Spring production of *Calanus finmarchicus* at the Iceland–Scotland Ridge

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Abstract

Distribution and reproduction activity of the calanoid copepod *Calanus finmarchicus* were studied in the waters between Scotland and Iceland in April 1997 during the expected time of the animals' ascent to surface waters following diapause. Ascent was taking place on both sides of the Iceland–Scotland Ridge, apparently from two separate overwintering centers. The population on the Faroe Shelf (FS) most likely came from the overwintering population in the Faroe Shetland Channel (FSC). Per capita egg production was highest on the FS (> 30 eggs female^{-1} d^{-1}) and lowest in the Iceland Basin (10 eggs female^{-1} d^{-1}). The maximum clutch size recorded was on the FS (145 eggs). As the maximum clutch sizes that females produced were between 40% and 77% (area averages of the station maximum rates) of their size-specific reproduction potential, it is argued that egg production rates were generally food-limited. Chlorophyll *a* concentrations were, at all but one station, under 1 μg L^{-1}. Chlorophyll-based ingestion could, theoretically, support the observed average egg production rates in the Iceland Basin and on the FS but only about 30% of the observed production at the stations in the East Icelandic Current (EIC). The carbon assimilated through ingestion of phytoplankton, *Calanus* own eggs and nauplii in the EIC was estimated to be too low to support the frequently observed production of clutches consisting of over 100 eggs. Cannibalism on eggs and nauplii was not likely to have constituted a significant component of dietary carbon intake. However, a combination of feeding and assimilation of reserved lipid remaining from overwintering could be sufficient to explain the observed per capita egg production rates. *C. finmarchicus* copepod stages 1–3 were only recorded in considerable numbers only on the FS. This suggests higher survival rates of eggs in the shelf waters.

1. Introduction

Because of its high biomass and wide distribution, *Calanus finmarchicus* is probably the most important mesozooplankter in the North Atlantic ecosystem (Conover, 1988; Heath et al., 2004). This

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organism represents an important food source for a number of juvenile fish species and thus, links lower and higher trophic levels in marine food webs. *C. finmarchicus* undergoes a period of dormancy mainly at pre-adult stage C5 (Hirche, 1998). Important overwintering sites of this species in the North Atlantic are at 500 1100 m depths in the Norwegian Sea Basin and Faroe Shetland Channel (FSC) (Heath et al., 2000), where concentrations are reported to be as high as 20,000 50,000 individuals m^{-2}. The appearance of copepodite stages C4 and C5 as well as recently molted females (C6), at the surface (0 100 m) has been noted in the beginning of April in the FSC with ascent being completed in May (Heath and Jónasdóttir, 1999). At station M, situated on the slope of the Norwegian shelf further north in the Norwegian Sea, the timing of the first appearance of females has been reported to be in late March (Hirche et al., 2001).

The period immediately following the animals' emergence from diapause and ascent from deep to surface waters is of interest as this is the very beginning of the animals' reproductive period. Studying *C. finmarchicus* in this phase of the life cycle in the open ocean is not a trivial task. First of all, the winter distribution area of this species is very extensive (Conover, 1988; Heath and Jónasdóttir, 1999; Heath et al., 2000). In addition, after surfacing in open ocean waters, females may be transported via various ocean currents to shelf areas. The timing of ascent varies throughout the distribution area (Heath, 1999), and in addition, the ascent of the whole overwintering population can take several months (Heath, 1999). This can result in the possibility of overlapping generations of newly ascended and first-generation females.

There are several studies where measurements of *C. finmarchicus* egg production have been made before the initiation of the spring bloom (e.g. Hay et al., 1991; Diel and Tande, 1992; Plourde and Runge, 1993; Meyer-Harms et al., 1999; Richardson et al., 1999; Mayor et al., 2006). Most of these studies report egg production rates at levels that, theoretically, cannot be supported by *in situ* food availability, e.g. phytoplankton and protozooplankton. Thus, it has been suggested that egg production by *C. finmarchicus* in surface waters during the period following ascent may be fueled by the metabolism of endogenous lipids (Plourde and Runge, 1993; Cabal et al., 1997; Irigoien et al., 1998; Niehoff et al., 1999; Richardson et al., 1999; Jónasdóttir et al., 2002) or protein (for *Calanus*

helgolandicus, Rey-Rassat et al., 2002a). Recently, studies have indicated the importance of cannibalism as a significant mortality factor on *C. finmarchicus* and *C. helgolandicus* eggs and nauplii (Basedow and Tande, 2006; Ohman and Hirche, 2001; Ohman et al., 2004), especially at low phytoplankton concentrations (Basedow and Tande, 2006). This recycled energy can thus be one of the factors that may explain the source of the missing carbon needed for the observed *C. finmarchicus* egg production before the spring bloom.

The purpose of the present study was to describe the reproductive physiology and activity of *C. finmarchicus* in the period immediately following ascent from diapause in the region of the Iceland Scotland Ridge. This is an area where *C. finmarchicus* overwinters, and it is thought to be an important site of ascent for a large proportion of the North Atlantic population of *C. finmarchicus*. We studied the condition, reproduction, and grazing of animals in the period immediately following ascent to surface waters and related these to food availability and other environmental parameters.

2. Methods

Samples were taken on a cruise on R/V *Dana*, 4 19 April 1997 at a network of 30 stations across the Iceland Scotland Ridge and the FSC (Fig. 1).
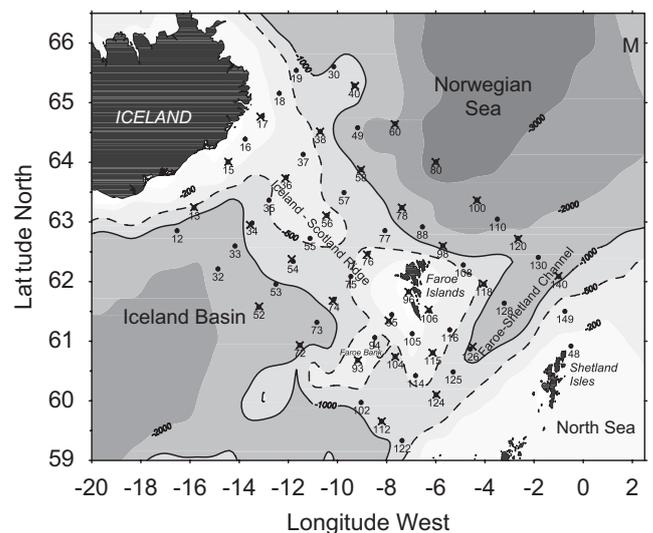
Fig. 1. R/V *Dana*, cruise 6/97, 4 19 April 1997. Sampling grid over the Iceland Scotland Ridge. Bullets indicate stations sampled for CTD, *Calanus finmarchicus* abundance and *C. finmarchicus* wax ester content, while crosses indicate stations where primary and secondary production, gut fluorescence and seston fatty acid composition were measured. M: approximate location of weather ship M.

2.1. Hydrographic and nutrient measurements

At each station, standard hydrographic measurements were taken with a Seabird[®] CTD (model $911+$) mounted on a rosette. Water samples were collected for analysis of dissolved nutrients (silicate, nitrate, nitrite and phosphate) from various depths between 3 and 100 m. Light penetration into the water column was measured with a Q Instruments photometer (cosine collector). A light attenuation coefficient (k) was calculated using the Lambert Beer relationship.

2.2. Phytoplankton measurements

Chlorophyll a fluorescence profiles through the water column were measured with a WETStar fluorometer mounted on the rosette. Fluorescence measurements were calibrated via linear regressions relating fluorescence to concomitantly measured chlorophyll a concentrations. At least one water sample (5 L) for chlorophyll calibration was taken from each station. A chlorophyll sample was always taken from the same depth as the primary production sample.

The surface layer was well mixed on all cruises to at least the depth of 1% surface light penetration. Thus, photosynthetic characteristics determined for phytoplankton at one depth (3 5 m) were taken as representative of the phytoplankton in the surface mixed layer. A 40 μCi $^{14}CO_2$ (as bicarbonate; Carbon 14 Center, Danish Hydraulic Institute, Denmark) was added to 250 mL samples. These were incubated at seven different photon flux densities (0 700 μmol photons PAR m^{-2} s^{-1}) on a rotating wheel in an artificial light incubator at $\pm 2\,°C$ surface seawater temperature. After 2 h of incubation, samples were filtered onto cellulose nitrate filters (0.2 μm), placed over concentrated HCl for 5 min to remove excess ^{14}C bicarbonate and frozen until later addition of scintillation fluid and counting.

Dark bottle DPMs were subtracted from light bottle DPMs prior to construction of a photosynthesis vs. light curve using standard methods (Steemann Nielsen, 1952). The maximum rate of photosynthesis (P_{max}) and the slope of the curve (α) were used to estimate total potential primary production.

2.3. Zooplankton sampling

Live zooplanktons were collected with a 1 m, 250 μm mesh plankton net with a 5 L closed cod end. The net was towed vertically from either 70 or 100 m. The contents of the cod end were immediately diluted into seawater from the collection station and sorting of specimens for experimental studies started within a few minutes.

Sampling to estimate the abundance of *C. finmarchicus* stages was carried out with an ARIES system (Dunn et al., 1993). The sampler was designed to collect a sequential set of discrete plankton net samples delineated by 2 min time intervals (approximately equivalent to 50 m vertically, 10 15 m^3 volume) during the descent and ascent legs of an oblique tow of a maximum 3000 m depth. The system was fitted with a 200 μm mesh net with a nose-cone diameter of 37 cm. The maximum number of samples collected in a single haul was 100. The system also carried two separate integrating nets (200 μm mesh net with a nose-cone diameter of 14.5 cm and a 95 μm mesh net with a nose-cone diameter of 6.8 cm), which were open throughout the descent and ascent legs of each tow (referred to as the pup-nets). A Valeport impeller flowmeter was mounted centrally in the mouth of the net and electronically integrated with the control and data logging systems. Flow data were logged at 1-s intervals throughout each tow and subsequently integrated over the duration of each sampling net exposure interval. Calibrations (revolutions m^{-1}) for each flowmeter were provided by the manufacturers, and checked *in situ* by reciprocal tows of the samplers at a fixed depth over a measured distance in a weakly tidal area with the collecting nets removed. In this way, the meters were in free-flow and subject to interference only by the rigid structures of the sampler during the calibration.

