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Calanus finmarchicus along the northern Mid-Atlantic Ridge: variation in fatty acid and alcohol profiles and stable isotope values, $\delta^{15}N$ and $\delta^{13}C$

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Fatty acid and alcohol profiles and stable nitrogen and carbon isotope values, $\delta^{15}N$ and $\delta^{13}C$, of *Calanus finmarchicus* CV were studied in June 2004 to estimate their trophic status along the northern Mid-Atlantic Ridge i.e. the Reykjanes Ridge (RR), extending from Iceland in the north to the productive region of the Sub-Polar Front (SPF) in the south. Two main groups of stations were defined in the study area based on fatty acid (FA) and fatty alcohol compositions, the stations in the RR area constituted one group and the stations in the frontal area constituted another. The sum of relative amounts of the dietary FAs was significantly higher in the RR area than in the frontal area. Conversely, the long-chained FAs, 20:1 and 22:1, were found in significantly lower relative amounts in the RR area than in the frontal area, thus indicating later ascent of the animals in the frontal area. Further support of this is provided by the fatty alcohols ratio 20:1/22:1 which differed significantly between the two areas. The $\delta^{15}N$ values were significantly higher in the frontal area compared to the RR area indicating higher trophic position and/or different pelagic-POM baseline in these areas.

KEYWORDS: Calanus finmarchicus; stable isotope; fatty acid; Mid-Atlantic Ridge

INTRODUCTION

The Mid-Atlantic Ridge (MAR) is mostly an underwater mountain range, which nearly splits the entire Atlantic Ocean floor from north to south. The Reykjanes Ridge (RR) is the northernmost part of the MAR extending between Iceland and the Charlie Gibbs transversal fracture zones (CGFZ) which is the deepest connection (>4000 m) between northeast and northwest North Atlantic. The complicated bottom topography of the MAR is believed to have a pronounced effect on the flow of currents, both deep water and near surface circulations (Sy *et al.*, 1992; Bower *et al.*, 2002; Søiland *et al.*, 2008), which in turn may keep pelagic organisms separated at depths. The North Atlantic Current crosses the MAR in the CGFZ region (45–52°N) from west to east, defining a boundary, the Sub-Polar Front (SPF), between the cold productive waters to the north and warmer less productive waters to the south (Sy *et al.*, 1992; Rossby, 1999). Fronts can serve as distribution barriers of species and induce

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formation of eddies and vertical mixing in their vicinity resulting in upwelling of nutrients and higher biological productivity in the frontal area.

The predominantly herbivorous copepod *Calanus finmarchicus* (Gunnerus, 1765) is a cold-temperate species with a main distribution off the east coast of North America at ~40°N in the south and west, to the North Sea in the east and to the arctic ice edge in the Norwegian and Barents Seas in the north (Conover, 1988; Harris, 1996). This species dominates the North Atlantic zooplankton biomass (Planque and Batten, 2000). It completes two or even three generations per year in the southern parts of its distribution range (Gislason and Astthorsson, 1996; Irigoien, 1999) whereas in the colder waters in northern parts only one generation is present (Falkenhaug *et al.*, 1997; Gislason and Astthorsson, 1998). *Calanus finmarchicus* develops via six naupliar and six copepodid stages after hatching from eggs. At late copepodite stages CIV-CV, present in late summer, the species descends from the surface water to overwinter at ~300–1800 m depth (Gislason and Astthorsson, 2000; Gislason *et al.*, 2007) in a state of dormancy (Marshall and Orr, 1972; Hirche, 1996). In late winter and spring they ascend to surface waters, moult into adults, and reproduce. Egg production is closely coupled to the phytoplankton spring bloom (Marshall and Orr, 1972; Hirche *et al.*, 1997). However, egg production has also been observed prior to the spring bloom when phytoplankton concentrations are extremely low indicating that *C. finmarchicus* are also able to use lipid reserves for egg production (Richardson *et al.*, 1999).

The neutral lipid class, wax esters, are the main storage lipids of *C. finmarchicus* and are produced during periods of phytoplankton blooms, before the animals enter dormancy (Sargent and Falk-Petersen, 1988; Lee *et al.*, 2006). Wax esters serve as an important energy source during food scarcity and diapause, and are also utilized for reproduction (Lee *et al.*, 2006). Thus, wax esters have been regarded as a long-term energy reserve. They consist of one fatty acid (FA) esterified to a long chain fatty alcohol in an equimolar amounts (Lee *et al.*, 1971a, 2006; Sargent and Henderson, 1986).

