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Original Article

Calanus finmarchicus basin scale life history traits and role in community carbon turnover during spring

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The copepod *Calanus finmarchicus* was investigated in four Subpolar Basins, Labrador, Irminger, Iceland, and Norwegian Seas, during spring, covering the time of ascent, grazing, and initiation of reproduction in the area. Lipid content, spawning activity, and stage composition and vital rates, such as egg and faecal pellet production were measured and linked to environmental parameters. Specific egg- and faecal pellet production rates varied with diatom biomass and were negatively correlated with temperature. Comparison of the various biological indicators revealed different life history traits *C. finmarchicus* has adopted in the different basins. In Labrador Sea, the females have invested in large eggs compared to the remaining basins. Labrador and Irminger Sea *C. finmarchicus* invest in size that we propose to be adaptation to cope with warmer overwintering habitats resulting in larger potential lipid storage capacity, while the Iceland and Norwegian Sea females can invest their remaining lipid storage in spring to fuel lipid-driven egg production. Grazing pressure on the phytoplankton community was estimated and compared between copepod and two dominating groups of protozooplankton; ciliates and heterotrophic dinoflagellates. Despite approximately the same biomass in the upper 100 m, the grazing impact of the protozoan grazers was an order of magnitude higher than the *C. finmarchicus* dominated mesozooplankton. This illustrates the importance to also include the smallest grazers when studying the spring bloom in high latitude marine ecosystems if the fate of the primary production should be fully understood.

Keywords: *Calanus finmarchicus*, egg production, grazing pressure, lipid content, carbon, life history traits and trade-offs.

Introduction

The Subpolar North Atlantic is a highly productive ecosystem, rich in commercially important fish stocks. While staying relatively dormant over the winter months, the initiation of the spring bloom initiates a highly productive chain reaction of intensive feeding activity, from heterotrophic protozoans to pelagic fish, birds, and whales. Fish migrations are tuned to the copepod production (Broms *et al.*, 2012) — where one of the main prey is the lipid rich and highly abundant copepod *Calanus finmarchicus* (Dalpadado *et al.*, 2000; Bachiller *et al.*, 2016).

The spring bloom is a key element in the global carbon cycling and consequently knowledge about its fate is essential for our understanding of the contribution of the Subarctic to global productivity and carbon sequestering. In this context, the copepods are important, not only as a base of fish production but also by accelerating the vertical carbon export through production of large fast sinking faecal pellets (Kobari *et al.*, 2008; Stamieszkin *et al.*, 2015). The larger copepods are the main grazers of phytoplankton during the spring bloom and produce fast sinking faecal pellets in association with the bloom (Dünweber *et al.*, 2010; Swalethorp *et al.*, 2011). However, to understand the role of Subpolar North Atlantic in the global carbon cycling and carbon-sequestering context the smaller grazers on the primary producers need to be included and considered. In particular, after the spring bloom when the *C. finmarchicus* have left the surface layers, the non-*Calanus* copepods components of the food web can be of major importance (Levinsen *et al.*, 2000; Møller *et al.*, 2006; Madsen *et al.*, 2008; Koski *et al.*, 2020). Also during the bloom when the copepods ingestion become saturated, the predation pressure on the protist relaxes, and the protozooplankton can build up high biomasses and dominate the grazing on the primary producers (Levinsen and Nielsen, 2002; Seuthe *et al.*, 2011; Riisgaard *et al.*, 2014).

Calanus finmarchicus it is probably the most studied of all marine copepod species, due to its life history success and for being a key species in the North Atlantic Ecosystem (Dalpadado *et al.*, 2000; Falk-Petersen *et al.*, 2007; Prokopchuk, 2009; Langøy *et al.*, 2012). It is an oceanic species that spends up to 10 months of the year overwintering in the deep water basins (Heath *et al.*, 2000; Melle *et al.*, 2014; Jónasdóttir *et al.*, 2019). In late-winter/spring, the populations ascent to surface waters and the individuals are carried with ocean currents onto the shelf seas where they feed on the developing phytoplankton and spawn, and the new generation prepares for the coming winter by accumulating large lipid reserves (Conover, 1988; Falk-Petersen *et al.*, 2009; Head *et al.*, 2013). The species descents as sub-adult stage 5 (C5) to the mesopelagic zone under the mixed layer depth, where it is quiescent in state of diapause. They use the lipid reserves for both buoyancy control and as energy for basic metabolism (Visser and Jónasdóttir, 1999) and contribute to the biological carbon pump by the means of the lipid pump (Jónasdóttir *et al.*, 2015; Visser *et al.*, 2017). Duration of diapause depends on the amount of lipids — or storage lipid fullness and overwintering temperatures (Wilson *et al.*, 2016; Jónasdóttir *et al.*, 2019). The metabolism, and thus the usage of the lipid energy

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depends on the temperature at the overwintering depths and therefore differs between habitats, and ocean areas (Jónasdóttir *et al.*, 2019). The amount of remaining lipids at ascent is expected to vary depending on the initial lipid content (copepod size), temperature at diapause (rate of lipid catabolism), and other strategies related to life history traits of diapause.

The timing of the ascent varies in the different places in the North Atlantic (Melle *et al.*, 2014). Once at the surface, *C. finmarchicus* is of a major importance as food for fish larvae and planktivorous fish such as sand eel (van Deurs *et al.*, 2009). Off shelf, *C. finmarchicus* is also heavily predated on by mackerel, herring, and blue whiting (Bachiller *et al.*, 2016). From copepodite stage 3 (C3) the copepods start directing energy towards lipid accumulation (Falk-Petersen *et al.*, 2009) and at stage C5 they descend as early as June to winter diapause (Melle *et al.*, 2014).

The spring bloom is also the key event in the life cycle of *Calanus finmarchicus*. It sets the schedule of life history events — from spawning to maturation to diapause. It is arguably the successful matching between life history strategy and the annual productivity cycle that make *C. finmarchicus* and its related cousin species, *C. glacialis*, and *C. hyperboreus,* so important for the ecology of Boreal and Subpolar Seas. To deal with a short growing season in the Subpolar Seas, *C. finmarchicus* has adapted several key life history traits. Such traits include body size, lipid accumulation, type of lipids they accumulate and deep winter diapause. These traits are adapted to the overwintering temperatures, to timing and length of spring bloom and to a one-year reproduction cycle.

Temperatures at the overwintering depths affect the rate of utilization of the storage lipids and therefore, length of diapause (Saumweber and Durbin, 2006; Wilson *et al.*, 2016). Diapause duration is a crucial trade-off that is controlled by lipid content and metabolism (Dahms, 1995; Pierson *et al.*, 2013). The trade-off for longer diapause is for example to develop larger body size and consequently increased lipid storage capacity. Body size and lipid capacity also dictate how much energy the copepod can direct towards gonad development and eventually their early preparation for egg production in spring. The type of lipid accumulated is also a trait to maximise energy per unit volume and to enable the copepods to stay at depth during overwintering (Visser and Jónasdóttir, 1999).

During the spring 2013 the research vessel G.O. Sars crossed four basins of the Subpolar Seas (SPS); the Norwegian Sea (NWS), Iceland Sea (ICS), Irminger Sea (IRM) and Labrador Sea (LS). This gave a unique opportunity to estimate and compare the biology of the copepod *Calanus finmarchicus* during spring ascent across SPS basins. The purpose of this investigation presented here was (i) to assess the *C. finmarchicus* vital rates across the SPS basins between Bergen, Norway to Nuuk, Greenland, (ii) to estimate time of ascent of *C. finmarchicus*, and (iii) to investigate possible life history traits developed by the different populations based on female body size, egg size and lipid content of copepodite stage 5 and females. While *C. finmarchicus* and other larger copepods are the major grazers during the spring bloom, smaller copepod species and protozoans take over as grazers on the primary producers after the bloom (Levinsen *et al.*, 2000; Madsen *et al.*, 2008; Koski *et al.*, 2020). However, knowledge on these small fast-growing protozooplankton in North Atlantic pelagic food webs is very limited. The second goal of the investigation was therefore to compare the role of the *C. finmarchicus* dominated mesozooplankton with the role of protozooplankton in carbon turnover.

Methods

Physical and biological sampling was carried out on the EuroBasin Trans-Atlantic cruise on the RV G.O. Sars (Marine Research Institute, Bergen Norway, cruise 2013107) from 1 May to 14 June 2013. The cruise track crossed the Subarctic Seas (SPS) covering 29 stations in the Norwegian Sea (n = 5), Iceland Sea (n = 5), Irminger Sea (n = 10), and Labrador Sea (n = 9) (Figure 1; Table 1) . The physical environment was measured by deploying a CTD equipped with an Aqua-III fluorometer at all stations (Drinkwater *et al.*, 2020). The fluorometer was calibrated for chlorophyll *a*. The phyto- and protozooplankton community were sampled from 10 m depth, assumed to represent the mixed layer. Water was sampled in 100 ml amber glass bottles. Protists were fixed with neutralized Lugol´s solution and counted and identified under compound light microscope, described in detail in Naustvoll *et al.* (2020). For the present study, we consolidated the counts into micro-plankton types; flagellates, dinoflagellates diatoms, and ciliates and present the data as carbon based concentration (see below). Water for nutrient analyses (silicate, nitrate, nitrite, and phosphate) was sampled with 10 L Niskin bottles from 7 to 10 depths. Water from the bottles was collected into 20 ml polyethylene vials, and conserved with 0.2 ml chloroform, stored at 4°C and analysed at shore with an autoanalyser as described in Bagøien *et al.* (2012). Here, we present average nutrient values from the upper 100 m.

Calanus finmarchicus stage abundance

Zooplankton for depth-stratified abundance, species and stage composition was sampled on 25 stations on the cruise track, but did not always fall on the same stations as the vital rates were measured (Figure 1). A MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System; Wiebe *et al.*, 1985) was used, equipped with eight nets (180 μm mesh size). The system was towed obliquely from 1000 m depth, sampling at 200 m intervals up to 200 m. The last four nets sampled layers between 200–100, 100–50, 50–25, and 25–0 m. In the present study, we used combined data on *C. finmarchicus* stage and abundance from the three last nets covering the upper 100 m of the water column to represent the population used for egg production and feeding measurements. Analysis of samples are presented in detail in Strand *et al.* (2020) where species identification of *C. finmarchicus* and *C. glacialis* was based on differences in stage specific length as presented in Skjoldal *et al.* (2013).