The catches in the pup-nets and descent-leg nets from ARIES were preserved in 4% formalin immediately upon recovery and returned to the laboratory for microscopic analysis. The ascent-leg ARIES nets were examined by eye to determine which ones contained high numbers of *Calanus*. A few nets showing peak plankton concentrations were put on ice and sub-samples of *Calanus* spp. individuals were sorted under a dissecting microscope with cold light source for biochemical analysis. The remainder of bulk material from each ascent-leg sample was preserved in 4% formalin.

The formalin preserved 200-μm-mesh pup-net and a subset of the descent-leg ARIES nets were analyzed to enumerate key taxonomic groups including *Calanus* spp. The numbers of individuals of each *Calanus* developmental stage C1 C6 (males

and females) were determined in each sample. *C. finmarchicus* and *C. helgolandicus* stages C5 and C6 males and females were distinguished by the curvature of the inside of the fifth pair of swimming legs; earlier stages were undistinguishable as they do not show this difference in curvature. *Calanus glacialis* was not distinguishable by routine microscopy from *C. finmarchicus* and *C. helgolandicus* at any stage.

2.4. Egg production and hatching measurements

To determine egg production rates, *C. finmarchicus* females were sorted from the 1 m diameter vertical haul under a stereomicroscope. A set of 22 25 active and apparently undamaged females were selected and individually introduced into 1 L bottles, filled with 64 μm filtered seawater taken from 5 m depth. Water was passed through a 64-μm sieve to remove all ambient eggs from the incubation water. Incubations took place in a temperature-controlled room for 24 h in darkness at temperatures corresponding to the *in situ* temperatures at the collection site. To minimize cannibalism on eggs, the bottles were kept upright and not rotated during the incubation so that eggs sank to the bottom of the bottle. After incubations, eggs and fecal pellets were collected by gently filtering the contents of each bottle through a 20-μm sieve. Eggs and pellets were immediately counted on the mesh under a stereomicroscope. The prosome lengths of the females were measured. Thereafter, the females were individually fixed in buffered 5% formalin for species confirmation and gonad-stage determination at a later date. All the eggs produced in the incubations for each station were then transferred to 500 mL glass bottles containing water (refiltered through a 20 μm mesh) from the incubations in which the eggs had been produced. The bottles were sealed without air bubbles and rotated on a wheel (1 rpm) for additional 48 h after which the remaining eggs and hatched nauplii were filtered through a 50 μm mesh and fixed in formalin for later counting.

Copepod per capita egg production rates are, generally, positively correlated with both body size (Jónasdóttir et al., 2005) and temperature (Runge, 1985). However, copepod size and temperature are generally inversely correlated (see table 53 in Mauchline, 1998). Therefore, in order to compare effects of environmental factors on egg production rates, we normalized egg production to both size and temperature (results not shown). As there was no significant difference between the normalized and original egg production rates, the original rates are used here.

2.5. Gut fluorescence

A separate net tow was made for the purpose of collecting females for estimating gut fluorescence. Immediately after the tow, the contents of the cod-end were gently sieved through a 250 μm mesh that was immediately placed in a $-84\,^{\circ}$C freezer. Samples were treated gently and frozen as quickly as possible to minimize gut clearance by the animals. Later, six replicates of 10 females each were picked out of the thawing sample and the pigments extracted in 90% acetone at 4 °C in darkness for 24 h. Fluorescence was measured on an Aminco® fluorometer using standard fluorometric procedures, with a reading before and after acidification (Parsons et al., 1984) and gut content was calculated as described in Båmstedt et al. (2000). Phytoplankton ingestion rate I was estimated as $I = k \times G$ (Båmstedt et al., 2000), where k is the gut clearance coefficient, estimated according to Dam and Peterson (1988) from the *in situ* temperature, and G is the measured gut fluorescence. The carbon chlorophyll relationship, $TPC = 190.34 + 62 \, \text{chl } a$ (Irigoien et al. 1998), was used, where TPC is total particulate carbon.

2.6. Gonad analysis

Gonad maturation stages were determined for all females that did not produce eggs during the egg production incubation period. The fixed females were individually stained with borax carmine in ethanol, and the classification of gonad maturation stages was made into four stages following the methods and description in Niehoff and Hirche (1996).

2.7. Lipid analysis

Copepods for lipid analysis were sorted from plankton samples collected during the ascent leg of ARIES tows and from the vertical plankton tows described above. Sorting was carried out immediately following the retrieval of the nets. Plankton samples were kept cold on ice during sorting. Intact and, preferably, live females were sorted into cryovials, which were flushed with N_2 gas and frozen in liquid nitrogen. At the end of the cruise,

the samples were transferred to a $-84\,°C$ freezer, where they were kept until analysis.

Three to five females were extracted in chloroform methanol (2:1, v/v) with a known concentration of hexadecane-3-one (ketone) as an internal standard. Lipids were analyzed by thin layer chromatography/flame ionization detection (TLC/FID) using an Iatroscan® MK-5. The extraction procedures and a detailed description of the analysis are found in Jónasdóttir (1999). The wax ester (WE) standards made for calibration were isolated from C5 *C. finmarchicus* wax esters, as suggested by Ohman (1997) and Miller et al. (1998). The copepods used for making those standards were collected from 1000 m depth in the FSC. The other standards for calibration were tristearine (triacylglycerol), palmitine acid (free fatty acid), cholesterol (sterol), and methyl manganate (phospholipid).

The fatty acid composition of the seston was determined on samples collected from the surface (3 5 m depth) using the water bottles mounted on the CTD rosette. Five litres of water was filtered through combusted glass fiber filters (GF/C). Immediately after filtrations, the filters were folded and placed in vials and the air was replaced with N_2 gas. The vials were then sealed and frozen at $-80\,°C$ until analysis could be carried out. Lipids were extracted from the samples by 24-h exposure to CH_2Cl_2 methanol (2:1, v/v) with a known amount of C_{17} fatty acid added to the sample as an internal standard. Fatty acids were analyzed by gas chromatography on a capillary column. The fatty acids were *trans*-methylated with BF_3 methanol to form fatty acid methyl esters (FAME). The FAME sample was injected ($1.8\,mL\,min^{-1}$) into a gas chromatograph (Hewlett-Packard 5890A) using splitless injection and helium as a carrier gas. The temperature program was increased in two steps from 80 to $160\,°C$ at $40\,°C\,min^{-1}$. After the sample was left at $160\,°C$ for 1 min, the temperature was increased from 160 to $220\,°C$ (at $3\,°C\,min^{-1}$). The samples remained at $220\,°C$ for 17 min. Peaks on chromatograms were compared to FAME standards for specific fatty acid identification and the integrated peaks compared to the peak area of the C_{17} standard.

2.8. Data analysis

All data were checked for normality and transformed, if necessary. Comparisons of means were performed with ANOVA or non-parametric tests when data did not meet requirements of normality. The large set of environmental variables was analyzed using principal component analysis (PCA). If two variables score above ±0.7 on the same component, the variables have a significant contribution to the same component and the variables are highly correlated (Meglen, 1992). The statistical programs SPSS® and Sigma Stat (Systat Software Inc.) were used for the analyses.

3. Results

3.1. Hydrography and dissolved nutrients

Average temperature and salinity distributions in the upper 70 m, from which the vertical haul zooplankton samples were taken, are shown in Fig. 2a and b. The lowest temperatures and salinities were observed in the East Iceland Current (EIC) and the highest in the Atlantic Current Water (ACW, Fig. 2c). Nutrient concentrations (data not shown) were uniformly high: NO_3 ranged from 10 to $13\,\mu M$, PO_4^{3} from 0.4 to $1.2\,\mu M$, Si from 2.6 to $7.8\,\mu M$ and NO_2 from 0.001 to $0.137\,\mu M$. The concentration patterns of NO_3, Si and PO_4^{3} were similar, with lowest values in the EIC and on the Faroe Shelf (FS), while the NO_2 concentration was lowest in the Iceland Basin and highest on the FS. We use the term FS for the area inside the 500-m contour around the Faroe Islands, including the Faroe Bank (Fig. 1).

3.2. Phytoplankton production and chemical composition

Chlorophyll *a* concentrations over the entire study area (0 70 m average) never exceeded $1\,\mu g\,L^{-1}$ (with the exception of station 60 with $1.2\,\mu g\,L^{-1}$) and were less than $0.5\,\mu g\,L^{-1}$ at most stations (Fig. 3a). Primary production ranged from between 0.1 and $0.5\,g\,C\,m^{-2}\,d^{-1}$. The highest primary production estimates (data not shown) were in the EIC and on the FS, i.e. in association with the highest chlorophyll concentrations. These same areas exhibited slightly reduced silicate and nitrate concentrations relative to the rest of the study area.