Stable isotopes and FA trophic marker techniques provide information on dietary assimilation over longer time periods (i.e. weeks to months) than the more traditional stomach content analyses (Fry, 1988; Rau *et al.*, 1992; Dahl *et al.*, 2003; Dalsgaard *et al.*, 2003), which reflects only recent feeding. In addition, stable isotopes may give information about trophic position of the species, while FAs and alcohols can provide valuable information on diet composition. Stable nitrogen values have been used to estimate trophic levels (Hobson and Welch, 1992; Dahl *et al.*, 2003; Tamelander *et al.*, 2006), while the carbon values may provide information about the carbon source (Peterson and Fry, 1987; Peterson, 1999; Søreide *et al.*, 2006a). A stepwise enrichment of stable carbon (^{13}C, ~1‰) and stable nitrogen (^{15}N, ~3–4‰) values occurs between trophic levels (Minagawa and Wada, 1984; Wada *et al.*, 1987; Fry, 1988; Hobson and Welch, 1992; Hobson *et al.*, 1995). Primary producers and some zooplankton species can be characterized by their specific FA profiles. Some of these FAs can be transferred relatively unchanged trough trophic levels (Lee *et al.*, 1971b; Graeve *et al.*, 1994; Dalsgaard *et al.*, 2003). Diatoms are known to have relatively high amounts of 20:5n3, 16:1n7 and C16 polyunsaturated fatty acids (PUFAs), whereas elevated amounts of 22:6n3 and C18 PUFAs are characteristic for dinoflagellates and *Phaeocystis* (Dalsgaard *et al.*, 2003). *Calanus* copepods biosynthesize *de novo* large amounts of C20 and C22 long-chain, high energy, monounsaturated FAs and alcohols (Dalsgaard *et al.*, 2003 for review). All these FAs are regarded as good trophic markers, i.e. are transferred relatively unmodified into neutral lipids of consumers.

The main objective of the present study was to investigate variation in stable isotope ratios (δ^{15}N and δ^{13}C) and FA and alcohol profiles of *C. finmarchicus* CV at stations along the RR, extending from Iceland in the north to the SPF in the south, to observe if the trophic status of *C. finmarchicus* over the RR and in the productive frontal area (close to the northern edge of the SPF), reflect the different environmental and hydrographic conditions. The project is a part of an international ecological study (MAR-ECO) to explore the macrofauna along the northern Mid-Atlantic, with its main objective to describe and understand the patterns and distribution, abundance and trophic relationships of organisms inhabiting the mid-ocean North Atlantic (Bergstad and Godø, 2003; Bergstad *et al.*, 2008).

METHOD

Study area

The study was carried out at six stations along the RR (Table I, Fig. 1) between Iceland and the SPF (~60–52°N). For simplification in this paper, stations 4, 8, 10 and 12 are called RR stations and 18 and 20 are referred to as the frontal area stations. The position of the SPF in this study was at 52°N and 30–35°W (Søiland *et al.*, 2008). The bottom depth at these stations ranged between 1300 and 3000 m, the deepest ones

Table I: Sampling locations and sampling date in June 2004

Stations	Lat (°N)	Long (°W)	Date
4	60.13	28.14	11 June
8	56.19	34.26	13 June
10	55.31	36.36	14 June
12	52.47	34.40	16 June
18	52.36	32.04	20 June
20	52.47	30.31	21 June