Calanus finmarchicus egg production and hatching

Live copepods were collected from the upper 100 m by a vertical gentle tow with a T-80 net (375 μm mesh size) with a 1 L non-draining cod-end. Immediately after the net retrieval, the sample was diluted into 10 L bucket containing surface seawater. In the laboratory, 20 active *Calanus finmarchicus* females were selected under stereomicroscope, and incubated to measure vital rates. Two different incubation methods were used and we refer to Table 1 for the stations those methods were used. In method-1, individual females were incubated in 400 ml containers, composed of 2 chambers

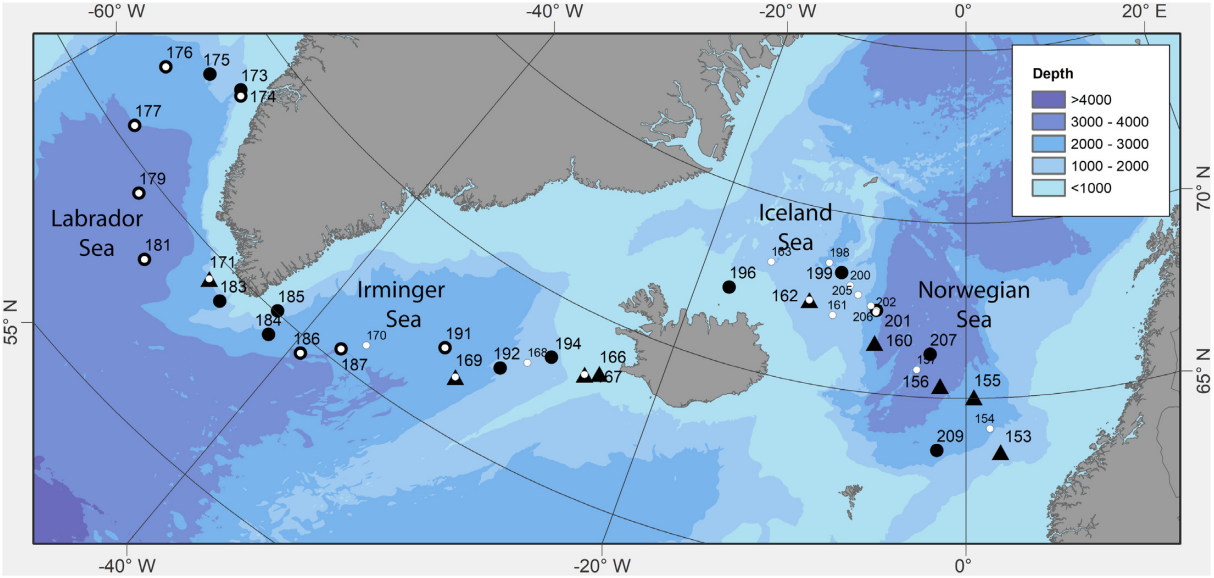

Figure 1. Sampling locations during G.O. Sars cruise May–June 2013. Station numbers as in Table 1. Sampling stations for *Calanus finmarchicus* vital rate measurements; solid black triangles stations from Bergen to Nuuk, solid black circles return stations from Nuuk to Bergen; White dots and station numbers with smaller font, mark the stations the multinet samples for zooplankton abundance were taken.

Table 1. Station details, Location: Latitude and Longitude in degrees, Norwegian Sea (NWS), Iceland Sea (ICS), Irminger Sea (IRM), and Labrador Sea (LS).

Station	Latitude	Longitude	Location	Date	Time UTC	Depth m	Measures
153	63.76	02.28	NWS	040513	10:30	212	E_1, SA, PL
155	65.06	−00.86	NWS	050513	08:00	1521	E_1, SA, PL
156	65.57	−02.39	NWS	060513	01:15	3246	E_1, SA, PL
160	66.70	−07.78	ICS	080513	06:45	1783	E_1, SA, PL
162	67.56	−12.50	ICS	100513	06:30	1756	E_1, SA, PL
166	63.83	−24.28	IRM	140513	22:45	224	E_1, SA, PL
167	63.51	−25.57	IRM	150513	04:45	315	E_1, SA, PL
169	61.91	−32.86	IRM	160513	13:00	2829	E_1, SA, PL
171	59.64	−46.32	LS	200513	12:00	1100	E_1, SA, PL
173	63.82	−53.04	LS	250513	01:30	87	$E_{1,2}$, SA, H, PL, ES, FP, CG
174	63.64	−53.54	LS	250513	09:30	1300	$E_{1,2}$, SA, H, PL, ES, FP, CG
175	63.08	−55.15	LS	250513	22:30	1864	$E_{1,2}$, SA, H, PL, ES, FP, CG
176	62.23	−57.36	LS	260513	11:00	2487	$E_{1,2}$, SA, H, PL, ES, FP, CG
177	60.83	−55.03	LS	270513	10:15	2935	$E_{1,2}$, SA, H, PL, ES, FP, CG
179	59.78	−52.28	LS	280513	12:00	3366	E_1, SA, CG
181	58.71	−49.15	LS	280513	17:00	3429	$E_{1,2}$, SA, H, PL, ES, FP, CG
183	59.25	−45.75	LS	290513	10:45	2120	E_2, SA, H, PL, ES, FP, CG
184	59.66	−43.00	IRM	300513	21:00	200	E_2, SA, H, PL, ES, FP, CG
185	60.08	−42.20	IRM	310513	02:00	251	$E_{1,2}$, SA, H, PL, ES, FP
186	59.95	−40.97	IRM	310513	13:30	2370	E_2, SA, H, PL, ES, FP, CG
187	60.63	−38.11	IRM	010613	22:00	2904	E_2, SA, H, PL, ES, FP, CG
191	62.13	−33.14	IRM	030613	01:30	2921	$E_{1,2}$, SA, H, PL, ES, FP, CG
192	62.65	−30.92	IRM	030613	21:30	2500	E_1, SA, CG
194	63.56	−27.01	IRM	040613	17:00	1151	$E_{1,2}$, SA, H, PL, ES, FP
196	67.18	−18.55	ICS	060613	22:30	370	E_2, SA, H, PL, ES, FP, CG
199	68.46	−10.54	ICS	070613	23:15	2102	$E_{1,2}$, SA, H, PL, ES, FP, CG
201	67.58	−07.56	ICS	080613	22:30	1947	$E_{1,2}$, SA, H, PL, ES, FP, CG
207	66.37	−03.79	NWS	110613	01:45	2437	E_2, SA, H, PL, ES, FP, CG
209	63.84	02.24	NWS	120613	06:15	1600	E_2, SA, H, PL, ES, FP, CG

Date (ddmmyy) and time (UTC: Coordinated Universal Time) of the first CTD, bottom depth (m). Measures are the vital rates measured at the stations, for *Calanus finmarchicus*: egg production rates (E), spawning activity (SA), egg hatching success (H), prosome length (PL), and egg size (ES), faecal pellet production (FP), community grazing (CG). E with underscore 1 and 2 indicates where the two different incubation methods for egg production measures were carried out (see text). Please refer to Figure 1 for zooplankton sampling locations.

separated by 375 μm mesh, filled with seawater screened at 90 µm (Stenevik *et al.*, 2007). In method-2 individual females were incubated in 50 μm screened seawater (from 6 m depth) in 600 ml polycarbonate bottles without a separation screen. Both methods aimed for 20 replicates. The bottles were incubated in a temperature-controlled room set at surface temperatures for 24 h. All samples were kept cool during sorting and preparation of the incubations.

After incubation, for both methods, the content of the bottles was filtered onto a 40 μm sieve, the female removed and

prosome length either measured directly or photographed for later measurements and eggs counted. Prosome length of the females was measured using a calibrated ocular scale in a Leica stereo microscope or the image was calibrated to pixel size and length measured using image-J (Rasband, 2011). In method-2 the diameter of the eggs were measured and faecal pellets were counted and their length and width measured using calibrated ocular scale under an inverted microscope. On average 40 eggs were measured from each station (range; 7–99 eggs) and 70 pellets (range: 18–110 pellets). For method-2, egg clutches from six of the 20 females were further incubated in 6×60 mm petri dishes at 5°C. After 4 days, numbers of nauplii and unhatched eggs were counted (total production) and the hatching success calculated as % nauplii of the total production. Spawning activity was estimated as the % of incubated females that produced a clutch over 2 eggs d^{-1}.

Calanus finmarchicus oil sac volume

From the photos of the life egg producing females taken for size as described above, and randomly attained C5s, the circumference lipid sacs were traced using Image-J (Rasband, 2011) calibrated to pixel size. The lipid sac area was converted into wax esters by using the formula, $\mu gWE = 0.167 \times A^{1.42}$ from Vogedes *et al.* (2010) where A is the area of the lipid sac in mm^2.

Community faecal pellet production

The faecal pellet production of the copepod community was measured in short-time incubations. Copepods were collected with a fast net tow from the upper 100 m using 180-µm WP-2 net with a large non-filtering cod end. At the retrieval 4×200 ml subsamples from the cod-end were immediately distributed into 4 incubation containers, made of clear PVC tubes, 40 cm high and with an inner diameter of 8 cm and incubated in dark at *in-situ* temperatures. The concentrations in the incubation cylinders ranged from 25 to 100 copepods L^{-1}. While the specific composition of the mesozooplankton community was not identified, the bulk was composed of *Calanus* spp. of different stages. The cylinders were equipped with a 200-µm false-mesh bottom to reduce copepod feeding on the faecal pellets. Prior to the addition of copepods, the incubation containers were filled with 1.8 L of 10 µm prescreened surface water. The experimental setup took less than five min after retrieval of the nets. After 60–80 min incubation at *in situ* temperatures, the copepods and faecal pellets were concentrated on 200 and 10 µm sieves, respectively and preserved in Lugol's solution. Pellets and copepod were subsequently counted and measured and converted to carbon values as described below.

Carbon conversions

Phyto- and protozooplankton abundances (presented in Naustvoll *et al.*, 2020) were converted to carbon using species carbon values from the website, http://nordicmicroalgae.org. If the size of the respective species in the sample was not known, we used the average size values for that species from the web site. Carbon was calculated from cell volume using the conversions for diatoms, dinoflagellates and ciliates given by Menden-Deuer and Lessard (2000) for the respective groups.

For specific rates, eggs and pellets were converted to carbon values based on their volume according to Swalethorp *et al.* (2011). Egg volume (EV in μm^3) was calculated as a sphere based on the measured egg diameter, and carbon content estimated from egg volume as $\mu gC_{egg} = 1.10 \times 10^{-7}$ x EV. Faecal pellet volume (FPV in μm^3) was calculated as a volume of a cylinder based on the measured length and width, and carbon was estimated using the equation $\mu gC_{pellet} = 4.3 \times 10^{-8}$ x FPV. Female daily pellet production was estimated as gC m^{-2} d^{-1} based on pellet production rates and female abundance.

Female carbon was calculated based on the formula for measured pre-bloom females from Disko Bay, Greenland (Swalethorp *et al.*, 2011); $mgC_{female} = 0.0018 \times PL^{4.10}$ where PL is the prosome length in mm.

Calanus finmarchicus time of spawning

We calculated the approximate time of spawning by using Bělehrádek's temperature function, $DT = a\ (T + 9.11)^{-2.05}$ where DT is development time in days and T is temperature (Bělehrádek, 1935). The stage parameter estimates "a" we take from Campbell *et al.* (2001) to estimate the time from eggs to stage C3.

Grazing budget

To compare the potential grazing impact of the copepods and protozooplankton community (ciliates and heterotrophic dinoflagellates) in the upper 100 m of the water column we calculated the potential grazing rate of the two groups and compared that to the standing stock of phytoplankton. The biomass of phytoplankton was calculated using the observed carbon: chlorophyll *a* ratio of 82 estimated from the present survey.

