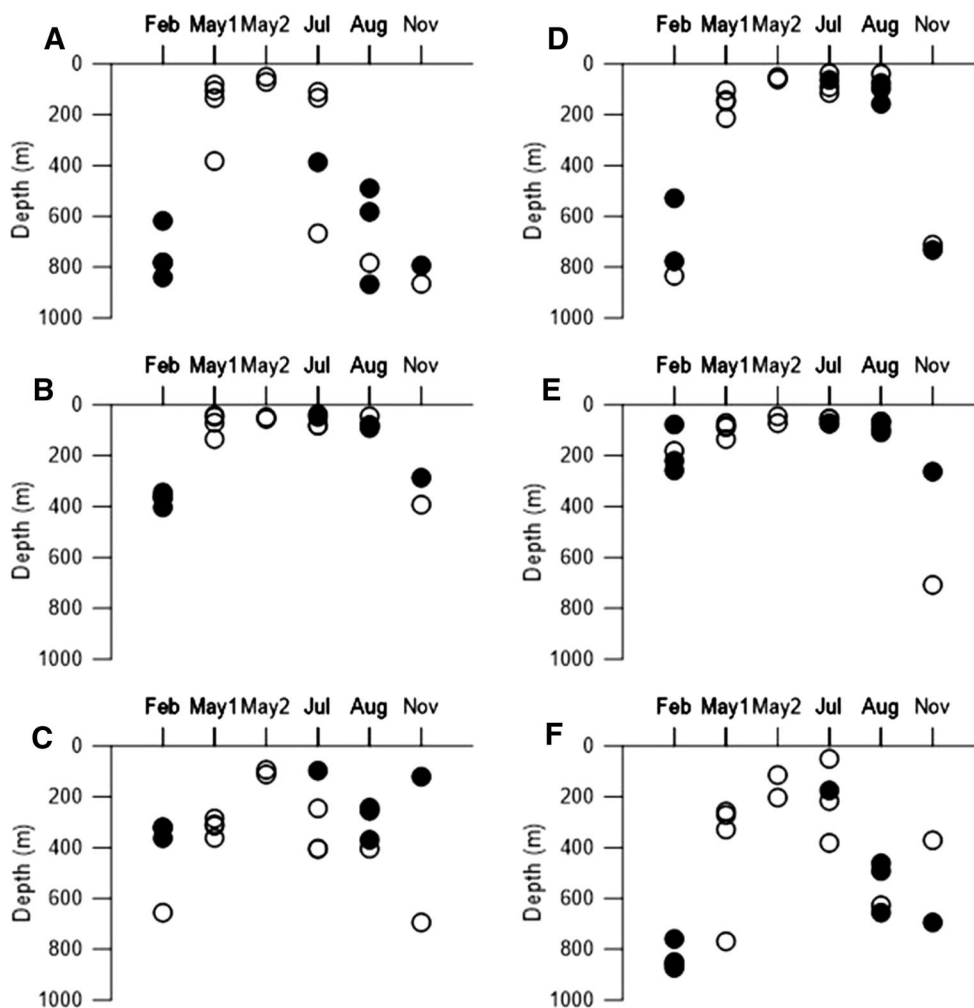
(Fig. 10a), the spring growth probably mainly took place in the upper layers (~ 0–50 m).

While *Pseudocalanus* spp. had a generally deeper depth distribution during winter than *C. finmarchicus*, the rise to the surface between February and May and descent after August took place at similar time for both groups. As with *C. finmarchicus*, the reproduction of both *P. minutus* and *P. acuspes* is linked to the phytoplankton spring bloom (Lischka and Hagen 2005; Renz et al. 2007) and they both accumulate large lipid reserves during summer for overwintering (McLaren et al. 1989; Norrbin 1991). In that sense, *Pseudocalanus* spp. and *C. finmarchicus* follow the same life history strategy. The annual maximum in July–August points to a one-year life cycle as has been observed for *P. minutus* and *P. acuspes* in Arctic environments (Kwasniewski 1990; Conover and Sifred 1993; Lischka and Hagen 2005).

Oithona spp.

As with *Pseudocalanus* spp., the stages of *Oithona* spp. were not separated and therefore it is difficult to evaluate when reproduction took place. From the distinct increase in total numbers that took place from May to July when the stocks were mostly found in the upper layers, it is considered most likely that breeding and growth took place during this period in the surface layers (Figs. 3b, 10b).

The seasonal depth distribution of *Oithona* spp. was generally similar to that of *Pseudocalanus* spp., except in February when *Oithona* spp. stayed much shallower than *Pseudocalanus* spp. (Figs. 10, 11). *Oithona* spp. is reported to have an omnivorous diet during all seasons (Lischka and Hagen 2007). The relatively shallow distribution of the species at most sampling times is indicative for the activity of the species throughout most of the year. From the Greenland Sea, Richter (1994) reported *Oithona* spp. as mesopelagic species year-round (0–500 m) showing continued development in the absence of phytoplankton production, but with the main breeding period in early summer in the surface layer. Similarly, in the western Arctic Ocean, abundance is generally greatest in the upper layers and reproduction probably occurs year-round (Ashjian et al. 2003).

Oncaea spp.

Although *Oncaea* spp was not classed to developmental stages in the present study, the increase in total numbers from May to July–August points to that the main growth of the population took place during the spring and summer months (Figs. 3b, 10c). From the seasonal depth distribution, the growth appears mainly to take place relatively shallow in the water column (Fig. 10c).

Of the species studied here, *Oncaea* spp. spent the shortest time in the surface layers, late May until July. At other times of the year, the animals stayed relatively deep. *Oncaea* spp. is mainly omnivorous (Kattner et al. 2003), and in the Iceland Basin and the Irminger Sea, the breeding activity appears not to be confined to a particular season of the year (Gislason 2008). In the Greenland Sea, the breeding season is more extended than that of *Oithona* spp. (Richter 1994).

Summary

As stated in the Introduction, the purpose of this study was to describe the population development, ontogenetic vertical migration, and life cycle of the dominant copepods in the Iceland Sea. The results demonstrate that the most abundant copepods differed in their life history strategies. *C. hyperboreus* is unique in that it has the deepest winter distribution, reproduces at depth in the absence of phytoplankton food, and spends relatively short time in the surface layers during summer (Fig. 11a). *C. finmarchicus* also hibernates at depth, however much shallower than *C. hyperboreus* and the reproduction at the surface is timed to the productive period of phytoplankton (Fig. 11b). Based on the seasonal stage structure, a 2- to 3-year life cycle is proposed for *C. hyperboreus* and a 1-year for *C. finmarchicus*. *Pseudocalanus* spp. appear to have a similar life history as *C. finmarchicus*, while occupying intermediate depths between *C. finmarchicus* and *C. hyperboreus* during the overwintering period (Fig. 11d). As judged by the relatively late increase in numbers of *M. longa* (July–August) and the presence of adults of both sexes throughout the year, the life history of this omnivorous species appears relatively decoupled from the phytoplankton spring bloom. The same applies to the omnivorous species *Oithona* spp. and *Oncaea* spp.

Compliance with ethical standards

Conflict of interest The author has no conflicts of interest to declare.

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