The fatty acid content of the particulate organic matter (POM) is presumed to derive mainly from phytoplankton. Specific fatty acids can be used as indicators of certain phytoplankton groups. Here, we use the signatures as suggested by Dalsgaard et al. (2003). The sum of the fatty acids 16:1n7,
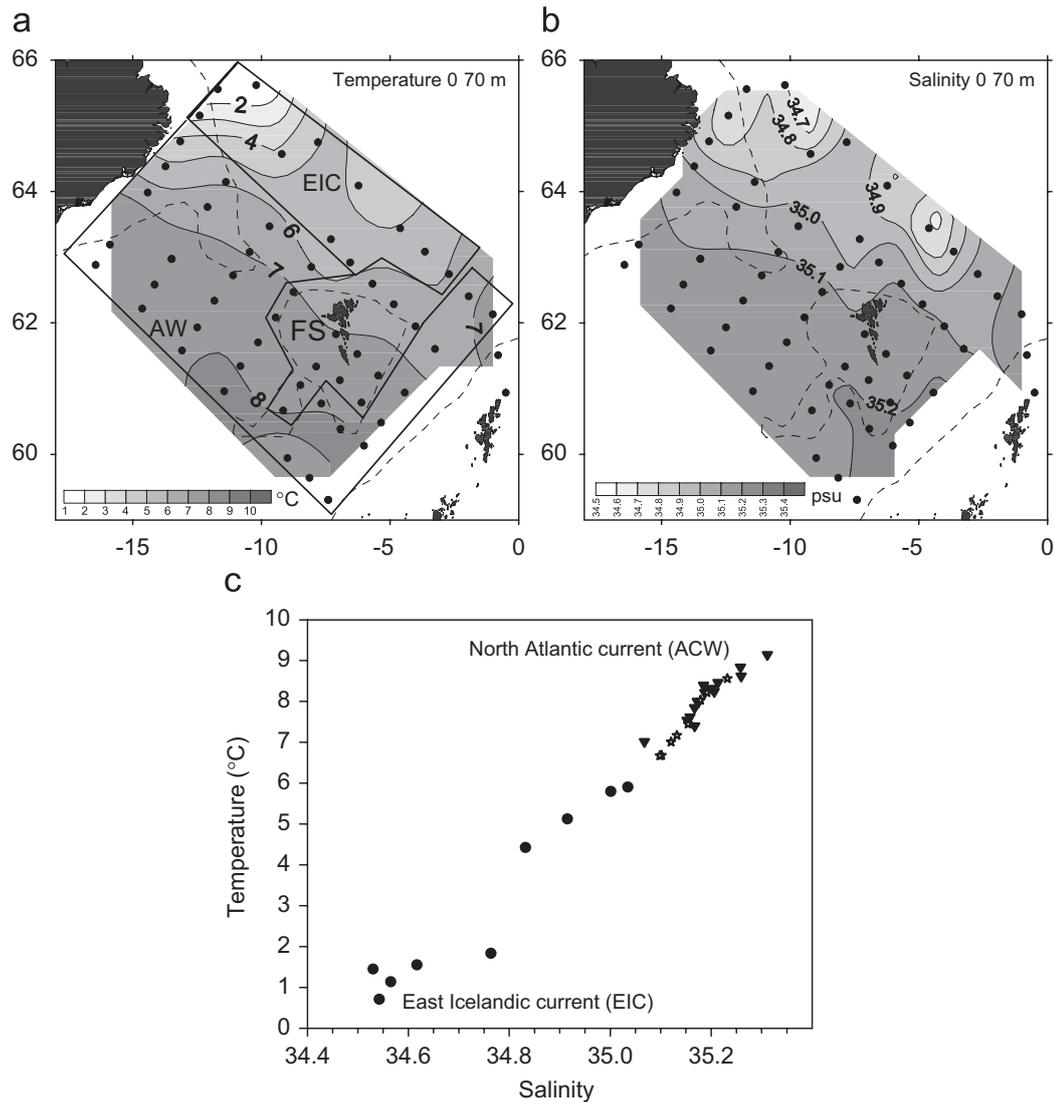
Fig. 2. (a) Temperature (°C) and (b) salinity distributions averaged over the upper 70 m of the water column, (c) T/S plot showing mixing of the two major water masses: the cold, less saline East Icelandic Current (EIC) and the warm saline North Atlantic Current Water (ACW). Areas of EIC, AW and FS are outlined in panel (a). The different symbols show the division into areas (see Section 3.5) based on water characteristics: (●) EIC, (▼) AW, (☆) FS (Table 1).

16:4n1 and 20:5n3 ($\sum$Bac) is used as an indicator of diatoms, the sum of 18:5n3 and 22:6n3 ($\sum$Din) as an indicator of the presence of dinoflagellates, the sum of 18:4n3 and 18:1n9 ($\sum$Pry) as an indicator of prymnesiophytes and the sum of the fatty acids 16:4n3, 18:2n6 and 18:3n3 ($\sum$Chl) as an indicator of chlorophytes. This analysis shows that the higher chlorophyll in EIC is due to significantly higher concentration of diatom markers compared with Atlantic Water (AW) and FS (ANOVA, post hoc LSD test $p < 0.05$; Fig. 3c and f). The markers of dinoflagellates, prymnesiophytes and chlorophytes (Fig. 3c–e) did not differ significantly between areas (Fig. 3f).

3.3. Distributions of stages C1–C6 of C. finmarchicus

Fig. 4 illustrates the distribution of *C. finmarchicus* copepodite stage abundances (C1–C6 female) integrated to the seabed (m^{-2}). The concentrations of adult females and C5s (Fig. 4b and c) were almost identical and dispersed over a greater area than the C4s. The highest concentrations were recorded northeast of the FS and in the FSC. Relatively high concentrations were also recorded along the southern slope of the Iceland–Scotland Ridge and on the southern FS. Stages C1–C3 (Fig. 4d) were recorded only around the Faroe Islands and off the Shetland Islands.
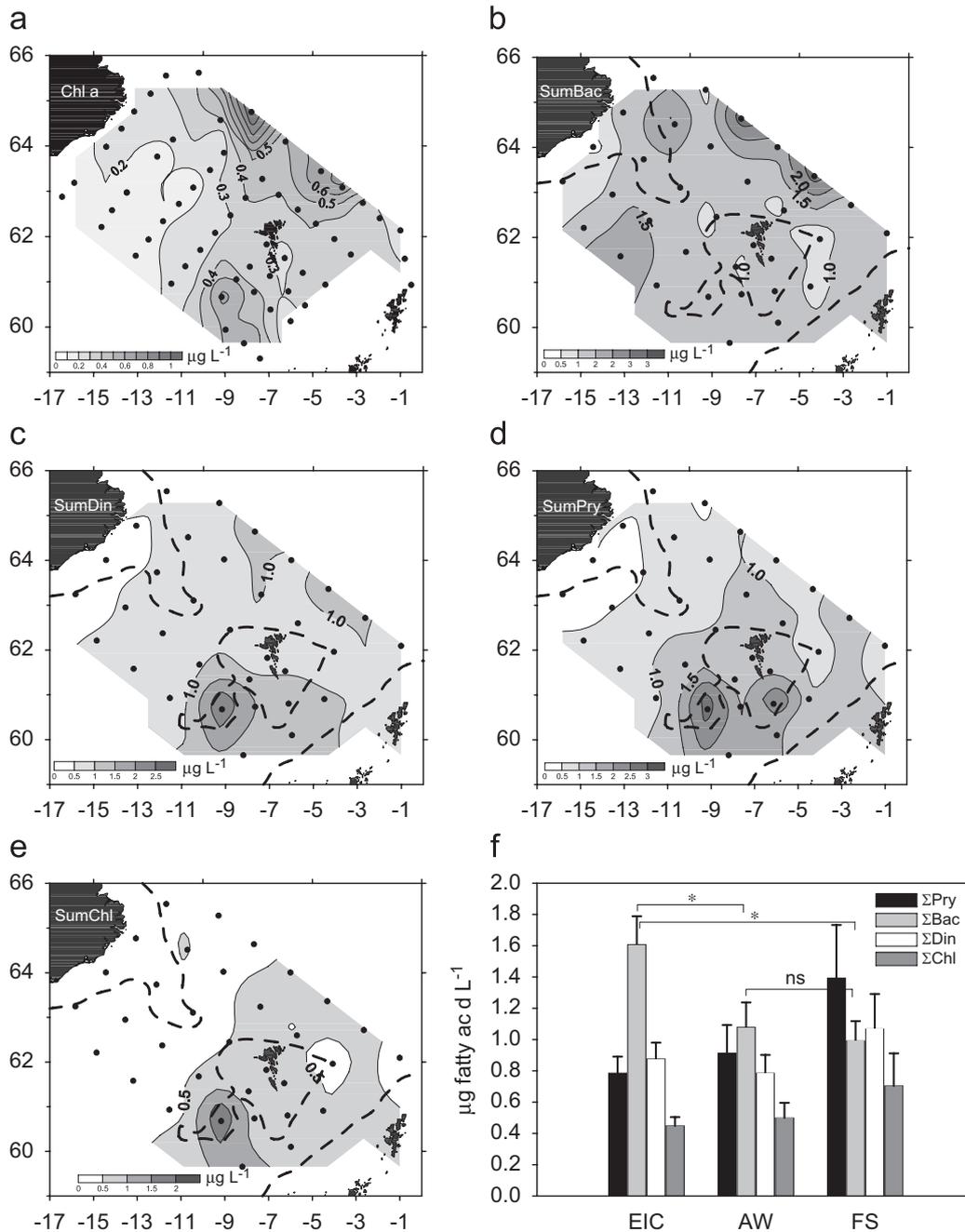
Fig. 3. Spatial distribution of (a) chlorophyll *a*, (b) diatom (SumBac), (c) dinoflagellate (SumDin), (d) prymnesiophyte (SumPry), and (e) chlorphyte (SumChl) fatty acid signatures (all in $\mu g\,L^{-1}$). (f) Average of the above four specific fatty acid signatures in the different areas: EIC, AW and FS. Difference in concentration of diatom fatty acid signature is indicated with [*]$p < 0.05$ and ns: non significant difference.

The size of the females differed significantly between the areas of Faroe Bank, Atlantic Basin and Norwegian Sea (Kruskal Wallis one-way analysis, d.f. $= 2$; $p < 0.001$). The observed difference was found to be between the females in the Norwegian Sea waters and on the Faroe Bank and the Atlantic Basin (Dunn's post hoc method, $p < 0.05$) but the difference in female size between Atlantic Basin and Faroe Bank was not significant (Dunn's post hoc method, $p > 0.05$; Fig. 5a).