The grazing of the protozooplankton was estimated from the general equations from Hansen *et al.* (1997), assuming maximum clearance rates for ciliates:

$$Log\,(C_{max}) = 1.491 - 0.23\ \log\,(P_{vol})$$

and for heterotrophic dinoflagellates:

$$\mathrm{Log}\,(C_{max}) = 0.851 - 0.23\ \log\,(P_{vol})$$

where C_{max} is the maximum specific clearance rate (10^5 h^{-1}) at 20°C and P_{vol} is the mean volume of the predator (ciliates and heterotrophic dinoflagellates, respectively). The average cell volumes of ciliates and heterotrophic dinoflagellates were calculated for each station. The clearance for each sampling station were adjusted for *in situ* temperatures by applying a Q_{10} of 2.8 (Hansen *et al.*, 1997). Average rates were calculated for each basin.

The specific copepod grazing rates were calculated for each station as the average of three independent methods (i) the specific egg production of the incubated *C. finmarchicus* females, (ii) the specific faecal pellet production of the incubated *C. finmarchcius* females, and (iii) the specific community faecal pellet production. From the specific pellet production the grazing rates were calculated assuming an assimilation efficiency of 68.2 (Conover, 1966) and the community grazing rate of the copepod community were calculated for each basin using the copepod biomass from Strand *et al.* (2020). The grazing rate applied in the carbon budget was the average of the specific egg production and the specific copepod community grazing using assimilation efficiency of 68.2 (Conover, 1966), multiplied with the copepod biomass m^{-2}.

Statistics

Statistical analyses were run using Sigma Plot statistical tools. All averages are presented with ± 1 standard error (*SE*).

Comparison of spawning activity between the four basins was analysed with one-way ANOVA. Due to difference in sampling size (unbalanced design) and failure to meet normality, the statistical comparison of the four basins was estimated by Kruskal–Wallis One Way ANOVA on ranks and included all basin differences in prosome length, egg size, lipid content, and vital rates. This method was also used to compare the two parallel egg production methods within each station. When differences were significant, ($p < 0.05$) Dunn´s method was used for multiple pairwise comparisons. Due to the multiple parameters potentially affecting vital rates and lack of linearity, we use principal component analysis (PCA) with temperature, nutrients, phytoplankton as chlorophyll *a*, phyto- and protozooplankton carbon, vital rates and female lipid content.

Results

Physical and chemical environment

The physical environment along the transect is presented in detail by Drinkwater *et al.* (2020) and nutrients are presented in Naustvoll *et al.* (2020). The 500 m temperature and salinity profiles along the cruise transect are presented spatially in Figure 2, but the temporal sequence is presented in Drinkwater *et al.* (2020). Focussing on the upper 100 m where the copepods were attained, the water mass properties varied greatly in temperature and salinity along the transect. Cold (0–4°C) and low saline (34–34.5 psu) water was observed in the LS. The western most stations of the IRM (St. 184 & 185) the East Greenland coastal current was clearly evident with subzero temperatures and low salinities (< 33.0 psu) while the Irminger Basin was generally warmer and more saline (5–8°C, >35 psu). Closer to Iceland (St. 192–166) the Atlantic current became gradually more apparent with warmer (6–8°C) and more saline (>35.0 psu) waters. In the Iceland Sea the water was < 0–5 °C with salinities between 34.5–35 psu that were also apparent in the western stations of the NWS (St. 160 and 201). The warm and saline Atlantic current was evident in the Eastern NWS but at the station closest to the Norwegian coast a less saline (33.5) but warm (>5°C) coastal current was apparent in the upper 100 m. The average temperature in the upper 100 meters of the water column ranged from −0.6 to 9.1°C (Table 2).

Nutrient concentrations (Figure 3b) averaged over upper 100 m ranged from being close to limiting to high: NO_3 ranged from 0.4 to 13 μM, PO_4 from 0.3 to 1 μM, Si from 0.7 to 7.2 μM and NO_2 μM from 0.03 to 0.23 μM. The concentration patterns of NO_3 μM, Si and PO_4 were very similar, with highest values in the IRM and similar in the remaining basins. The temporal resolution is presented in Naustvoll *et al.*, (2020).

Phytoplankton

The fluorescence based chlorophyll *a* concentration, averaged for the upper 50 m ranged from 0.3 to 7.9 μgChl *a* L^{-1} and the total phytoplankton carbon ranged from 42 to 467 μgC L^{-1}. The highest concentrations of both chlorophyll *a* and phytoplankton carbon were at the coastal stations around southern tip of Greenland where the biomass were primarily diatoms (Figure 3a). Diatoms constituted also about 50% of the phytoplankton carbon biomass in the Labrador Sea and at the coastal station southwest of Iceland. On the remaining stations, the biomass was predominantly composed of flagellates and dinoflagellates. The absence of diatoms in combination with high Si concentrations indicates that the spring bloom had not been initiated at those stations at the time of sampling. The phytoplankton community and bloom dynamics is described with the temporal resolution and discussed in more detail by Naustvoll *et al.* (2020).

Calanus finmarchicus abundances

The total abundance of *C. finmarchicus* in the upper 100 m of the water column ranged from 1000–20 000 ind. m^{-2} (Figure 4a). Copepodite stages 1–3 were observed in highest abundance and proportions (Figure 4b) in the two most coastal LS (174 and 171) and NWS stations (157 and 154). The overwintering stages C5 and C6 (females and males) were observed mostly at comparable concentrations (ca 3000 ind. m^{-2}) along the transect with the exception of stations 170 and 191 in the IRM and coastal stations in the NWS (157 and 154) where the abundance was between 5000–11 000 ind. m^{-2}. Stage C4 was observed in highest abundances and proportions of the population in ICS, and in lower abundances in all the remaining basins.

Calanus finmarchicus vital rates

Incubation method-1 (400 ml 2-chambers separated with a screen) and method-2 (600 ml bottles) gave different egg production rates when used at the same stations. Method-2 gave consistently higher egg production rates by an average of 1.7 times of method-1 (0.7–2.9 times). However, the difference was only significant for stations 179, 191, and 201 (Kruskal–Wallis One-Way Analysis of Variance on Ranks, $p < 0.05$). Therefore, at the stations where both methods were used the rates were averaged.

The proportion of spawning females (spawning activity: SA) varied from 6 to 100% d^{-1} (Figure 5a), with lowest proportion in the central IRM (6% d^{-1}, St. 167) and at the shelf break in the NWS (25% d^{-1}, St. 207). Overall, the average spawning activity in the basins ranged from 45 to 60% and was not significantly different between basins (Table 3, One-way ANOVA, $F_3 = 0.40$, $p = 0.75$).

Station 209 in NWS was the only station with no egg-producing females. Average egg production rates varied from 3 to 56 (St. 187 and 167 in the IRM) eggs $female^{-1}$ day^{-1} (Figure 5a) and maximum clutch size was observed to be 205 eggs $female^{-1}$ in the IRM (Table 2). Clutch size was over 100 eggs at 12 stations across the basins and was on average highest in the IRM and lowest in NWS. Hatching success was generally high (Figure 5c). The lowest average H% was 58 ± 16% in the ICS (St. 196), 79 ± 19% in the NWS (St. 207), and highest in IRM and LS, 97 ± 1% and 96 ± 2% (St. 184 and 181, respectively).

The time since spawning calculated by the Bělehrádek's temperature function based on stage 3 copepodites, showed that the C3's were from early April in the Norwegian and Irminger Seas and from mid April in the Labrador and Iceland Seas (Table 3).

Egg size presented as egg volume varied between stations (Table 2) with the significantly largest eggs in the LS and smallest in the remaining Basins ($H_3 = 339.1$, $p < 0.001$). Consequently, eggs in the LS had the highest carbon content on average (Table 2, Figure 5d). *Calanus finmarchicus* female size differed across the SPS, with largest females in the Labrador Sea and smallest in the Eastern Norwegian Sea (Figure 6a).

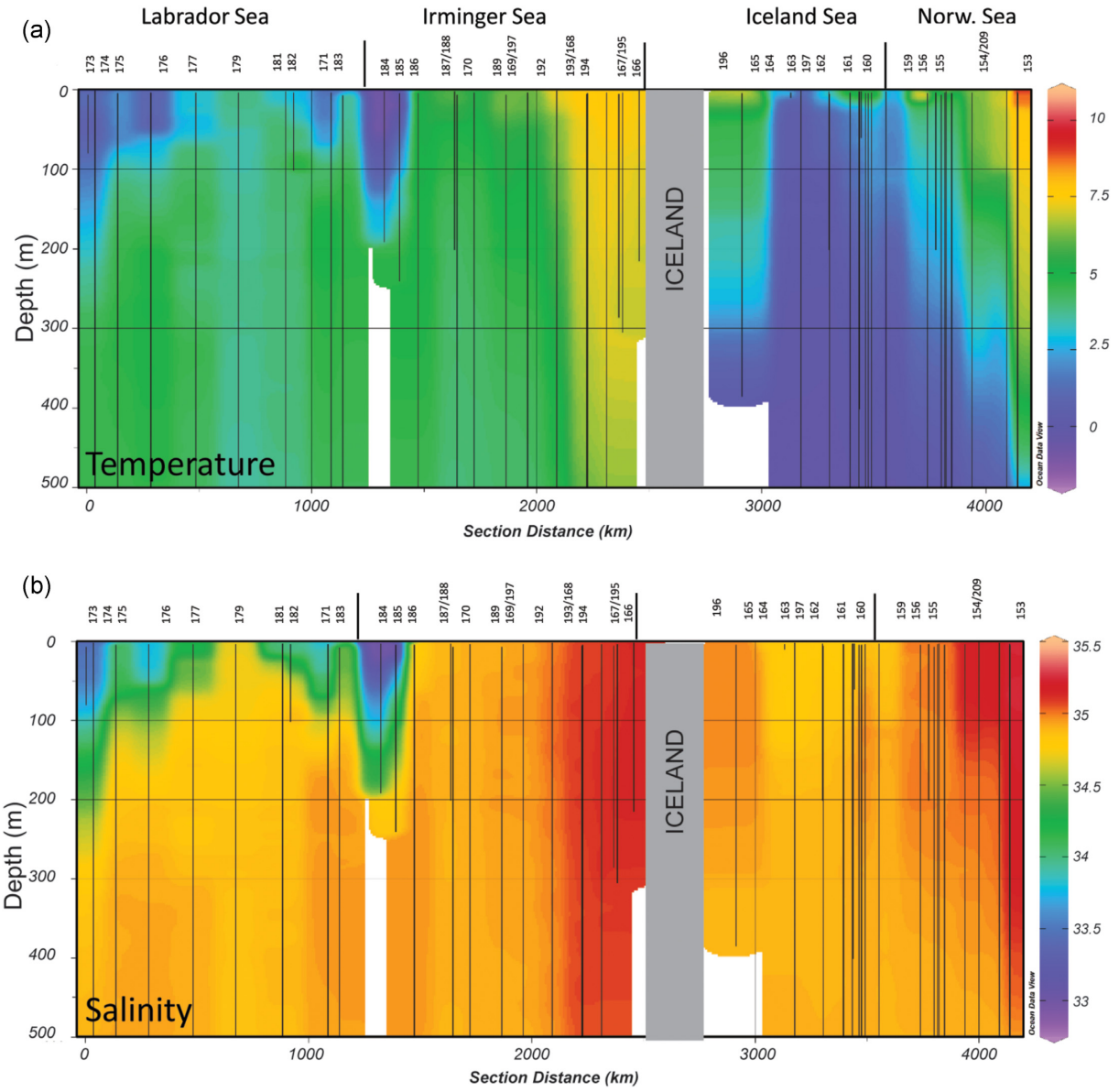

Figure 2. Upper 500 m profile of (a) Temperature (°C) and (b) Salinity across the transect from West: Labrador Sea (km 0) to East: Bergen (km 4450). Station numbers are as in Figure 1 and Ocean Basins as in Table 1. Figure generated in Ocean Data view.