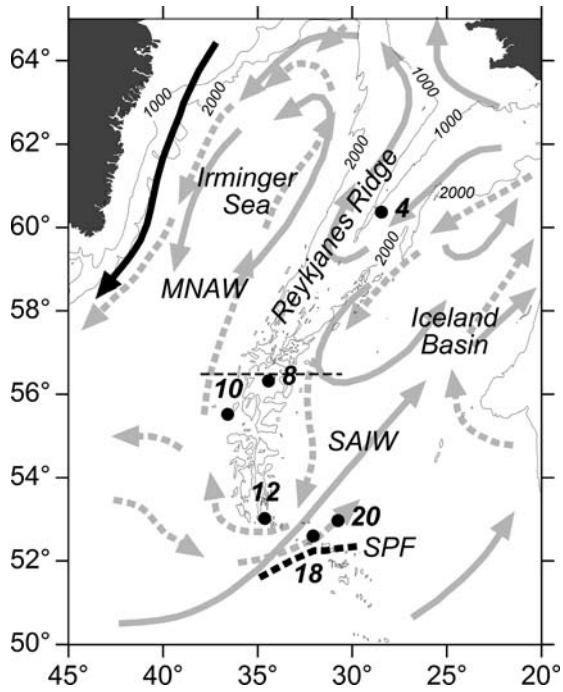

Fig. 1. Map of the study area showing the sampling stations. Inserted on the figure are the main ocean currents in the upper layers, adapted from Valdimarsson and Malmberg (1999) and Dietrich *et al.* (1980), and the main overflow paths adapted from Hansen and Østerhus (2000). The Sub-Polar Front (SPF) is adapted from Gaard *et al.* (2008). Grey arrows, Atlantic Water; black arrow, Polar Water; grey broken arrows, main overflow paths. Thin black broken line denotes the boundary between the Modified North Atlantic Water (MNAW) and the Sub-Arctic Intermediate Water (SAIW). Thick black broken line denotes the SPF.

(Stns 12, 18 and 20) were in the CGFZ area. The depth on each side of the ridge is around 2000–3000 m.

Sampling

Samples were collected from the RV *G.O. Sars* between 11 and 21 June 2004. Temperature and salinity were recorded with a Sea Bird Electronics SBE 911plus CTD. Seawater samples for chlorophyll *a* were collected from 8–10 depths in the upper 200 m and filtered through GF/C glass fibre filters, which were frozen for later analysis. Seawater for nutrient analyses was collected from ~12 depths in the upper 200 m. *Calanus finmarchicus* was sampled by vertical hauls (from 100 m depth to surface) with a Juday net with 180 μm mesh. The net hauls were not quantitative in this study. For FA and alcohol analyses, three replicates including 8–10 individuals of *C. finmarchicus* CV were picked out of the samples and stored in chloroform:methanol 2:1 (v/v) solution at −80°C. Bulk samples containing mainly *C. finmarchicus* were frozen in plastic trays at −80°C and CV of *C. finmarchicus* were picked out later in the laboratory for stable isotope analyses.

Laboratory analyses

Stable isotope ratios were analysed for *C. finmarchicus* CV. Three replicates including ~60 individuals each were analysed for each station. Stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) were analysed at the Institute for Energy Technology (IFE), Kjeller, Norway. The samples were dried at 60–70°C to constant weight and homogenized in a mortar using a glass pestle. According to protocols of the IFE (Søreide *et al.*, 2006b), lipids were removed by Soxhlet extraction for 2 h by using a solvent consisting of 93% dichloromethane (DCM) and 7% methanol, in order to reduce variability due to isotopically lighter lipid (Hobson and Welch, 1992). To remove traces of carbonates, the samples were acid rinsed with 2N HCl and dried at 80°C. Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of the residual material were analysed on a Micromass Optima, Isotope Ratio Mass Spectrometer and expressed as per mill (‰) enrichment relative to international standards according to the relationship:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

where X (‰) is ^{13}C or ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard for $\delta^{13}C$ is Pee Dee Belemnite (PDB: USGS 24) and for $\delta^{15}N$ is atmospheric air (IAEA-N-1 and IAEA-N-2).

Fatty acid and alcohol compositions were analysed for *C. finmarchicus* CV.

Lipid classes, FAs and fatty alcohols were analysed at UNILAB, Tromsø, Norway. The samples were homogenized in chloroform:methanol 2:1 (v/v), and total lipid was extracted and weighed. A sub-sample of the extract was separated into a polar and a neutral lipid fraction, using solid bond extraction–fractionation as described by Kaluzny *et al.* (Kaluzny *et al.*, 1985).

Relative compositions (%) of FA methyl esters and fatty alcohol acetates were determined on an Agilent 6890 N gas chromatograph, equipped with a fused silica, wall-coated capillary column with an Agilent 7683 injector and flame ionization detection. Hydrogen was used as the carrier gas with an oven thermal gradient from an initial 60 to 150°C at 30°C min^{-1}, and then to a final temperature of 230°C at 1.5°C min^{-1}. Individual components were identified by comparing them to known standards, and were quantified using HPChemStation software (Hewlett-Packard).