3.4. Wax ester content in adult female *C. finmarchicus*

Wax ester contents in individual females in the upper 100 m are listed in Table 3. Females collected in the upper 100 m of the water column had considerably lower wax ester concentrations than in those found in deeper waters (100–1000 m, Fig. 5b). The highest wax ester contents in the females in the upper layer were 6 ± 1, 13 ± 4, and
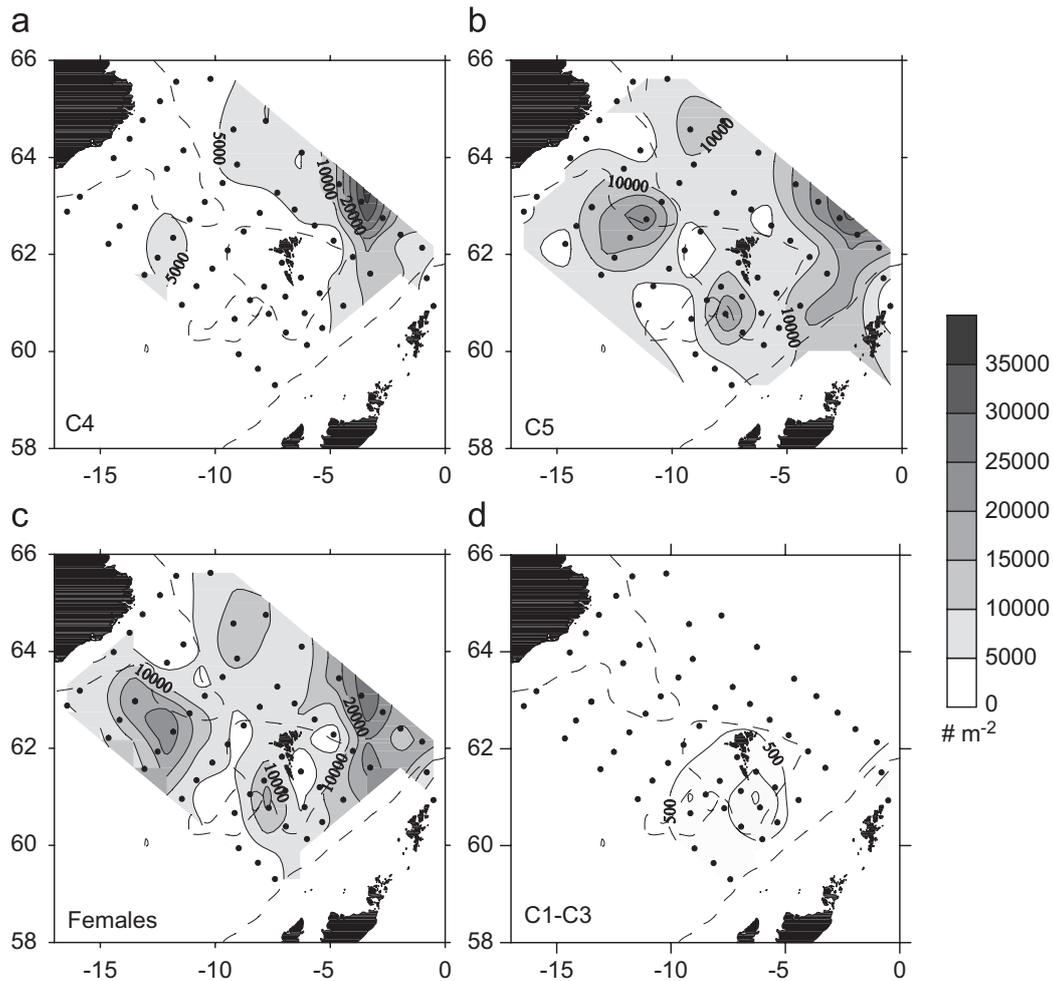
Fig. 4. Spatial stage distribution of *Calanus finmarchicus* abundance (number m^{-2}): (a) copepodite stage 4, C4, (b) copepodite stage 5, C5, (c) adult females, and (d) sum of copepodite stages 1 3, C1 C3, integrated over the entire water column.

$29 \pm 6 \mu g$ WE female ^{1}, respectively, when values were pooled from the stations on the Faroe Bank, Atlantic Basin and Norwegian Sea. The highest concentration recorded was $209 \mu g$ WE female ^{1} at 400 m depth (1.8°W, 62.4°N), whilst south of Iceland, the highest wax ester concentration in females was 96 μg at 700 m depth (16°W, 62.8°N).

3.5. Reproductive biology

Based on stage distribution (Fig. 4), lipid contents (Fig. 5b), and water masses (Fig. 2c), we divided the female *C. finmarchicus* wax ester encountered into three groups: Norwegian Sea sampled in the EIC (waters $<6\,°C$), Iceland Basin and FSC sampled in the ACW (waters $>6.5\,°C$ with bottom depth $>500\,m$), and FS (in waters $>6.5\,°C$ with bottom depth $<500\,m$, including the Faroe Bank). We identify these groups by the areas where they were

sampled: EIC, AW and FS (Fig. 2a) with different symbols in the figures.

Generally, the percentage of females in the population with fully mature gonads (%G4) was high (60 100%) over the entire study area (Er/Er4 ratio in Table 1). The lowest proportions ($<70\%$) recorded were at station 13 south of Iceland. The distribution of actively reproducing females in the population showed a pattern similar to that of gonad maturity, with the highest percentages of actively reproducing females being found on the FS (Table 1). Average egg production rates differed significantly between the areas (Fig. 6a), with the highest rates being recorded on the FS (31 ± 6 eggs female ^{1} d $^{1} \pm$ S.E.) and lowest in the AW (10 ± 3 eggs female ^{1} d $^{1} \pm$ S.E.; Table 1). This difference was significant between AW and FS (two-way ANOVA, LSD $p < 0.001$). Maximum clutch size (maximum number of eggs produced per female;

a

b
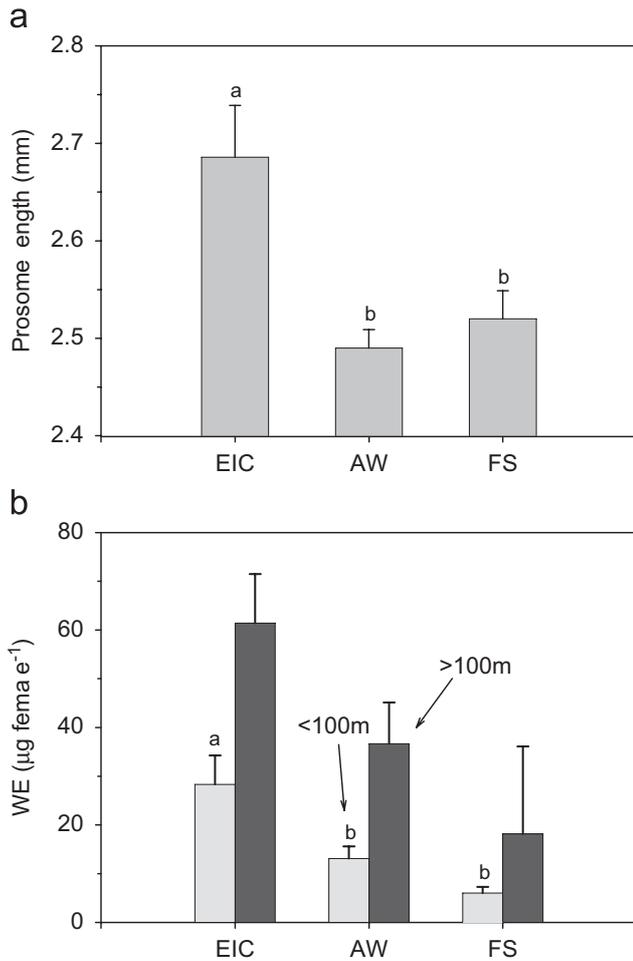
Fig. 5. *Calanus finmarchicus* averages of measurements at stations in the three different regions: AIC, AW, and FS. (a) Female prosome length (mm), (b) WE: wax ester content ($\mu g\,female^{-1}$) in females in the upper 100 m of the water column (light bars) and deeper than 100 m (dark bars). Whiskers indicate ± 1 S.E. Different letters above the bars indicate a significant difference in the respective measurements between areas.

Table 1) was highest on the FS but also high in the EIC. The highest average egg production rate and maximum clutch size were both recorded in waters with only $0.3\,\mu g\,chl\,a\,L^{-1}$ (Fig. 6b and c). As a result of the high production rates at this low and the highest measured chlorophyll concentrations ($1.2\,\mu g\,L^{-1}$), no significant linear relationship could be established between chlorophyll concentration and average egg production rate or maximum clutch size.

Egg production rates recorded in this study were not related to either copepod size or temperature (data not shown). The temperature in the study area ranged from 0 to 8 °C, and the prosome length of the incubated females ranged from 2.0 to 3.3 mm (Table 1). Campbell and Head (2000) explained egg production rates of *C. finmarchicus* on the Scotian

Shelf during spring, summer and autumn with the percentage of females at gonad stage 4 (GS4; fully ripe). However, over 60% of the females in our study were already in GS4, and we could not establish the equivalent relationship (Fig. 6e).

At over half of the stations, egg-hatching success was between 90% and 100%. However, at seven stations, hatching was below 50% (Table 1). On two of these, hatching failed almost completely (1–2% hatching). The lowest values for hatching success were recorded at stations south of the FS, at a few stations in the Norwegian Sea and south of Iceland. The low hatching was associated with low egg production rates, and there was a positive but not significant relationship between hatching and egg-production rates (Fig. 6d).

Analysis of Er4 or hatching, female size, wax ester content, temperature and food availability (chlorophyll *a* and seston fatty acid composition) at all stations ($n = 30$) using PCA resulted in a highly significant positive correlation between egg production and the signature fatty acids for prymnesiophytes ($\sum$Pry; Table 2). Linear regression analysis resulted in a weak but significant linear correlation between Er4 and $\sum$Pry ($R^2 = 0.26$; $p < 0.05$). Additionally, a significant ($p < 0.05$) linear relationship with low R^2 was between Er4 and $\sum$Din ($R^2 = 0.22$) and $\sum$Chl ($R^2 = 0.15$). Hatching success was significantly correlated with the incubation temperature ($n = 30$, $R^2 = 0.18$; $p < 0.05$).

The same analysis was carried out on the variables for the three different areas: EIC, AW and FS. The PCA analysis showed that egg production rates of females in EIC were highly positively correlated with the prymnesiophyte and chlorophyta fatty acid markers (Table 2) and there was a weaker correlation with incubation temperatures and dinoflagellate fatty acid markers. Hatching success in the EIC did not correlate with any of the measured parameters. In the AW, egg production did not correlate with any of the variables, while hatching and incubation temperatures were highly correlated in the PCA analysis and linear correlation was significant ($n = 14$, $R^2 = 0.4$; $p < 0.05$). On the FS, PCA showed a high correlation between egg production and chlorophyll *a* concentration as well as the concentrations of all specific algal fatty acid indicators. Here, the only significant linear relationships were between Er4 and the prymnesiophyte fatty acid markers $\sum$Pry ($n = 8$, $R^2 = 0.51$; $p < 0.05$). No correlations were found between hatching and the variables measured at the FS stations.