There was no relationship between station averaged prosome lengths and station averaged egg volumes (linear regression, ANOVA on regression, n = 17, $F_1 = 0.25$, $p = 6.3$, values in Table 2).

Faecal pellet production of the females incubated in method-2 was measured as a proxy for *C. finmarchicus* feeding activity. The faecal pellet production was highest in the IRM with average 45 ± 3 pellets female^{-1} d^{-1} followed by 39 ± 3, 29 ± 4, and 23 ± 2 pellets female^{-1} d^{-1} (Average ± 1 *SE*), in ICS, NWS and LS, respectively (Figure 5b). Specific egg- and faecal pellet production rates (Figure 7a and *C. finmarchicus* rates in 7b) ranged from 0.01 to 0.13 d^{-1} at the different stations. NWS had the lowest specific egg production rate and both LS and NWS lowest specific faecal pellet production rates differing from the rates in the IRM and ICS (Table 3). The total female pellet production estimate was 0.9, 2.2, 4.6, and 1.3 mgC m^{-2} d^{-1} in LS, IRM, ICS, and NWS, respectively.

Integrated zooplankton community biomass and grazing potential

The depth integrated biomass of the three investigated zooplankton groups (mesozooplankton, ciliates, and dinoflagellates) were in the same order of magnitude (1000–1500 mgC m^{-2}) in the four basins, with the exception of the Irminger Sea, where the biomass of the heterotrophic dinoflagellates peaked (Figure 8a). When the trophic role of the three groups were compared, the fast turnover of the protozooplankton compared to the copepods is evident resulting in one order of magnitude higher grazing impact on the phytoplankton biomass compared to of the impact of mesozooplankton (Figure 8b).

Calanus finmarchicus lipid content

Wax ester (WE) content of females was on average 107 ± 6 µg female^{-1} in the LS, but under 20 µg female^{-1} and significantly lower in the other basins (Kruskal–Wallis One Way ANOVA;

Table 2. *Calanus finmarchicus* egg, faecal pellet, and female statistics.

Station	Location	T_{100}°C	n	Clutch size range	Clutch size average	Egg vol. $\mu m^3 \times 10^5$	Egg carbon ng egg^{-1}	Pellet vol. $\mu m^3 \times 10^6$	Pellet Carbon ng $pellet^{-1}$	Female prosome mm	Female carbon µg
173	LS	1.0	8	24–95	53 ± 9	23.8 ± 0.5	262 ± 6	4.3 ± 0.11	186 ± 4.9	2.72 ± 0.03	111 ± 4
174	LS	0.9	30	2–86	38 ± 5	23.1 ± 0.5	254 ± 6	3.4 ± 0.19	145 ± 8.0	2.85 ± 0.03	136 ± 6
175	LS	2.7	16	5–69	30 ± 5	Nm	Nm	2.9 ± 0.17	124 ± 7.4	2.80 ± 0.02	125 ± 4
176	LS	1.9	35	2–62	22 ± 3	22.7 ± 0.4	250 ± 5	1.6 ± 0.13	69 ± 5.4	2.82 ± 0.02	128 ± 5
177	LS	3.5	30	2–111	36 ± 5	22.9 ± 0.9	251 ± 10	3.2 ± 0.15	139 ± 6.4	2.87 ± 0.02	138 ± 5
179	LS	3.6	33	2–205	57 ± 8	20.5 ± 1.0	225 ± 11	2.5 ± 0.09	107 ± 9.5	2.91 ± 0.02	147 ± 5
181	LS	3.9	31	2–137	44 ± 6	22.2 ± 0.5	244 ± 6	3.7 ± 0.11	159 ± 8.6	2.91 ± 0.02	126 ± 4
171	LS	2.0	21	2–110	33 ± 6	Nm	Nm	Nm	Nm	2.67 ± 0.03	103 ± 5
183	LS	4.2	13	28–95	56 ± 5	22.5 ± 0.3	247 ± 3	2.7 ± 0.14	118 ± 6.1	2.84 ± 0.03	132 ± 5
Average		2.6 ± 0.4			40[a] ± 2	22.4 ± 0.4	247 ± 4	3.3[a] ± 0.07	141[a] ± 3.0	2.81[a] ± 0.01	130[a] ± 2
184	IRM	− 0.6	11	2–89	52 ± 9	19.9 ± 0.8	219 ± 8	3.7 ± 0.13	161 ± 5.8	2.66 ± 0.05	103 ± 7
185	IRM	0.2	34	2–183	55 ± 8	18.8 ± 0.8	206 ± 9	3.8 ± 0.13	164 ± 5.6	2.74 ± 0.03	115 ± 5
186	IRM	5.6	29	2–140	51 ± 7	14.9 ± 0.8	164 ± 8	2.0 ± 0.09	85 ± 3.9	2.84 ± 0.02	132 ± 5
187	IRM	5.2	1	57	57	17.2 ± 0.4	189 ± 5	1.8 ± 0.07	79 ± 3.2	2.87 ± 0.04	140 ± 8
191	IRM	5.6	11	2–118	47 ± 11	Nm	Nm	1.7 ± 0.08	74 ± 3.4	2.88 ± 0.02	139 ± 4
169	IRM	5.7	21	2–166	59 ± 10	Nm	Nm	Nm	Nm	2.78 ± 0.02	120 ± 3
192	IRM	6.7	19	2–136	66 ± 9	16.5 ± 1.0	181 ± 11	1.8 ± 0.08	78 ± 3.5	2.86 ± 0.02	137 ± 4
194	IRM	7.7	34	10–110	55 ± 4	18.0 ± 1.6	198 ± 18	2.1 ± 0.15	90 ± 6.6	2.83 ± 0.02	129 ± 4
167	IRM	7.5	10	8–195	67 ± 18	Nm	Nm	Nm	Nm	2.60 ± 0.04	91 ± 6
166	IRM	7.3	15	3–66	32 ± 5	Nm	Nm	Nm	Nm	2.58 ± 0.04	89 ± 6
Average		5.1 ± 0.9			54 ± 3	17.4[a] ± 0.6	192[a] ± 7	2.6[a] ± 0.07	114[a] ± 2.8	2.81[a] ± 0.01	125[a] ± 1.9
196	ICS	5.1	34	2–137	38 ± 6	17.3 ± 0.6	190 ± 6	2.2 ± 0.07	93 ± 3.2	2.72 ± 0.04	111 ± 6
162	ICS	0.4	9	3–39	19 ± 4	Nm	Nm	Nm	Nm	2.76 ± 0.04	117 ± 7
199	ICS	1.4	8	49–98	76 ± 6	17.5 ± 0.6	192 ± 7	1.2 ± 0.08	51 ± 3.3	2.76 ± 0.02	118 ± 4
160	ICS	1.7	26	4–92	44 ± 5	Nm	Nm	Nm	Nm	2.69 ± 0.04	106 ± 6
201	ICS	2.7	7	2–53	14 ± 7	17.8 ± 0.6	195.9 ± 6.0	2.2 ± 0.10	93 ± 44.6	2.70 ± 0.04	108 ± 4
Average		2.2 ± 0.8			40[a] ± 3	18.0[a] ± 1.6	198[a] ± 18	1.8[a] ± 0.06	79[a] ± 2.4	2.72 ± 0.01	112 ± 2
207	NWS	4.7	5	11–52	35 ± 8	17.5 ± 0.1	193 ± 2	1.5 ± 0.07	66 ± 3.1	2.64 ± 0.03	98 ± 4
156	NWS	3.8	13	2–54	29 ± 5	Nm	Nm	Nm	Nm	2.62 ± 0.04	95 ± 6
155	NWS	8.6	21	2–39	17 ± 2	Nm	Nm	Nm	Nm	2.66 ± 0.03	100 ± 5
209	NWS	6.3	0	0		No eggs	Nm	2.0 ± 0.10	88 ± 41.9	2.58 ± 0.03	90 ± 5
153	NWS	7.3	13	2–30	10 ± 3	Nm	Nm	Nm	Nm	2.58 ± 0.02	87.9 ± 3.6
Average		6.1 ± 0.9			20 ± 2	17.5[a] ± 0.1	193[a] ± 2	1.9[a] ± 0.07	80[a] ± 2.9	2.58 ± 0.01	93.1 ± 1.9

Average temperature ($temp_{100}$) in the upper 100 m of the water column, number of females with >two eggs (n), minimum and maximum clutch size >two eggs (# eggs), clutch size average (# eggs ± *SE*) average egg- and faecal pellet volumes ($\mu m^3 \pm SE$) and females (mm ± *SE*) and respective calculated carbon content in ng for eggs and pellets and µg for females (see text). Average ± *SE* is given for each Basin. Nm: not measured. Locations as in Table 1. Stations arranged from West to East, as in figures. Statistical comparison of means of the basins. Same lower case letters next to basin averages are not significantly different (Dunn's Pairwise Comparison $p << 0.05$i>).