Statistical analyses

Redundancy analysis (RDA) was performed on FA and alcohol relative compositional data (i.e. the sum of FAs and alcohols being 100%). RDA is a constrained ordination analysis and represents multivariate data in a reduced number of axes of the greatest variability. In ordination methods, the first axis always explains most of the variance in the data set, the second axis the second most variance and so on. With the help of an ordination diagram, it becomes easier to visualize the similarity structure. Samples with low amounts of FAs and alcohols (<0.5%) were excluded from the analysis because the precision of their determination was too low. The remaining percentage was subjected to RDA to explore spatial differences in FA and fatty alcohol compositions of *C. finmarchicus* CV. Stations were used as explanatory variables, and the FA and fatty alcohol compositions as response variables. To test for significant differences in FA and fatty alcohol compositions between stations, a Monte Carlo test with 999 permutations was applied. This multivariate statistical analysis was performed in CANOCO 4.5 for Windows®. Individual samples (*n*) were used in the analysis, but in the Table III, only mean values are presented.

The Shapiro–Wilk's test was used to test for normality of the stable isotope and the selected FAs and alcohol data. This test was performed in Statistica version 6 for Windows® (StatSoft Inc.). As both isotope ratios, $\delta^{15}N$ and $\delta^{13}C$, data were normally distributed, analysis of variance (ANOVA) was conducted to analyse for differences in stable isotope ratios of *C. finmarchicus* CV among stations within areas (i.e. the RR and the frontal area) followed by multiple comparisons, performed by Tukey's honestly significant difference test (HDS). Differences in stable isotope ratios and selected FAs and alcohol relative amounts of *C. finmarchicus* CV were tested between the two areas with ANOVA, where all stations within each area were pooled. These tests were performed using R 1.9.1. Individual samples (*n*) were used in all analyses.

RESULTS

Environmental conditions

Søiland *et al.* (Søiland *et al.*, 2008) have described the physical oceanographic conditions for this area. Thus, we here only include a condensed description for stations represented in the present study. Above 500 m depth, two main water masses occurred, Modified North Atlantic Water, MNAW ($T > 7°C$, $S > 35$) north of 57°N (Stn 4), while the rest of the stations belonged to a water mass called Sub-Arctic Intermediate Water, SAIW ($T < 9°C$, $S > 35$) (Fig. 1). The water was stratified at all stations mainly because of a thermocline (~60 m depth). Low-saline Labrador Sea Water (LSW) was observed at ~1500 m depth (Søiland *et al.*, 2008).

The phytoplankton biomass was generally low being mostly confined to the surface layer (40–50 m) above the thermocline (Fig. 2). In the surface layers (0–50 m), concentrations of chlorophyll *a* increased from ~0.4 μg L^{-1} at station 4 to ~0.6–0.9 μg L^{-1} at stations 8, 10, 12 and 20 (Table II). The highest concentrations were observed in the frontal area, at station 18 (~1.7 μg L^{-1}).

Concentrations of the essential nutrients (nitrate, phosphate and silicate) were lower in the surface mixed layer (0–50 m) than deeper (Fig. 2). In general, the concentrations of nutrients were similar at the RR stations 4, 8, 10 and 12, with average values of ~9.3–9.9 μmol L^{-1} for nitrate, ~0.7 μmol L^{-1} for phosphate and ~2.3–3.3 μmol L^{-1} for silicate (Table II). In the frontal area, at stations 18 and 20, the concentrations were lower for nitrate (~5.6–7.7 μmol L^{-1}) and phosphate (~0.6 μmol L^{-1}) than in the RR area. Concentrations of silicate were similar at station 18 (~2.7–3.7 μmol L^{-1}) and the RR stations (~2.3–3.3 μmol L^{-1}), and was higher at station 20 in the frontal area (~3.7 μmol L^{-1}).

Stable isotope ratios

Stable nitrogen isotope ratios ($\delta^{15}N$) for *C. finmarchicus* varied from very low value of 3.5‰ (mean value) at station 8 to 4.9‰ at station 18 (Table II). The $\delta^{15}N$ values of *C. finmarchicus* within the RR area did not differ significantly (ANOVA $F_{3,8} = 0.916$, $P = 0.476$) while in the Frontal area, the $\delta^{15}N$ values from station 18 were significantly higher (ANOVA $F_{1,4} = 8.266$, $P = 0.045$) than from station 20 (Table II). The $\delta^{15}N$ values were significantly higher (ANOVA $F_{1,16} = 17.87$, $P < 0001$) in the frontal area than in the RR area.