Table 1
Calanus finmarchicus reproduction characteristics

Station area	Date	nEr and nEr4	Er	Er4	% Prod. fem.	E_{max}	Prosome length (mm)	H%	n eggs
13 AW	09.04.97	23/14	1.8 ± 1.1	2.9 ± 1.7	13.0	21	2.54 ± 0.04	95	391
15 AW	08.04.97	23/22	9.3 ± 2.9	9.7 ± 3.0	43.5	45	2.45 ± 0.03	1	213
34 AW	10.04.97	24/22	5.5 ± 2.0	6.0 ± 2.2	33.3	38	2.48 ± 0.02	96	132
36 AW	11.04.97	22/19	5.0 ± 2.2	5.8 ± 2.6	27.3	35	2.59 ± 0.03	63	118
38 EIC	11.04.97	24/24	16.3 ± 3.4	16.3 ± 3.4	58.3	51	2.45 ± 0.03	98	391
40 EIC	07.04.97	22/19	6.3 ± 3.2	7.2 ± 3.7	26.1	45	2.71 ± 0.05	38	135
52 AW	13.04.97	23/18	0.8 ± 0.7	1.0 ± 0.9	4.3	17	2.45 ± 0.02	42	18
54 AW	12.04.97	25/21	13.6 ± 3.0	16.2 ± 3.3	54.2	41	2.47 ± 0.03	99	336
56 AW	12.04.97	24/23	8.4 ± 2.6	8.8 ± 2.7	33.3	38	2.57 ± 0.03	97	49
58 EIC	12.04.97	23/19	6.8 ± 3.0	8.2 ± 3.5	21.7	39	2.69 ± 0.04	100	156
60 EIC	07.04.97	24/19	20.5 ± 6.8	25.9 ± 8.2	41.7	109	2.88 ± 0.03	63	505
72 AW	13.04.97	23/22	11.7 ± 2.3	12.3 ± 2.4	56.5	35	2.47 ± 0.03	100	283
74 AW	14.04.97	24/22	9.3 ± 1.5	9.6 ± 1.6	73.9	24	2.51 ± 0.02	98	226
76 FS	14.04.97	23/19	17.6 ± 3.9	21.3 ± 4.3	52.2	52	2.53 ± 0.03	90	408
78 EIC	14.04.97	23/22	37.0 ± 7.6	37.2 ± 8.0	62.5	130	2.69 ± 0.02	98	850
80 EIC	06.04.97	23/18	12.8 ± 4.4	16.3 ± 5.4	39.1	63	2.81 ± 0.02	32	297
93 FS	17.04.97	24/21	48.0 ± 6.5	51.2 ± 6.5	78.3	94	2.54 ± 0.03	76	1153
95 FS	16.04.97	25/18	10.5 ± 3.6	14.6 ± 6.5	33.3	62	2.56 ± 0.03	47	263
96 FS	16.04.97	24/24	48.0 ± 5.8	48.0 ± 5.8	91.7	111	2.37 ± 0.03	70	1136
98 FS	15.04.97	23/23	28.9 ± 3.7	28.9 ± 3.7	82.6	57	2.48 ± 0.03	99	665
100 EIC	06.04.97	23/18	24.9 ± 7.7	32.1 ± 9.2	43.5	120	2.78 ± 0.02	37	587
104 AW	17.04.97	25/24	7.7 ± 2.7	7.0 ± 2.7	33.3	46	2.44 ± 0.03	2	193
106 FS	16.04.97	23/18	19.7 ± 5.5	25.2 ± 6.4	62.5	80	2.47 ± 0.03	82	447
112 AW	18.04.97	23/20	5.0 ± 2.8	5.3 ± 3.2	13.0	50	2.31 ± 0.03	98	138
115 FS	16.04.97	22/22	59.8 ± 8.8	59.8 ± 8.8	81.8	145	2.61 ± 0.04	93	1316
118 FS	15.04.97	24/24	16.9 ± 4.6	16.9 ± 4.6	50.0	68	2.62 ± 0.03	51	373
120 EIC	05.04.97	23/22	25.5 ± 4.8	26.7 ± 4.9	83.3	78	2.48 ± 0.03	99	603
124 AW	17.04.97	24/17	15.0 ± 4.3	21.1 ± 5.4	41.7	58	2.45 ± 0.03	99	352
126 AW	15.04.97	24/24	41.2 ± 6.9	41.2 ± 6.9	75.0	106	2.55 ± 0.03	99	1077
140 AW	05.04.97	23/22	8.6 ± 4.3	9.0 ± 4.5	26.1	78	2.58 ± 0.03	95	200

Station numbers and the areas: AW, FS, and EIC (Fig. 2a); sampling date (dd.mm.yy); nEr and nEr4: number of females at all gonad development stages (Er) and numbers of females in gonad development stage GS4 (Er4), Er and Er4: (eggs female^{-1} d^{-1}) egg production rates; Er4 include only ripe females in gonad stage GS4; % prod. fem.: % of incubated females that produced > 1 egg; E_{max}: number of eggs in the largest clutch, prosome length (mm); H%: % eggs that hatched; n eggs: number of eggs incubated for hatching. All means with ± 1 S.E.

3.6. Feeding

Fecal pellet production of the females in the egg production incubations was very low, with a maximum of five pellets being produced over the 24-h incubation. Gut fluorescence was also low, with the highest value recorded 7 ng chl a female^{-1} (Fig. 7b). There was a significant difference in gut fluorescence between animals caught during night and day ($n = 177$, T-test; $p < 0.001$; Fig. 7a), where night is the time between sunset and sunrise. There was also a significant difference in gut fluorescence between the nighttime stations ($n = 77$, Kruskal Wallis ANOVA on ranks; $p < 0.001$) as well as between the daytime stations ($n = 98$; $p < 0.001$). Gut fluorescence was significantly correlated with chlorophyll a concentration ($n = 31$, $R^2 = 0.67$; $p \ll 0.0001$; Fig. 7b). Calculation of phytoplankton ingestion rates resulted in rates ranging from 0.8 88 µg C female^{-1} d^{-1} (Table 3). The averages were 5 ± 1, 15 ± 2 and 39 ± 9 µg C female^{-1} d^{-1} (± 1 S.E.) for EIC, AW and FS, respectively.

4. Discussion

4.1. Population structure

We encountered two main centers of abundance of *C. finmarchicus*; one in the EIC and one south of the Iceland Scotland Ridge in the Iceland Basin. Stages C4 C6 were presumed to represent animals that had survived through the winter and were in
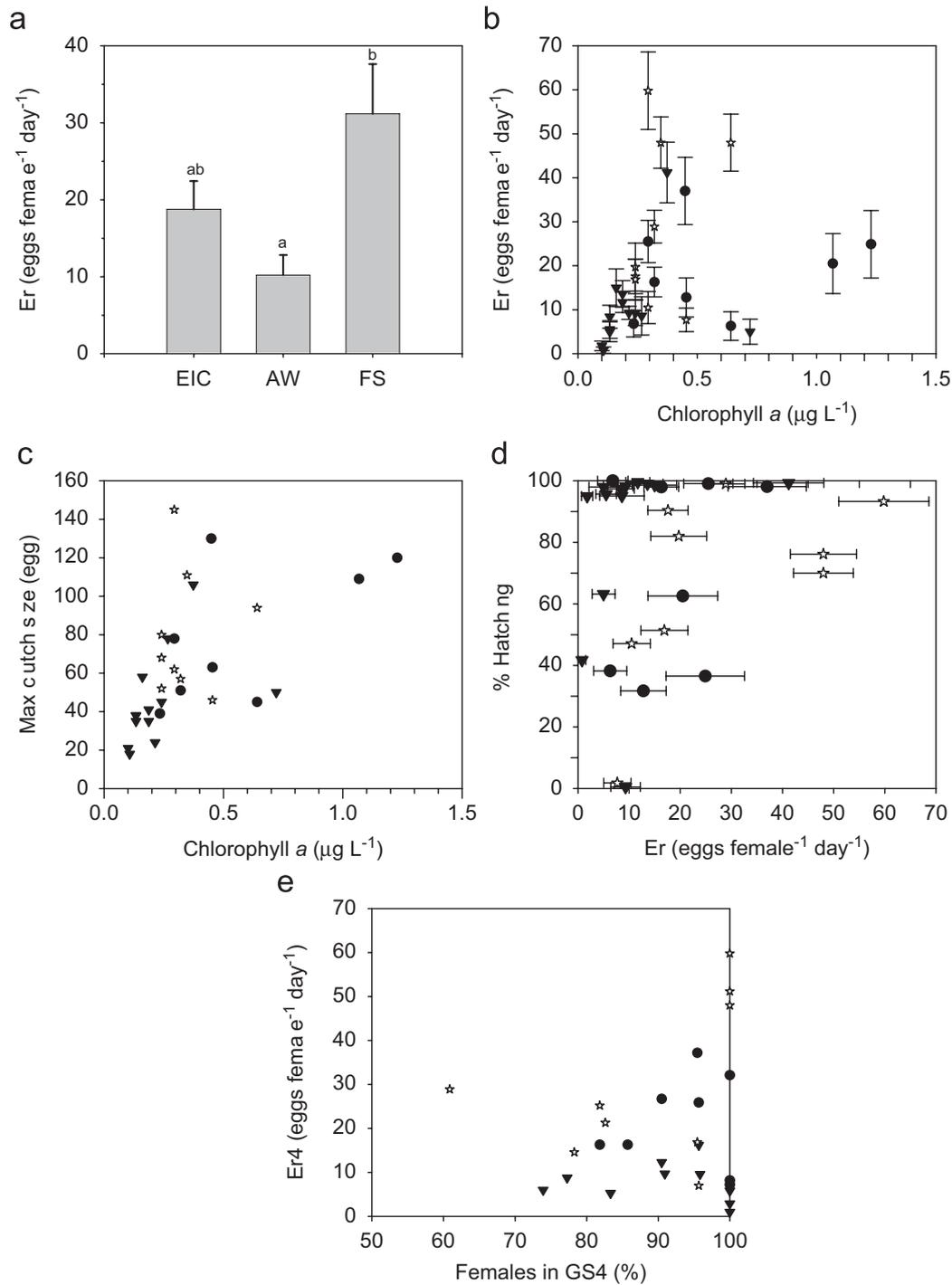
Fig. 6. *Calanus finmarchicus* (a) average egg production (eggs female^{-1} d^{-1}) in EIC, AW, and FS; (b) average egg production and (c) maximum clutch size (eggs female^{-1}) in relation to chlorophyll *a* concentrations (µg L^{-1}); (d) correlation between average egg production rates (Er: eggs female^{-1} d^{-1}) and hatching (%); and (e) the percentage of females at gonad stage GS4. Whiskers indicate ± 1 S.E. Measurements over different areas (see Section 3.5) are indicated by: ($\bullet$) EIC, ($\blacktriangledown$) AW, and ($\star$) FS. Different letters above the bars in (a) indicate a significant difference in the respective measurements between areas.