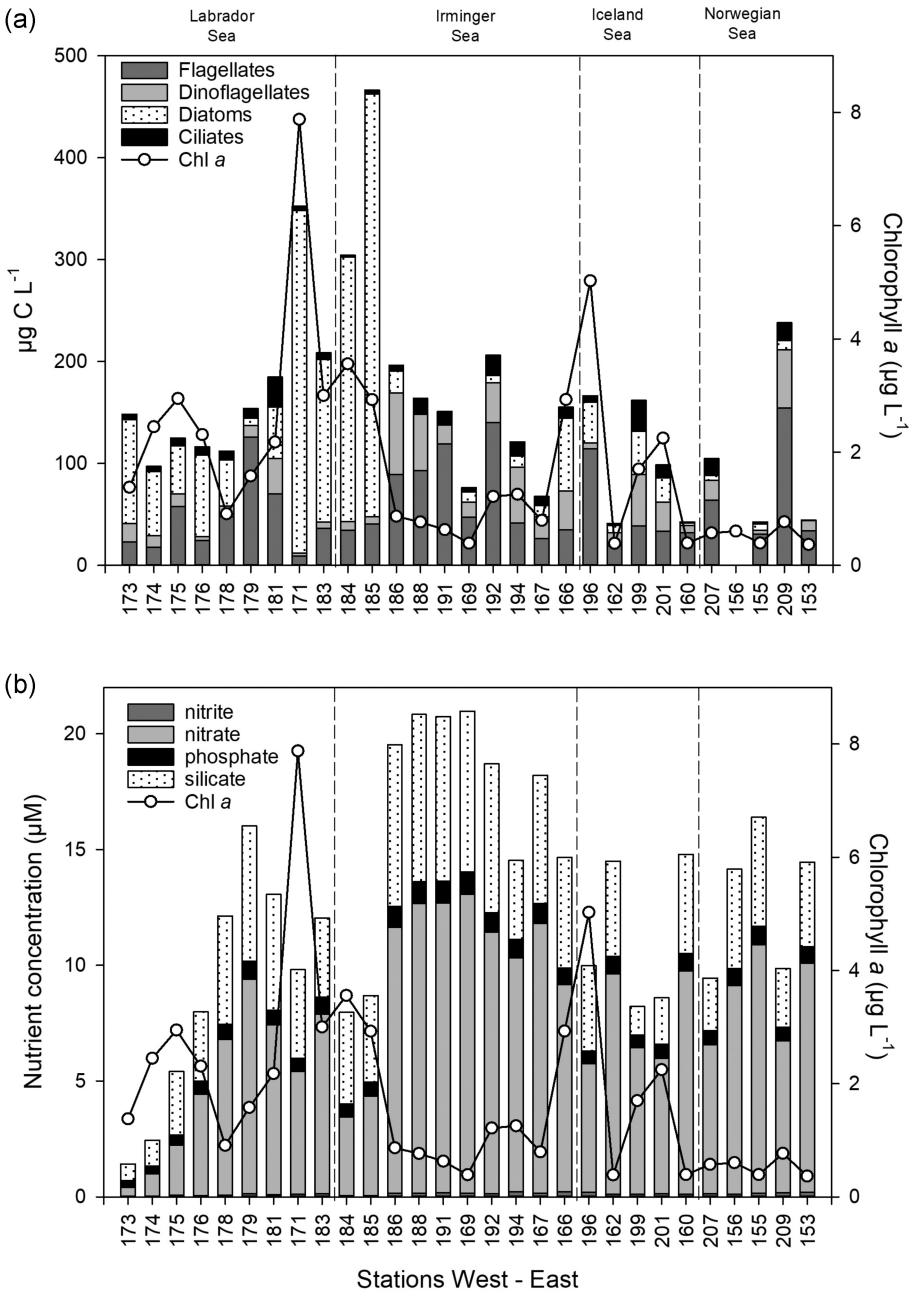

Figure 3. (a) Carbon based concentration (µgC L^{-1}) of different micro-plankton types (flagellates, dinoflagellates diatoms, and ciliates) and (b) Nutrient concentration (µM) averaged over the upper 50 m of the water column across the cruise trajectory. Chlorophyll *a* concentration (µg L^{-1}) overlaid as line graph over both panels. Stations arranged from West to East.

$H_3 = 174.7, p < 0.001$; average ±1 *SE*: 19 ± 2, 16 ± 2 and 13 ± 3 µg female^{-1} for IRM, ICS, and NWS, respectively). The average WE content in stage C5 measured 197 ± 15, 154 ± 13, 102 ± 14, 73 ± 9 µg indiv.$^{-1}$ ± 1 *SE*, in LS, IRM, ICS, and NWS, respectively (Figure 6b, Table 3).

Correlation with environmental parameters

The first two components of the PCA resulted in explaining 60% of the total variance variability of the data (Figure 9). The grouping of the entities showed that the vital rates (SpEp, SpFp, and female spawning activity) were positively correlated with the chlorophyll *a* and diatoms, and negatively with WE content of females. There was no correlation with the perpendicular group composed of the nutrient components, flagellates, and dinoflagellates.

Discussion

The main purpose of the present study was specifically to evaluate the state of *C. finmarchicus* populations during and after ascent from diapause in early spring across the SPS. The focus was on reproduction and grazing, in relation to numerous of physical and biological parameters to compare time of ascent and advancement of reproduction and grazing pressure in the basins covered. However, the information gained went well beyond the initial purpose and provides a base for a proposition of different life history traits *C. finmarchicus* has adopted

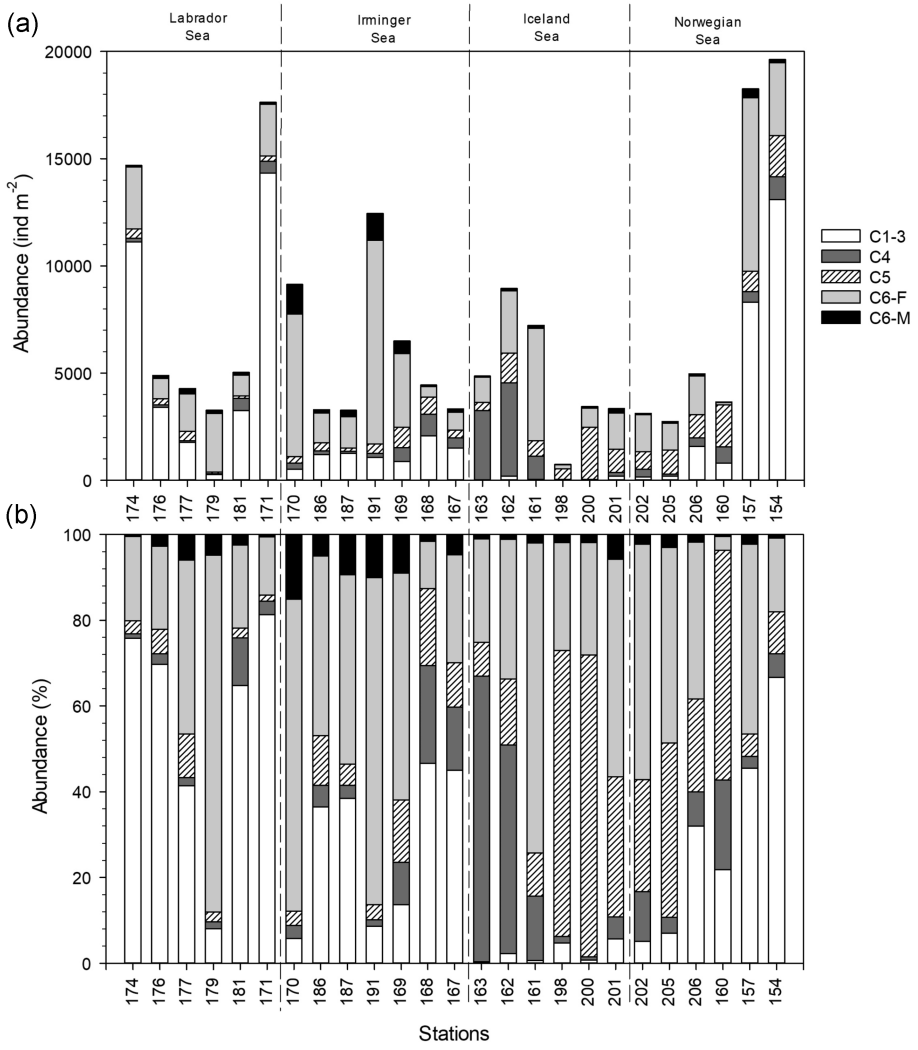

Figure 4. *Calanus finmarchicus* in the upper 100 m of the water column. (a) Abundance of stages C1–C6 (number m^{-2}) and (b) the relative stage composition (%) across the cruise trajectory. Copepod stages C1-3 are combined, C6-F: females C6-M: male.

in relation to the different environmental stressors. Table 4 summarises the general basin scale findings compared in the synthesis below.

Spring in the Subpolar Seas

The general environmental scene across the SPS was pre-spring bloom in IRM, early- to late spring bloom in ICS and NWS, and advanced bloom in LS (Figure 3b, Naustvoll *et al.*, 2020). The state of the bloom is estimated from silica and nitrate concentrations (Figure 3b) and nutrient depletion (Table 4, Naustvoll *et al.*, 2020). The *C. finmarchicus* populations had ascended from diapause in all basins (Strand *et al.*, 2020) and the observed station variability in egg production and grazing rates were best explained by food availability characterised by diatom biomass (Figure 9). Lipid content (WE) of females varied and was negatively correlated on PC2 with vital rates (with 21% explanation of the total variability), that is, high WE content coincide to low vital rates (early stage of production) and consequently, low lipid content with of more active grazing and egg production.

The time of spawning only shows approximation when the individuals at copepodite stage C3, were spawned based on day of sampling and the temperature at the respective stations. In this, we assume that the C3s sampled are of the first generation and the time of estimated spawning is close to the time of ascent. However, ascent is not a synchronous event and has been show to last about 60 days in the Faroe Shetland Channel (Heath, 1999). To better estimate initiation of spawning the population structure has to be taken into account and modelled, an exercise beyond the scope of the present study. In this study, however, this rough estimate is useful in the basin comparison of the populations, as it can be used in concert with other indicators to better compare the status of the population ascent. The female lipid content and presence of lipid rich stage 5 copepodites are such indicators (Jónasdóttir, 1999; Jónasdóttir *et al.*, 2008, 2019) while combination of the vital rate parameters, such as spawning activity, clutch sizes in combination with the stage composition can give an idea on the advancement of reproduction.

Life history traits

One of the most important and longest lasting periods in *C. finmarchicus* life cycle is overwintering to which the species

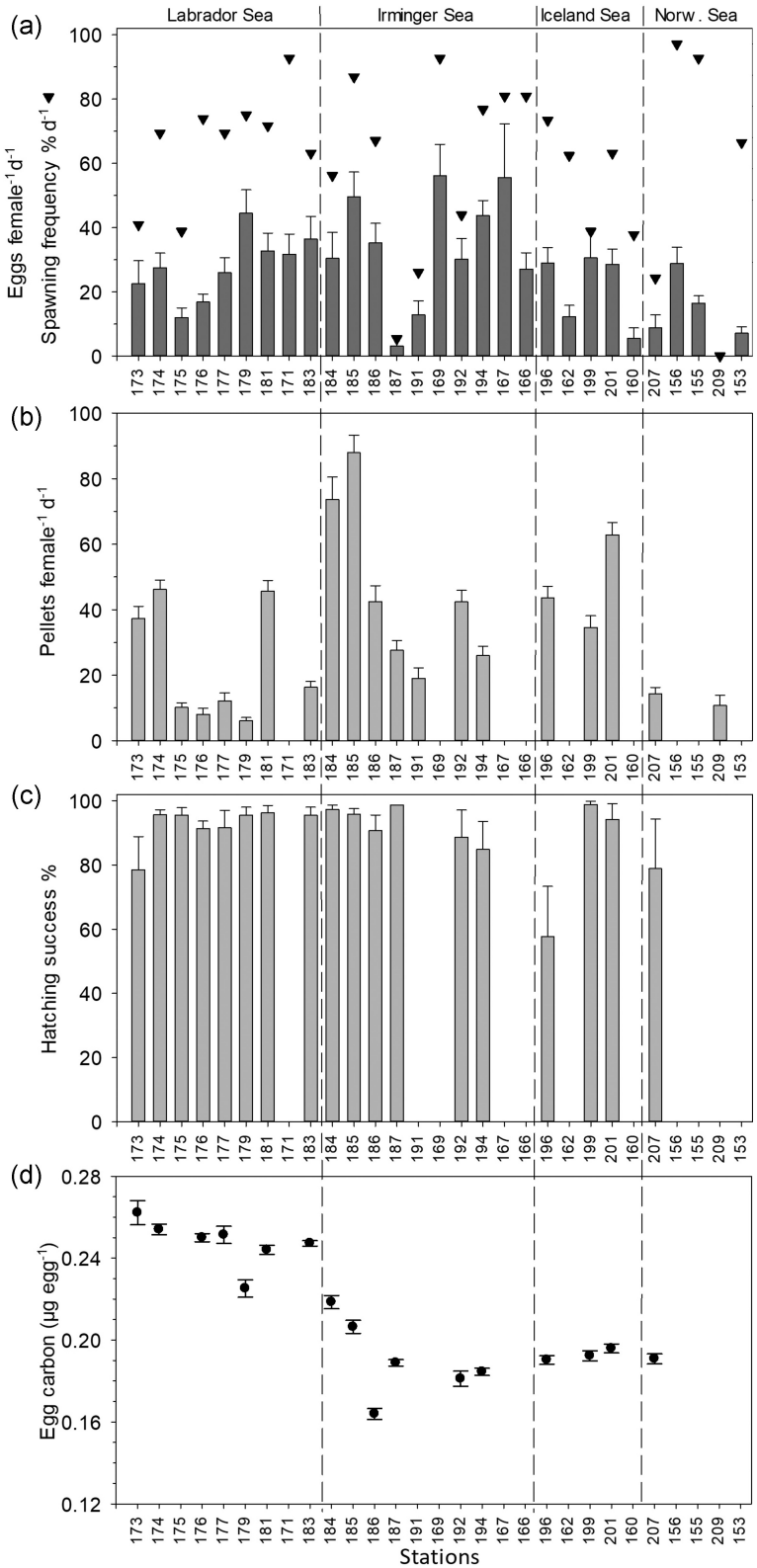

Figure 5. *Calanus finmarchicus* (a) egg production rates (eggs female^{-1} d^{-1}, histograms) and on same axes spawning frequency (% d^{-1}, filled triangles), (b) faecal pellet production (pellets female^{-1} d^{-1}), (c) hatching success (%) and (d) carbon content of eggs (µgC egg^{-1}). All means + *SE*. No bars in (a) station 209 is due to zero egg production rate but in (b) and (c) indicate lack of measurement (see Table 1).

must adapt in order to endure. The overwintering temperatures *C. finmarchicus* populations experience in the four basins differ considerably, ranging from sub-zero, −0.4 and −0.2°C in the Iceland and Norwegian Seas to 3.4 and 3.8°C in the Labrador and Irminger Seas, respectively (Heath *et al.*, 2000, 2004; Table 4). To their respective overwintering habitats, *C. finmarchicus* have adapted their lipid accumulation to cover their energy need and subsequent lipid utilisation

Table 3. Comparison of *C. finmarchicus* vital rates and other measures in the ocean basins (location as in Table 1).

Location		SER %	SPP %	SPP_{comm} %	Spawning activity %	WE C6 μg ind^{-1}	WE C5 μg ind^{-1}	Day of spawning	% pop C1-3
LS	Range	0–29	0–14	1–14	40–91	0–354	17–356	64–106	8–81
	Med	2.8	1.3	4.7	61	105	213	84	67
	Av	$5.3^{a} \pm 0.3$	3 ± 0.3	4.9 ± 1.6	$59^{a} \pm 2$	107 ± 6	$198^{a} \pm 14$	84 ± 6	57 ± 11
IRM	Range	0–47	0–26	0.6–2	6–91	0–172	51–276	35–128	6–47
	Med	3.7	3.1	1.4	68	7	137	111	37
	Av	$5.7^{a} \pm 0.4$	$5.8^{a} \pm 0.5$	1.5 ± 0.3	$58^{a} \pm 3$	$19^{a} \pm 2$	$154^{a} \pm 12$	99 ± 10	28 ± 7
ICS	Range	0–27	0–12	2–10	17–64	0–122	55–262	43–120	0–22
	Med	1.4	3.1	3.2	57	6	103	91	4
	Av	$4.3^{ab} \pm 0.5$	$3.5^{a} \pm 0.3$	5.1 ± 2.4	$48^{a} \pm 4$	$15^{a} \pm 2$	$109^{ab} \pm 14$	84 ± 14	5 ± 1
NWS	Range	0–12	0–7	2–3	0–92	0–188	4–188	60–140	5–67
	Med	0.7	0.7	2.7	42	0	51	95	39
	Av	$2.4^{b} \pm 0.3$	1.1 ± 0.2	2.7 ± 0.7	$47^{a} \pm 8$	$12^{a} \pm 3$	$62^{b} \pm 7$	107 ± 11	37 ± 13

The range, median (Med) and average (Av ± *SE*) of values for specific egg production rates (SER) faecal pellet production rates (SPP) and community faecal pellet production (SPP_{comm}), all as %, spawning activity (%), wax ester (WE) content of females (C6) and stage 5 copepodite (C5) (μg individual^{-1}), day of the year spawning occurred, calculated from the stage 3 copepodite (see text), and % of stage C1–C3 of the *C. finmarchicus* population. Vital rate averages with same lower case superscript letters are not significantly different between the basins (Dunn's Pairwise Comparison $p < 0.005$). No statistics performed on "Day of Spawning."

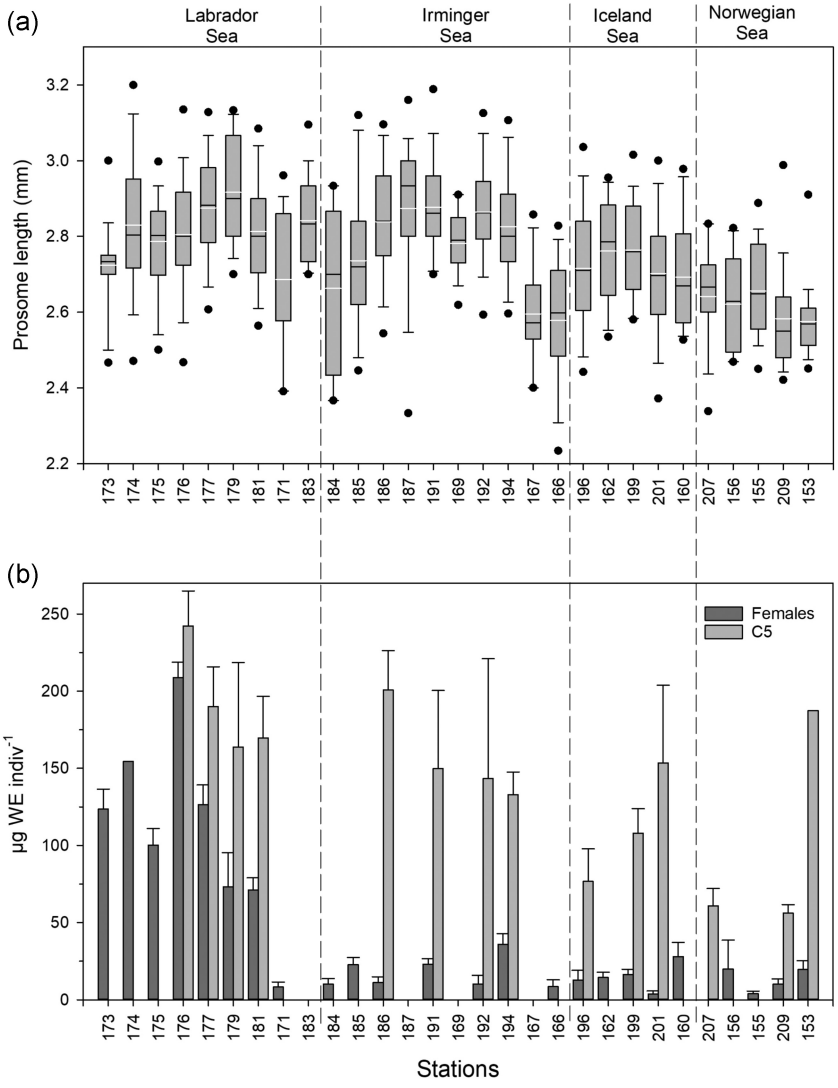

Figure 6. *Calanus finmarchicus* (a) female prosome length. Mean (white line) median (black line) and boxes, whiskers and dots show 25/75, 19/90, and 5/95 percentiles respectively. (b) Wax ester content (μg individual^{-1} ± 1 *SE*) of females and stage C5.