the process of ascending to the surface, while stages C1 C3 were assumed to be the first-generation offspring of the current production season. C4 C6 in the EIC were animals apparently ascending from the depths of the Norwegian Sea into the FSC. C4 individuals (Fig. 4a) were a significant component of the ascending population on both sides of the Iceland Scotland Ridge including the FSC. The

Table 2
Egg production rates Er4, regression coefficients R^2 and significant relationships (loading $> \pm 0.6$) emerged from principal component analysis (PCA)

Er4	All stations (n 30)		EIC (n 8)		AW (n 14)		FS (n 8)	
	R^2	PCA Er4/var	R^2	PCA Er4/var	R^2	PCA Er4/var	R^2	PCA Er4/var
Chl a							ns	0.84/0.83
T			ns	0.97/0.60				
$\sum$Din	0.22*		ns	0.97/0.71			ns	0.84/0.91
$\sum$Bac							ns	0.84/0.80
$\sum$Chl	015*		0.59*	0.97/0.84			ns	0.84/0.96
$\sum$Pry	0.26*	0.73/0.64	0.74*	0.97/0.90			0.51*	0.84/0.94

Significance of regression slope is indicated with *$p < 0.05$. PCA loadings are shown as loading of Er4/loading of variable. EIC: area in the East Icelandic Current; AW: area in the Atlantic Water; and FS: Faroe Self including Faroe Bank, as in Table 1. Chl a: Chlorophyll a concentration; T: temperature; $\sum$Bac, $\sum$Din, $\sum$Chl, and $\sum$Pry: fatty acid indicators of diatoms, dinoflagellates, chlorophyta, and prymnesiophyta; ns: linear regression not significant; ( ): no correlations.

distribution pattern of the C4, C5 and adult females (total water column integration; Fig. 4) showed a clear separation of the Norwegian Sea and Iceland Basin centers by the Iceland Scotland Ridge. Heath et al. (2000) showed that the depth distribution of overwintering stages was shallower in the Norwegian Sea (400 100 m) compared to the Iceland Basin (1400 1600 m). Further support for this interpretation of the location of major sites of ascent on both sides of the Iceland Scotland Ridge can be derived from the relatively high wax ester content of the surface females, especially at the eastern stations (Fig. 5b), a region which Heath et al. (2004) showed to be a major overwintering site. Females at the surface in the EIC contained up to 110 μg WE. Assuming an approximate requirement of 2.8 and 3.5 μg WE d [−1] for respiration alone (Ingvarsdóttir et al., 1999; Jónasdóttir, 1999) at 4 and 7 °C surface waters, respectively, 110 μg WE would last (without feeding) for about 40 and 25 days, respectively.

According to Gaard and Hansen (2000), *C. finmarchicus* on the FS probably originate from the overwintering stock in the EIC area and FSC. The female prosome length on the FS in the present study were significantly smaller (FS: 2.52 ± 0.16 mm; ± 1 S.D.) than compared to EIC (2.68 ± 0.21 mm; Section 3.3) and thus more comparable to the size of females in the AW (2.49 ± 0.16 mm; Fig. 5a). Prosome-length measurements of *C. finmarchicus* females, overwintering in the Norwegian Sea and FSC (Jónasdóttir, unpublished data) showed that females in the FSC and on the FS in the present study were of comparable sizes. This may indicate that at the time of our study, the females on the FS did not originate from the EIC but, instead, from the AW and FSC. The origin of the animals on the FS is, at any given time, highly dependent on the strength of the surface currents at the time of ascent (Heath et al., 1999).

Stages C1 C3 copepodites were observed at appreciable concentration only on the FS (790 m [−2]). Using the development models of Corkett et al. (1986) at FS temperatures, we estimate that these young stages originated from eggs spawned about 3 weeks earlier. Development time to stage C1 in the EIC would have been about 29 days but, due to higher temperatures, 17 days in the AW. The question then arises whether the low abundance/absence of younger stages in the AW and EIC (average 47 and 23 individuals m [−2], respectively) could be due to higher cannibalism in these waters as compared to FS, thus allowing the population to flourish only on the FS. Since the C4 C6 population recently ascended from overwintering represented a major fraction of the zooplankton biomass, cannibalism on eggs and nauplii could be an important factor. Predation on conspecific eggs has been estimated in the laboratory for *C. helgolandicus* (Bonnet et al., 2004) and on nauplii for *C. finmarchicus* (Basedow and Tande, 2006). We made use of these laboratory estimates to perform a simple simulation of potential cannibalism to see if it could explain the lack of C1 C3 stages in the off-shelf waters.

The simulation tracked consumption by the observed numbers of C5 and C6 female copepodites present at each station, from a simulated population of eggs and nauplii comprising a succession of daily
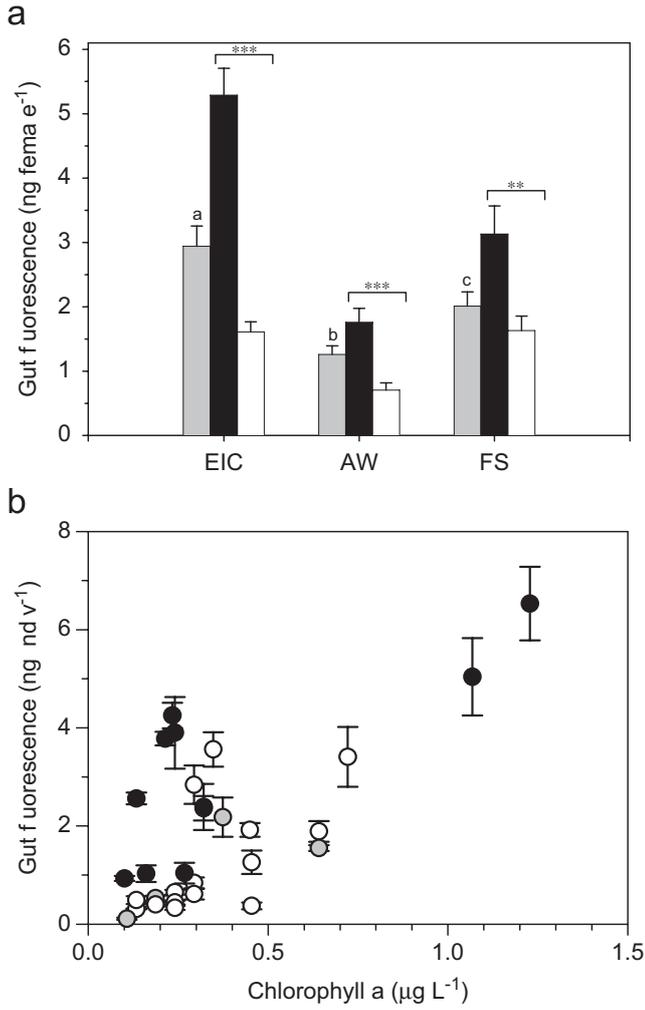
Fig. 7. *Calanus finmarchicus* (a) gut fluorescence (ng pigment female^{-1}) in the different areas. Light bar: 24 h average, black bar: night average, white bar: day average. (b) Correlation between gut fluorescence and chlorophyll *a* concentration. Open circles: animals sampled during daylight, gray circles: animals sampled during dusk or dawn and black circles: animals sampled during nighttime. EIC: area in the East Icelandic Current, AW: area in the Atlantic Water and FS: Faroe Self including Faroe Bank, as in Fig. 2. Whiskers indicate ± 1 S.E. Different letters above the bars indicate a significant difference in the respective measurement between areas, and significant differences between day and night measurements in part (a) is indicated with $^{**}p < 0.001$, $^{***}p < 0.0001$.

cohorts assuming constant daily population egg production over time. The concentration (N, L^{-1}, averaged over the upper 150 m of the water column) of individuals of age a (days, $a \geqslant 0$) at time t (days, $t \geqslant 0$) in a cohort born on day $t-a$ ($t \geqslant a$) was given by

$$N_{a+1,t+1} = N_{a,t} - i_{a,t}$$

subject to the limit that $N \geqslant 0$. $N_{a=0}$ was the daily population egg production, assumed constant over

time, and estimated from the observed per capita egg production rates by ripe females (G4 Er, Table 2), female abundance ($N_{C6female}$, L^{-1}, averaged over the upper 150 m), and the fraction of females at stage G4. The term $i_{a,t}$ was the number of prey eaten by the C5 and C6 predators (N_{C5} and $N_{C6female}$, L^{-1}; Fig. 8b) according to

$$i_{a,t} = I_t \times \frac{N_{a,t}}{\sum_{a=\text{stage } 1}^{a=\text{stage } 2} N_{a,t}}$$

Here, the term 'stage' referred to $a = 0$, $a =$ age at egg hatching, or $a =$ age at end of $N1$, and I was the total daily consumption of eggs or nauplii from the multi-cohort population of prey by the C5 and C6 female copepodites: for eggs ($a \leqslant$ age at hatch),

$$I_t = (N_{C5} + N_{C6female}) \frac{48.2 \times \sum_{a=0}^{a=\text{hatch}} N_{a,t}}{179.6 + \sum_{a=0}^{a=\text{hatch}} N_{a,t}}$$

according to data for *C. helgolandicus* (Bonnet et al., 2004). For nauplii (age at hatch $< a \leqslant$ age at end of $N1$),

$$I_t = (N_{C5} + N_{C6female}) \times 0.43 \times \sum_{a=\text{hatch}}^{a=\text{end of } N2} N_{a,t} + 0.07$$

according to data for *C. finmarchicus* (Basedow and Tande, 2006). The ages at hatching and the end of $N1$ were estimated from the mean temperature over the upper 150 m of the water column at each station according to Corkett et al. (1986). Finally, the equilibrium daily consumptions of eggs and nauplii were averaged over the three water masses EIC, AW and FS, and expressed as fractions of the daily egg production.

The results of this simplified model show that about 0.3 l eggs and nauplii were potentially ingested per predator per day (Fig. 8c). Taking predator concentrations into account, this corresponds to approximately 13–17% of the egg and $N1$ production in the EIC and AW potentially being removed daily by cannibalism and hatching failure, while only 3% was removed on the FS (Fig. 8d.). The stage duration for $N1$ was longest in the EIC, which results in a greater risk of predation for this stage in the EIC than in AW and FS. It is possible that the egg predation model for *C. helgolandicus* was not applicable for *C. finmarchicus*. Basedow and Tande (2006) showed in their study that *C. finmarchicus* exhibits higher ingestion rates on nauplii than Bonnet et al. (2004) reported for *C. helgolandicus*, and the same could be true for

Table 3
Energy gained with food and used for production of eggs

Area	Station	Chl a (mg m^{-2})	Ingestion rate (µg C female^{-1} d^{-1})			C need for observed Er (µg C)		Ingested C% of need		Er% of potential		WE$_{0-100}$ (µg female^{-1})
			Phyto.	Egg	Nauplii	Er4	E_{max}	I/Er4	I/E_{max}	Er4	E_{max}	
EIC	38	32.0	0.8	0.1	0.1	16.3	51	6	2	16	50	1 ± 1
	40	64.1	3.6	0.0	0.0	7.2	45	50	8	6	36	33 ± 10
	58	23.4	3.6	0.2	0.2	8.2	39	48	10	7	31	26
	60	106.8	12.2	0.4	0.2	25.9	109	49	12	18	77	81 ± 3
	78	44.9	3.4	0.2	0.2	37.0	130	10	3	30	104	20 ± 0
	80	45.4	3.6	0.1	0.0	13.4	63	28	6	10	47	38 ± 10
	100	122.8	6.7	0.7	0.3	32.1	120	24	6	24	91	111 ± 6
	120	29.4	3.8	0.3	0.3	26.7	78	17	6	25	74	27 ± 17
AW	13	10.0	15.7	0.0	0.0	2.9	21	545	75	3	19	29 ± 18
	15	24.0	13.8	0.0	0.0	9.3	45	149	31	9	44	8
	34	13.4	4.9	0.4	0.3	5.7	38	98	15	5	36	21
	36	13.4	7.7	0.0	0.0	5.5	35	140	22	5	30	9 ± 5
	52	10.7	13.7	0.0	0.0	0.9	18	1455	76	1	17	14
	54	18.7	15.4	0.2	0.2	16.2	41	98	39	16	39	20 ± 14
	56	13.4	14.1	0.0	0.0	8.8	38	162	37	8	34	5 ± 1
	72	18.7	9.7	0.0	0.0	11.7	35	83	28	11	33	7
	74	21.4	17.3	0.1	0.1	9.7	24	181	73	9	22	33 ± 2
	104	45.4	13.6	0.1	0.0	7.7	46	178	30	8	45	13 ± 2
	112	72.1	29.7	0.0	0.0	5.5	50	538	59	6	56	5
	124	16.0	25.6	0.0	0.0	18.0	58	143	44	17	56	4
	126	37.4	7.3	0.1	0.1	41.2	106	18	7	37	95	10
	140	26.7	22.5	0.0	0.0	9.0	78	250	29	8	68	22
FS	76	24.0	22.3	0.0	0.0	21.3	52	105	43	19	47	4
	93	64.1	22.3	0.0	0.0	50.1	94	45	24	45	85	2 ± 2
	95	29.4	65.8	0.0	0.0	11.9	62	553	106	11	55	6 ± 0
	96	34.7	28.1	0.0	0.0	48.0	111	59	25	50	117	2 ± 1
	98	32.0	23.2	0.1	0.1	28.9	57	81	41	27	54	13 ± 6
	106	24.0	88.2	0.0	0.0	25.2	80	350	110	24	76	3 ± 1
	115	29.4	22.2	0.4	0.4	59.8	145	38	16	51	123	14
	118	24.0	38.6	0.1	0.1	16.9	68	230	57	14	58	17 ± 13

Areas as in Table 1. Chlorophyll concentration (mg Chl a m^{-2}); carbon based ingestion (µg C female^{-1} d^{-1}) of phytoplankton (phyto.), eggs and nauplii; carbon need for the observed egg production rates (Er) where Er4 and E_{max} are the average egg production rate of females in gonad developmental stage 4 (GS4) and the maximum clutch size, respectively. Ingested carbon (I) in relation to the carbon need for the observed egg production rates Er4 and E_{max} (%), Er% of potential: percent of eggs produced in relation to the potential egg production of the female of the given size (%), wax ester (WE) content of females in the upper 100 m of the water column (µg female^{-1} ± 1 S.E.). See Section 4.1.1 for calculations.

ingestion of eggs. However, such species differences are probably irrelevant in the present study at these low egg and naupliar concentrations (1 3 eggs and nauplii L^{-1}) as Bonnet et al. (2004) and Basedow and Tande (2006) employed up to 120 eggs L^{-1}, and 20 nauplii L^{-1}, respectively, in their experiments. The large difference in the potential impact of predation on eggs and $N1$ between the FS and the other two regions suggests that predation could, possibly, contribute appreciably to the lack of early stage copepodites in the EIC and AW, while the mortality rate was sufficiently low in the FS to allow the population to develop. There was also lower predator pressure on the FS as the ratio between C5 and C6 females and C1 C3 stages was considerably higher in EIC and AW, suggesting higher predator pressure by *C. finmarchicus* in these waters (Fig. 8b). However, this difference in stage composition could also be caused by a different timing of reproduction in the areas, reproduction starting earlier and/or developing faster because of higher temperatures on the FS.
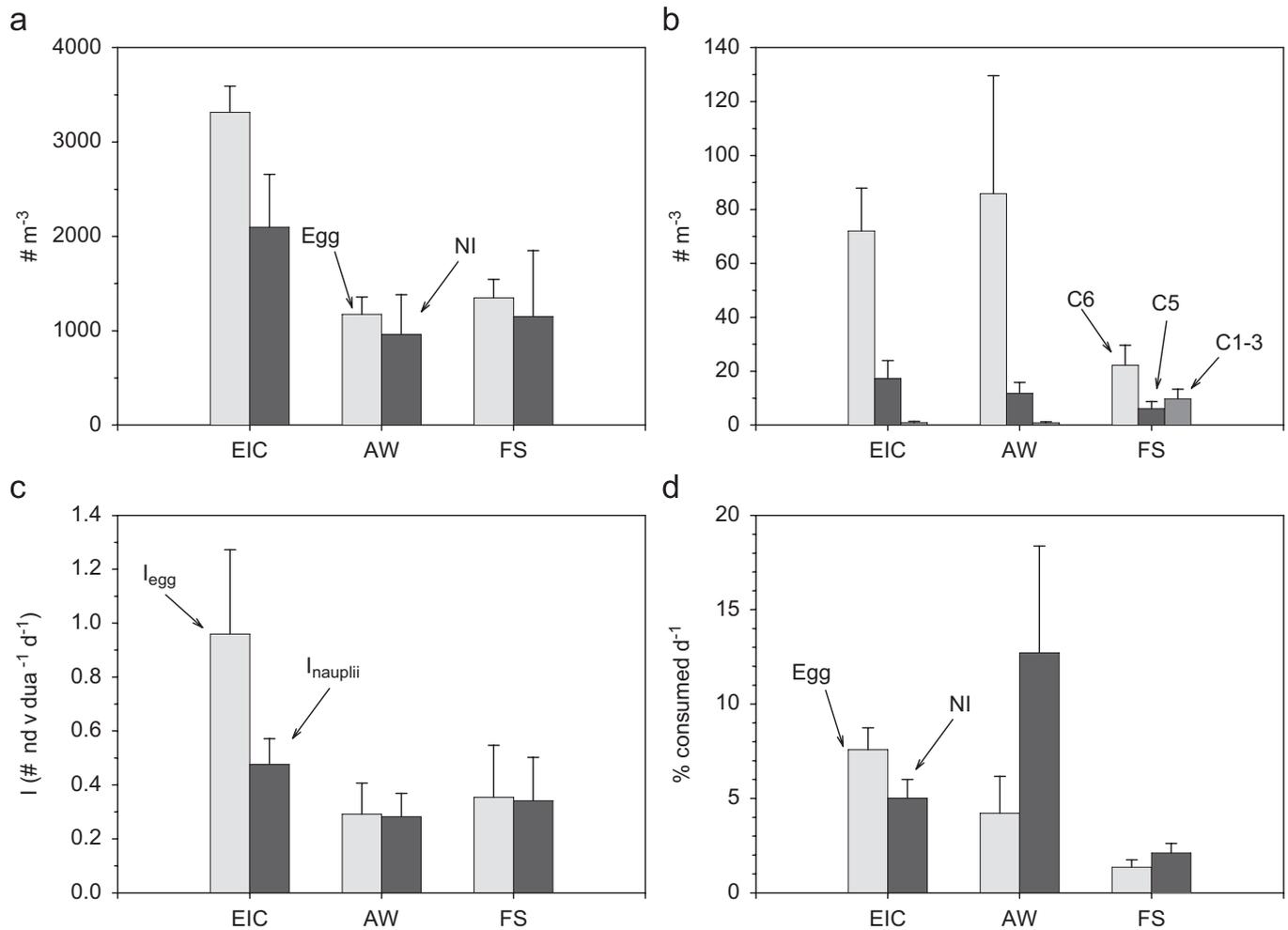
Fig. 8. (a) Abundance of *Calanus finmarchicus* eggs (light bars) and naupliar stage 1 (NI; dark bars; number m^{-3}); (b) abundance of females (C6), copepodite stage C5 and C1 C3 combined in the upper 150 m (number m^{-3}); (c) estimated ingestion rates of eggs (light bars) and nauplii 1 (dark bar) by the potential predators (C5 and C6 females) (number individual^{-1} d^{-1}); and (d) percent of total eggs (light bars) and nauplii (dark bars) consumed by the potential predators in areas EIC, AW and FS (as in Fig. 6). Whiskers indicate $\pm$1 S.E.