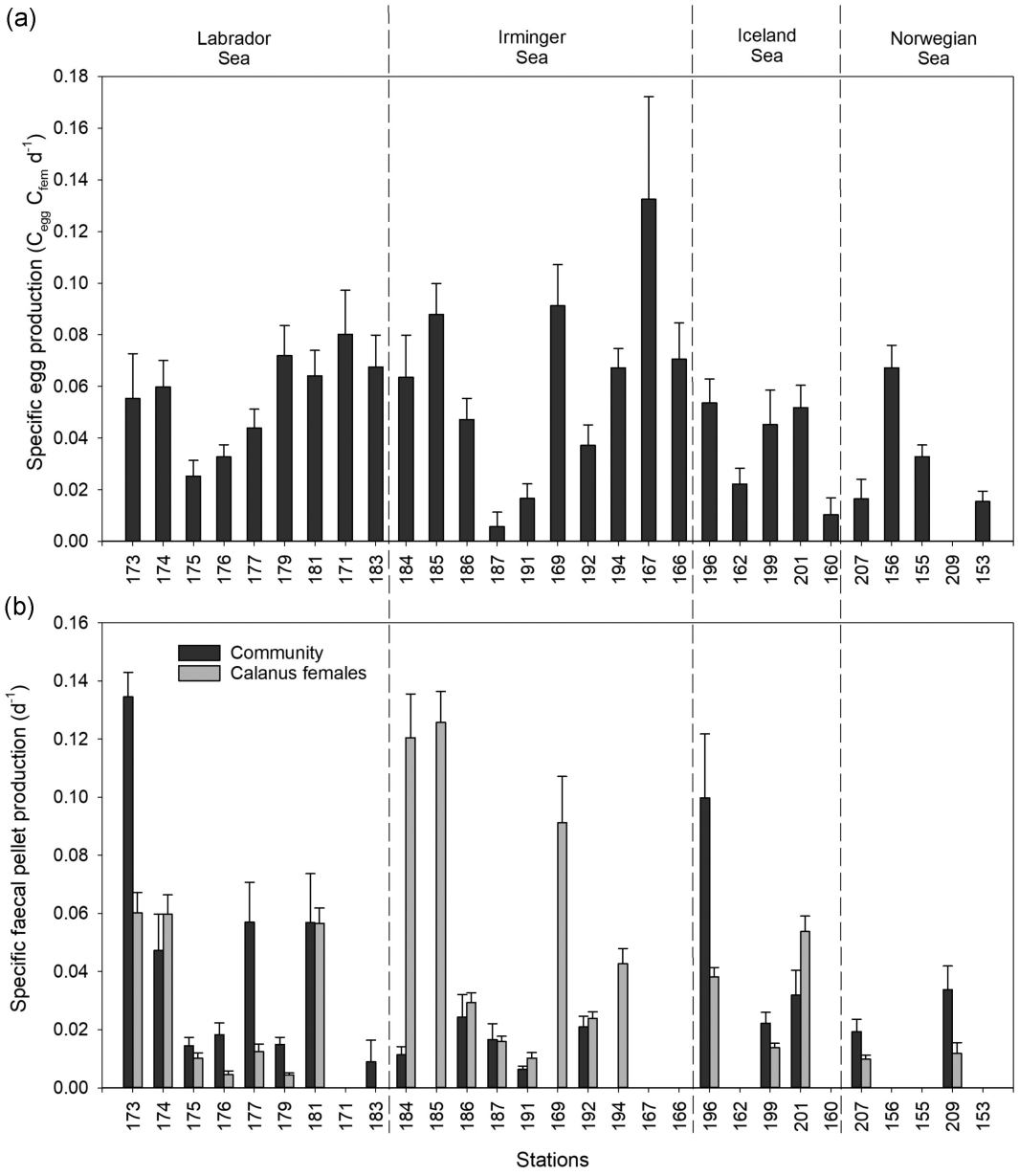

Figure 7. (a) *Calanus finmarchicus* specific egg production (C_{eggs} C_{female}^{-1} d^{-1}) (b) dark bars: zooplankton community and light bars: *C. finmarchicus* specific faecal pellet production (d^{-1}) mean ±1 *SE*.

during winter (Jónasdóttir *et al.*, 2019). Jónasdóttir *et al.* (2019) estimated the length of diapause for *C. finmarchicus* populations in North Atlantic basins, based on individual size of C5s in diapause (i.e. lipid storage capability) and the temperatures at the respective overwintering depths (Table 4). They concluded that a conservative diapause length for *C. finmarchicus* was about two months shorter in the Labrador and Irminger Seas than in the Iceland and Norwegian Seas (156, 144, 206, and 200 days for LS, IRM, ICS, and NWS, respectively). Size is therefore an important factor to include in our assessment of the life history traits in the different basins. According to metabolic theory (Arrhenius, 1889), larger body size results in lower specific metabolic rate (Visser et al, 2017) and is therefore an additional beneficial factor at higher overwintering temperatures.

LS

In Labrador Sea the females were large and lipid rich, indicating short time since ascent and early reproduction stage. The egg production of *C. finmarchicus* in the LS is an income breeding strategy, where spawning is strongly related to the initiation of the spring bloom (Head et al, 2000). The present observation of high female lipid content supports this finding and shows that the females do not seem to mobilise their lipid reserves to initiate egg production or energy demanding gonad development before the bloom. This strategy could be an adaptation to variation in the timing and magnitude of the spring bloom, and could provide an energy buffer to deal with such annual variations. The large eggs produced, may be and adoption to make the eggs and young more robust to survive, in case of early ascent, but the timing of the spring bloom is

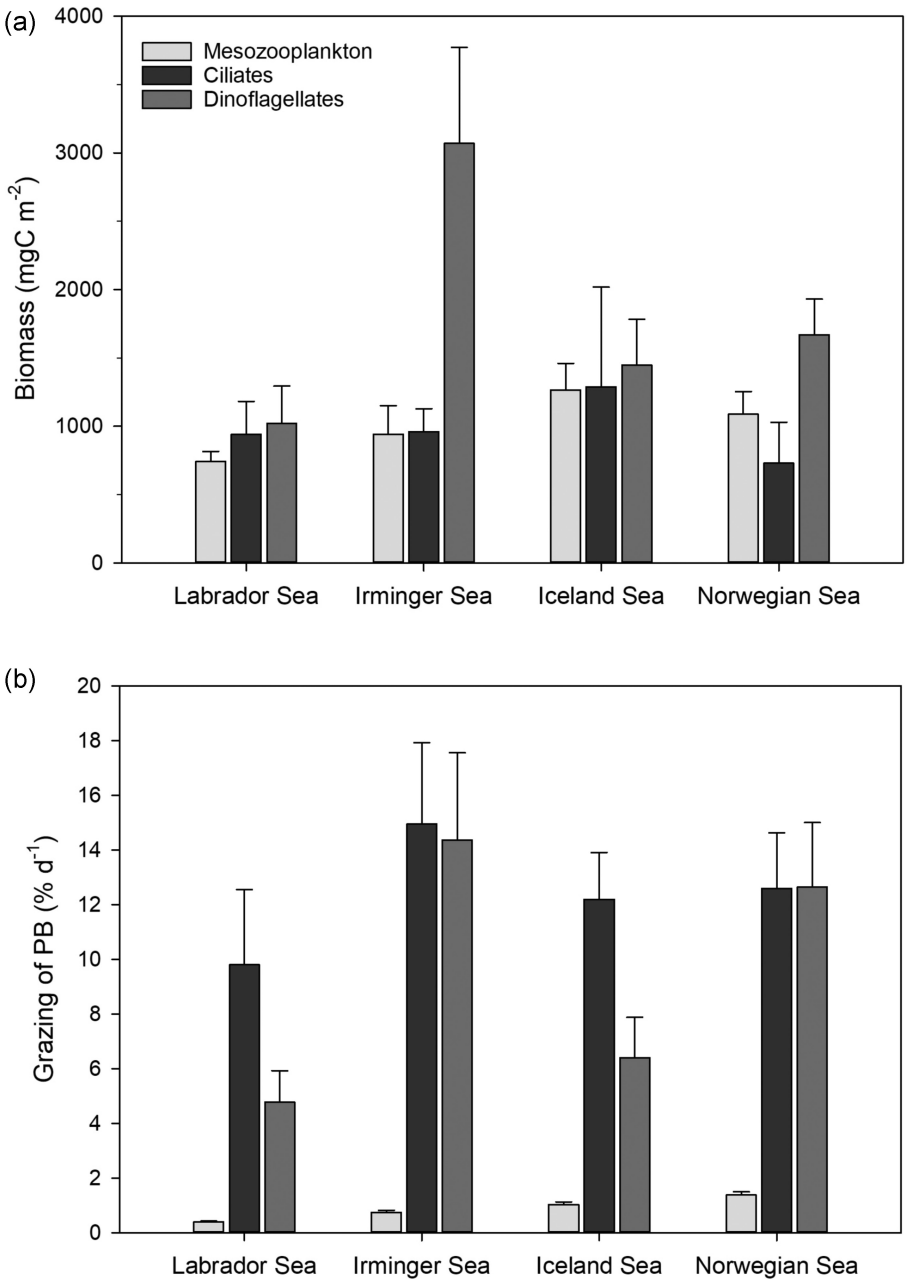

Figure 8. (a) Biomass in the four ocean basins (mgC m^{-2}) and (b) the grazing (as % d^{-1}) of the phytoplankton biomass (PB) by mesozooplankton, cilate, and heterotrophic dinoflagellates, respectively.

critical for the offspring (Head *et al.*, 2000) and therefore a driver for such adaptations. The egg production and feeding rates were low, though about 60% of the females were actively spawning during the one-day incubations. The few C5s present were very lipid rich. All of this support the indication of early state of egg production.

The high proportion of the young development stages (C1-3) in the LS (Table 3 and 4) does not match that impression of lipid rich females indicating recent ascent. The possible reasons for the discrepancy can be as suggested by Strand *et al.* (2020), that the young stages represent earlier reproduction by females with main egg production on the LS shelf areas. It is unlikely that the young stages belong to *Calanus glacialis* as one could suspect in the LS. While it is difficult to morphologically distinguish the younger stages of the cousin species, their size difference is considerable in the LS (Madsen *et al.*, 2001), and in the present analyses C1–C4 speciation was based on size (Strand *et al.*, 2020). Most of our observations were in the central LS, where Head et al (2013) have also shown lagged egg production compared to the LS shelf areas. They showed that in May and June the central LS was dominated by females and recently ascended C5s. The composition shown here, and in all basins, most likely presents a mixture of the production by mainly newly ascended females and females further along in their reproduction cycle in this case from the shelf regions.

The eggs produced by *C. finmarchicus* in our Labrador Sea incubations were significantly larger, compared to the eggs produced in the other basins. The LS egg-carbon content corresponds well with the published measures from the western part of the *C. finmarchicus* distribution area, i.e. the Scotian

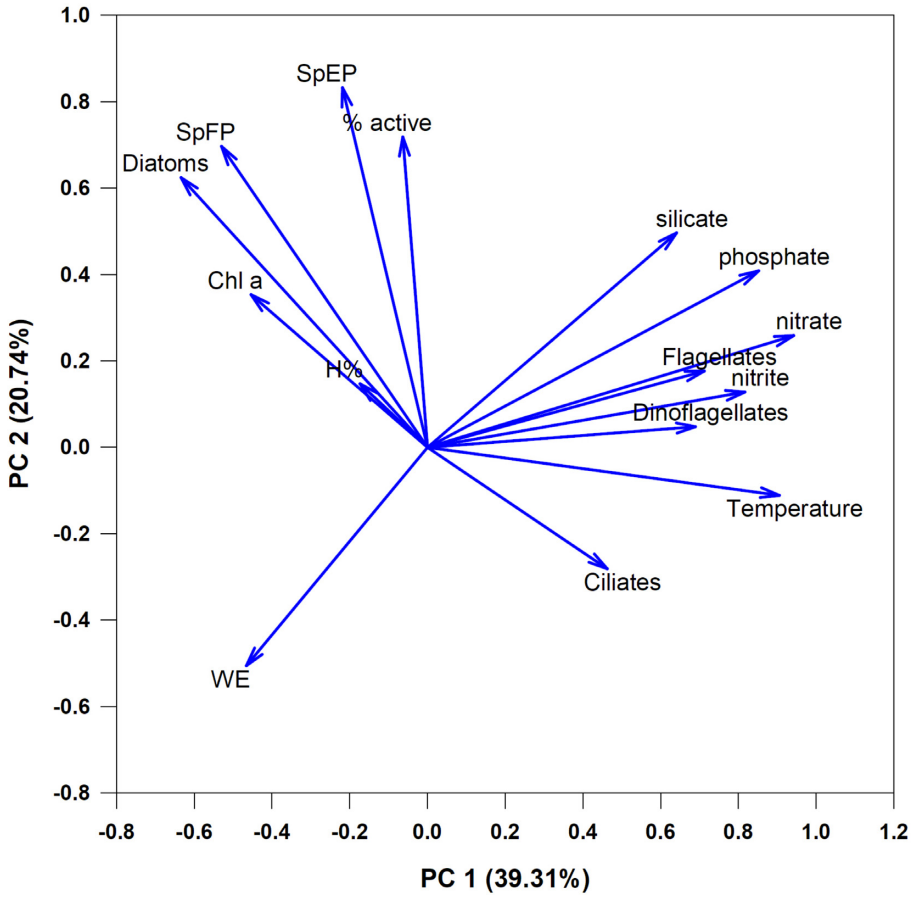

Figure 9. Principal component biplot of environmental variables and vital rate measurements. Loadings on PC1 and PC2 explain 39.3 and 20.7% of the variation of the data, respectively. Based on 16 complete sets of observations. % active: Number of females actively producing eggs per day, SpE; Specific Egg production (d^{-1}); SpFP: Specific Faecal pellet production (d^{-1}), H%: hatching percentage, WE: female wax ester content (μg ind^{-1}). Ciliates, dinoflagellates and diatomes as μgC L^{-1}, Chl a: Chlorophyll a (μg L^{-1}), Silicate, Nitrate, Nitrite and Phosphate μM, T: Average temperature in the upper 100 m.