4.2. Reproduction biology

On the basis of the high dissolved nutrient and low chlorophyll *a* concentrations ($\leqslant 1 \mu g L^{-1}$ at all but one station; Fig. 3a), it is reasonable to conclude that the spring bloom had not yet taken place at any location in our study area. Concurrent measurements on the Faroe Bank (Gaard, 1999) and at station M, about 2°E from these stations (see Fig. 1 for location, Meyer-Harms et al., 1999), showed pre-spring-bloom levels of chlorophyll *a* between 0.2 and 0.7 $\mu g L^{-1}$. At both locations, the spring bloom began about month later, i.e. mid-May, with peak chlorophyll *a* concentrations being about 3 $\mu g L^{-1}$. The gut fluorescence levels in the EIC (Fig. 7a and b) were similar to the levels determined during pre-spring bloom at station M reported by Irigoien et al. (1998). A concurrent study by Gaard

(2000) on the FS also showed the peak abundance of *C. finmarchicus* (stages C1 C6) to be about 1 month after our study, i.e., in May, with the first generation beginning to develop during April, in accordance with our observation.

Because of the low phytoplankton concentrations and frequently observed high egg production rates, three questions arise: (1) Would the potential consumption of phytoplankton by *C. finmarchicus* in the region be sufficient to supply the carbon needed for such high egg production rates during the pre-bloom period? (2) Was the production food limited? and (3) What controlled the observed egg production rates?

4.2.1. Carbon demand

To estimate the carbon demand for the eggs produced, we assumed the carbon content of eggs to

be 250 ng C egg [1], which is an average of four published carbon values of *C. finmarchicus* eggs: 191, 231, 250 and 347 ng C egg [1] (Hygum et al., 2000; Ohman and Runge, 1994; Cabal et al., 1997; Mayor et al., 2006). We assumed a gross growth efficiency (GGE) of 25%, an upper value obtained for *C. helgolandicus* feeding on a dinoflagellate by Rey-Rassat et al. (2002b). Our calculations showed that the chlorophyll-based ingestion could support the observed average egg production of the GS4 females (Er4) in the AW (288±35%) because of low egg production rates, and FS (182±65%) because of high ingestion rates. In the EIC, however, chlorophyll-based ingestion could support only 29±6% of the observed Er4 as the ingestion rates were low because of low temperatures (Table 3). Ingested eggs and nauplii contributed only an additional 1% of the potential ingested carbon required for the observed egg production. Many females in our study had clutch sizes of over 100 eggs (Table 1). The maximum clutch size of 145 eggs was close to the observed size-related maximum for this species (Fig. 9, see also Jónasdóttir et al., 2005). In these instances, phytoplankton, egg and nauplii ingestion could not meet the carbon demand for the maximum egg production rates observed, but only accounted for 7±1%, 40±6% and 53±13% (±1 S.E.) of the C demand in the EIC, AW and FS, respectively (Table 3).

No determination of heterotrophic microplankton biomass was made during the present study, but ingestion of ciliates can also be a significant source of carbon for *C. finmarchicus* (Ohman and Runge, 1994; Mayor et al., 2006). *C. finmarchicus* ingestion rates on ciliates were estimated to be 0.032 μg C female [1] d [1] at pre-bloom conditions at station M (Irigoien et al., 1998), but Mayor et al. (2006) estimated the spring ingestion rates in the Irminger Sea to be about 0.4 μg C female [1] d [1]. Mayor et al. (2006) also reported a slight selection for ciliates during the spring period. Nevertheless, compared to phytoplankton ingestion rates, the ciliate carbon ingested can be expected to constitute only a minor contribution to the diet of *C. finmarchicus* during our study, at least in the oceanic areas AW and EIC. On the FS, where phytoplankton production appeared to be more advanced than in the other two areas (significantly lower diatom fatty acid signal, slightly higher dinoflagellate and prymnesiophyte fatty acid signals compared to the EIC), one might predict that there could be a more active microbial food web in this region compared with the rest of the study area. This would include higher ciliate concentrations representing a potential non-chlorophyll food source for the *Calanus*. Therefore, the above comparison with the heterotrophic community measured at station M and the Irminger Sea at the same time may not apply for the FS community.

An alternate source of energy for the observed rates of egg production in the EIC is the lipid reserves in the females. While there are no studies that report direct measurements of utilization of internal lipids for producing eggs for
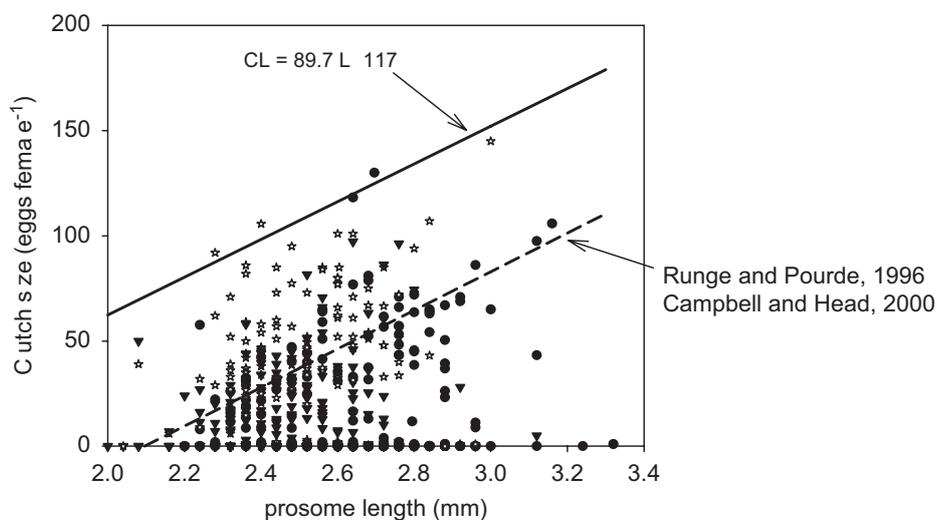
Fig. 9. Relationship between egg production rates Er4 (eggs female^{-1} d^{-1}) of *Calanus finmarchicus* and prosome length (mm). Solid line is the regression showing egg production potential of *C. finmarchicus* at given length (Jónasdóttir et al., 2005), and the dotted line is the regression from Runge and Plourde (1996) and Campbell and Head (2000) through all their clutch size measurements.

C. finmarchicus, numerous studies show, based on lipid or carbon depletion, that internal lipid reserves are a likely source of energy used for gonad development (Pasternak et al., 2001; Pasternak et al., 2004) and egg production (e.g. Richardson et al., 1999; Mayor et al., 2006) for this species. According to Richardson et al. (1999), 20 µg C (ca. 25 µg WE) could fuel the production of approximately 100 *C. finmarchicus* eggs based on 30% efficiency for catabolism of wax ester to eggs. If this is the case, then wax ester concentrations in females at the surface in the EIC (Fig. 5a) would appear to have been sufficient to support the production of the maximum egg clutch sizes recorded here. The GGE for internal lipids is not known for *Calanus* but can be assumed to be higher than for phytoplankton. All of the above calculations are sensitive to the chosen GGE. If GGE is higher than 30% for internal lipids, more eggs can be produced per unit wax ester, and similarly, if the GGE for phytoplankton is lower than the 25% chosen here, less of the observed egg production can be explained by phytoplankton ingestion. This is a very important issue to resolve in order to be able to make accurate estimates of carbon sequestering for reproduction.

4.2.2. Food limitation

The egg production potential of *C. finmarchicus* is influenced by the size of the female (Runge and Plourde, 1996; Jónasdóttir et al., 2005). We used the regression on maximum published clutch sizes of *C. finmarchicus* vs. prosome length of the female presented in Jónasdóttir et al. (2005) to calculate the reproductive potential of *C. finmarchicus* in the present study (Table 3; Fig. 9). When average Er4 egg production rates are considered, *C. finmarchicus* appeared only to be producing at 1 50% of its maximum capacity in our study area. Females producing the largest clutches were producing from $43 \pm 6\%$ of their capacity in region AW (range 17 95%) to $64 \pm 9\%$ (range 31 104%) and $77 \pm 10\%$ (range 47 123%) in EIC and FS, respectively. This indicates food limitation for egg production at many stations but also a large difference in reproduction characteristics of the individual females in these populations.

4.2.3. Control of egg production rates

It appears that in many, but not all, of the stations food availability and potential internal lipid reserves can explain the carbon demand for the observed egg production. This does not, however, explain what controls the production   why is there such a low production when the observed ingestion could fuel much higher rates? When the egg production rates of *Calanus* in the different areas were compared and analyzed with respect to the food environment, temperature, size and wax ester content, significant correlations with different phytoplankton communities (specific fatty acid indicators) appeared (Table 2). The egg production rate was strongly correlated with prymnesiophyte, dinoflagellates and chlorophyte fatty acid indicators but, interestingly, not to the diatom fatty acids that appeared to be the main component of the phytoplankton biomass in the EIC. We believe that the females in this area had recently ascended from overwintering and that their internal lipid stores could have contributed to the observed production. The egg production rates observed in the AW cannot be explained in the same way, as the rates were much lower than expected with the potential chlorophyll ingestion rates in this water mass. The Er4 could not be explained by any of the measured variables (Table 3). On the FS, the observed egg production rates correlated best with food abundance composed of all main phytoplankton groups.

4.2.4. Hatching

While the hatching success of *C. finmarchicus* eggs was over 80% at half of the stations, there were seven stations where hatching was under 50%. At two of these, eggs totally failed to hatch. These two stations were far apart, one off the south coast of Iceland and the other in the FSC off the southern FS. No correlations were apparent with the measured environmental variables when all stations were combined. When the hatching results were separated into the three different areas, it was still not possible to explain the pattern in hatching on the basis of differences in environmental variables, with the exception of a temperature relationship for hatching in the EIC and AW. The most likely reason for this temperature dependence in the EIC is that the time given for the eggs to hatch (i.e. incubation time) was too short in the cold EIC water as the low hatching (32 62%) was in waters under $2\,^\circ\text{C}$ while hatching was 100% in 4.5 6 $^\circ\text{C}$ waters. Based on measurements from Nova Scotia and Tromsø (Corkett et al., 1986), *C. finmarchicus* eggs needed 78 and 92 h to hatch at 3 and $2\,^\circ\text{C}$, respectively, which is longer than given in this study (72 h at $3\,^\circ\text{C}$). However, this cannot explain the

poor hatching at stations in the AW, as temperatures were over 7 °C and incubation time should have been ample for hatching. If females were producing eggs partly or fully from their lipid reserves, we would not expect to find a correlation with any concurrent environmental measurements, as the lipid reserves are based on food ingested during the previous summer. Removing the low hatching results from the EIC dataset did not yield in any significant correlations relating hatching at the remaining stations to the measured variables.

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