Table 4. Summary of *Calanus finmarchicus* metrics, temperature, nutrients, and state of spring bloom in Labrador, Irminger, Iceland, and Norwegian Seas.

	LS	IRM	ICS	NWS	Source
Female size	Large	Large	Small	Small	This study
Female lipid at ascent	High	Low	Low	Low	This study
C1–C3% population	57	28	5	37	This study
C4 and C5 presence	Low	Low	High	Low	This study
C5 lipids	Very high	High	High	Low	This study
Egg size	Large	Small	Small	Small	This study
Approx. time of accent	Mid April	Early April	Mid April	Early April	This study
Surface T°C	2.6	5.1	2.2	6.1	This study
Overwintering T°C	3.4	3.8	−0.4	−0.2	1
Diapause duration days	156	144	206	200	2
Spring bloom	Strong bloom	Not started	Occurring	Late bloom	3
Nitrate usage mol m^{-2}	0.5	0.2	0.4	0.4	3

"High", "Low", "Large" and "Small" are a relative comparison between the basins with details given in Tables 2 and 3. Presence of stages refers to Figure 4. Source: 1. Heath *et al.*, 2000, 2. Jónasdóttir *et al.*, 2019, 3. Naustvoll *et al.*, 2020.

Shelf, Labrador Sea, and Disko Bay (Ohman and Runge, 1994; Cabal *et al.*, 1997; Swalethorp *et al.*, 2011).

IRM

Two of the stations sampled in the Irminger Sea were in the 0°C Greenland coastal current that differed considerably form the remaining IRM stations. The remaining stations were more similar with a temperature gradient from 5 to 7°C towards the Icelandic coast. In IRM, *C. finmarchicus* showed the highest egg production activities of the four basins, highest clutch sizes, feeding rates but similar spawning activity as in the LS. The females had order of magnitude lower lipid content compared to the similarly sized females in the LS but similar to ICS females, indicating longer time at the surface. This is despite pre-spring bloom state given for IRM (Table 4, Naustvoll *et al.*, 2020). The proportion of females in the population structure was high, and the abundance of C1-3 stages considerably higher than in the Iceland Sea, even though

initiation of egg production was estimated to be later, mid-April. This could partly be due to higher surface temperatures, hence faster development rates.

Jónasdóttir *et al.* (2019) estimated that the IRM overwintering population would have a limited ability to survive diapause due to their small size (their observation of 2.1 mm of both female and C5 size at depth in diapause). They suggested that the overwintering population represented in their study was connected to the Iceland Basin where the population has similar small body size. However, the current females in the surface waters did not differ from the LS females of 2.8 mm and the observed Greenland Sea females in Jónasdóttir *et al.* (2019). This supports the proposition of Jónasdóttir *et al.* that the IRM population during spring could be advected with the East Greenland Current from the Greenland Sea stock, and may not represent the overwintering stock in the IRM. This calls for further investigation of the source(s) of the IRM *C. finmarchicus* population at surface and in winter diapause.

ICS

The demographics in the Iceland Sea were mostly similar to the LS with the exception of significantly lower lipid content of the females (Tables 3 and 4). The relatively low lipid content would indicate that the females had been at the surface at some time having mobilized the lipids into gonad development, or had utilized more lipid during the longer overwintering period (Jónasdóttir *et al.*, 2019). The higher relative abundance of the overwintering stages C4 and C5 (Gislason, 2018) and the lipid rich C5s, clearly indicate recent time of ascent and the low specific egg and faecal pellet production rates indicated early stage of reproduction. The daily spawning activity was not significantly different from the other basins (Table 3). Overwintering at sub-zero temperatures does not require high lipid utilization (Jónasdóttir, 1999) and smaller sized *C. finmarchicus* can survive long overwintering periods (Table 4). We propose that the ICS *C. finmarchicus* have adopted the strategy to utilize lipids for gonad development and initiation of egg production partially based on lipids (partial capital breading) as has been reported for the Norwegian Sea population (Richardson et al, 1999; Jónasdóttir et al, 2008).

NWS

The demographics in the Norwegian Sea differed considerably from the other basins. Norwegian Sea Basin as presented here is a mixture of oceanic stations and shallower shelf stations, with higher productivity and warmer coastal current in the latter. Females had low lipid content. The clutch sizes, specific egg production and grazing rates were less than half of the rates in the other basin and 47% of the females were actively spawning. *C. finmarchicus* has a one-year life cycle in most of the oceanic areas, but the populations in the Norwegian Sea may at times manage two generations (Kristiansen *et al.*, 2021). This population that has overwintering in the −0.5°C Norwegian Sea Deep Water (Heath, 1999; Heath *et al.*, 2000) has been recorded to start ascent from diapause as early as February/March with all the population at the surface in May (Heath, 1999; Kristiansen *et al.*, 2021). Therefore, it is likely that the young stages do not only represent the second generation but a mixture of first and second generations (Strand *et al.*, 2020).

In summary, the analysis of the different traits (egg size female size, lipid utilisation) in the four basins shows that the populations may have adopted slightly different life history strategies. The Labrador Sea females investing in their eggs, while the females in the other basins have smaller eggs. Production of large eggs is a major life history trade-off where the female sets more maternal investment in fewer, larger eggs compared to the bet-hedging strategy, producing many small eggs with lower survival potential (e.g. Auel, 2004). While several studies have previously reported sizes of *C. finmarchicus* eggs (i.e. Ohman and Runge, 1994; Cabal *et al.*, 1997; Swalethorp *et al.*, 2011), this is the first study to our knowledge, that has compared *C. finmarchicus* egg sizes in the different ocean basins. There is also an indication that there is a gradient from income- (LS) to a semi-capital breeding strategy (NWS). The large LS and IRM females will, according to metabolic theory, have lower specific metabolic rate during diapause (Arrhenius, 1889; Visser et al, 2017), that would to some degree counteract their higher metabolism at higher overwintering temperatures (LS: 3.5 IRM: 3.8°C, Heath *et al.*, 2000). Therefore, being large, investing in larger lipid storage capacity is a trade-off to extend overwintering duration at higher temperatures. The smaller sized Iceland and Norwegian Sea *C. finmarchicus*, are more tuned to their low overwintering temperatures (−0.4 to −0.2°C, Heath *et al.*, 2000), burning relatively less lipids and potentially ascending with high levels of lipids (Jónasdóttir, 1999). They can therefore put more investment in bet-hedging strategy, being ready for the spring bloom with lipid driven gonad development and egg production (Niehoff *et al.*, 1999; Richardson *et al.*, 1999).

Community grazing

Based on the zooplankton biomass (Strand *et al.*, 2020), protozooplankton samples (Naustvoll *et al.*, 2020) and the measured faecal pellet rates we established some coarse carbon budgets for the basins in consideration. Across the four basins, the biomass of the two protozooplankton groups, ciliates and heterotrophic dinoflagellates were of the same order of magnitude as the biomass of the total copepod community (Figure 8a). However, considering the grazing rates on phytoplankton biomass (PB), the impact of each group of protozooplankton was one order of magnitude higher than the grazing impact of the total copepod community, 5–15% and 0.5–2% PB d^{-1}, respectively. These estimates fit well with other studies at same temperatures in the Arctic and subarctic areas (summarized in Menden-Deuer *et al.*, 2018) at similar temperatures. However, the implication of the grazing of the protozooplankton and copepod community are very different. The copepods export carbon out of the surface layer while the protozoans recycle nutrients, serve as prey for the post bloom copepod community and thereby preserve carbon in the surface layer after the main bloom. In spite of lower grazing pressure by the copepod community, their high production of fast sinking faecal pellets ranged from 1–5 mgC m^{-2} d^{-1} by the female population only, and is similar to the estimates presented by Wassman and Slagstad (1993) during spring bloom in the Barents Sea. This underscores the importance of *C. finmarchicus* in exporting carbon out of the surface layer in all basins during spring and generally in carbon turnover in the SPS ecosystem.

Conclusion

The crossing of the Sub Arctic Seas during spring/summer resulted in two significant findings. First, the relatively minor

role of *C. finmarchicus* in the turnover of the primary production in comparison with the protozoan community. This is true even pre- or during the spring bloom, stressing the importance of also consider protozooplankton in the energy flow of the Subpolar Ecosystems. The second finding reviled different life history strategies *Calanus finmarchicus* has adapted related to the observed demographics in the four Basins. Female size, lipid storage capacity and investment in eggs are the key traits of success in seasonal environments (Visser *et al.*, 2020; Sainmont *et al.*, 2014). Life history traits reflect long-term adaptations to the species mean environment and *C. finmarchicus* utilizes the plasticity of the traits to encompass the different environments and has by this flexibility, ensured being the most successful copepod species in the North Atlantic subpolar basins.

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Data availability statement

The physical oceanography data underlying this article are available in ICES data base https://gis.ices.dk/geonetwork/srv/eng/catalog.search#/metadata/561291a5-f26c-43aa-8310-e59fb2208809. The egg production data for method-1 and C. finmarchicus abundance data are available in Pangea https://doi.pangaea.de/10.1594/PANGAEA.819905 and egg production method- 2 in https://doi.pangaea.de/10.1594/PANGAEA.820732. The phytoplankton and nutrient data will be shared on reasonable request to the co-author Lars Naustvoll.

Author contribution

SHJ is the main author, conducted on-ship measures of vital rates and lipids, analysed the data, synthesized the results, and was the main writer of the manuscript. LN conducted on-board egg production measures, a provided data on protozooplantkon, FWT, MDA, and JG all conducted on board the measures and provided comments to the manuscript, WM provided zooplankton and production data and contributed to the manuscript writing, and TGN conducted and analysed on-ship measures of vital and grazing rates and is the second main writer of the manuscript.

Conflict of interest

All authors declare that they have no conflicts of interest.

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