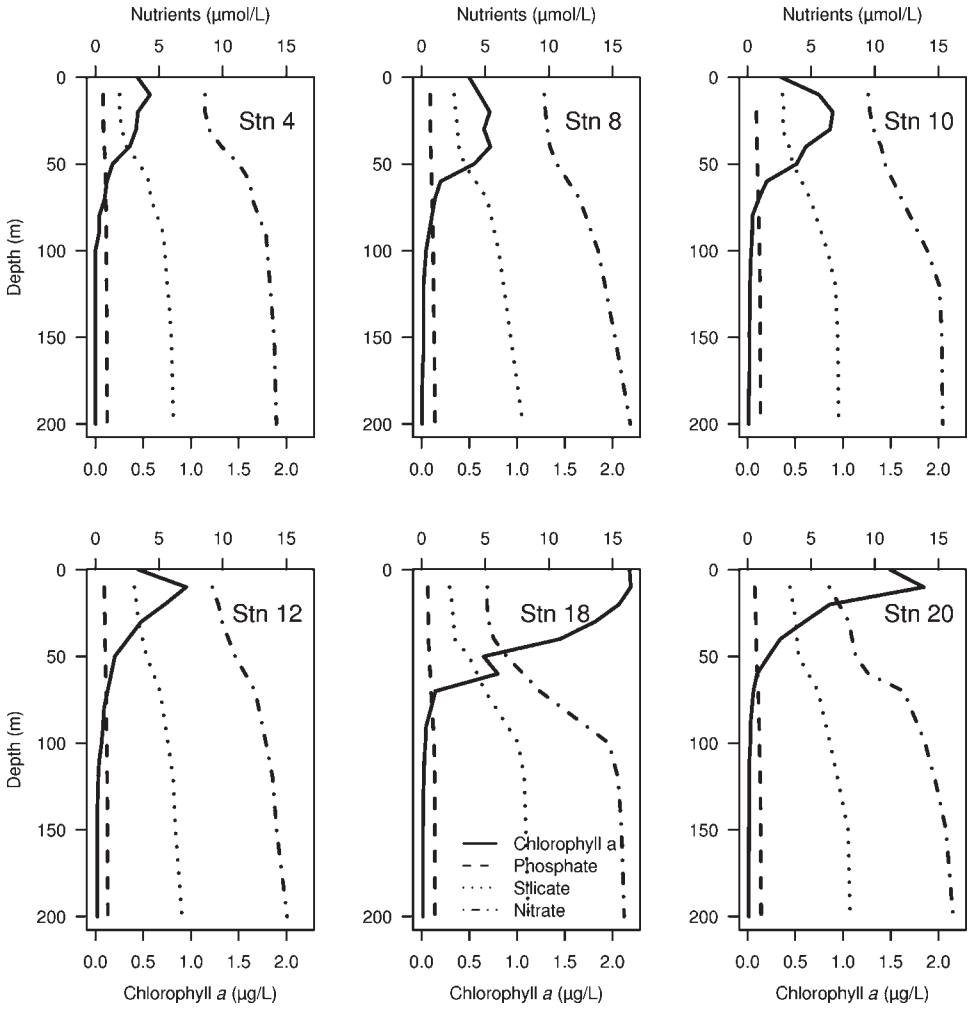

Fig. 2. Vertical profiles for the chlorophyll *a* and nutrients (phosphate, silicate and nitrate) in June 2004 at stations 4, 8, 10, 12, 18 and 20. Samples were taken in June 2004.

Table II: Average chlorophyll a and nutrients (nitrate, phosphate and silicate) in the upper 50 m as well as stable nitrogen and carbon isotopes ratios for C. finmarchicus CV at stations 4, 8, 10, 12, 18 and 20

Area	Station no.	Chl *a* (µg L^{-1})	Nitrate (µmol L^{-1})	Phosphate (µmol L^{-1})	Silicate (µmol L^{-1})	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Reykjanes Ridge						A	A
	4	0.42	9.33	0.66	2.28	-20.2 ± 0.0^{a}	3.6 ± 0.2^{a}
	8	0.64	9.93	0.71	2.80	-21.5 ± 0.3^{b}	3.5 ± 0.2^{a}
	10	0.65	9.95	0.73	3.00	-20.9 ± 0.0^{b}	3.9 ± 0.1^{a}
	12	0.60	9.76	0.72	3.32	-21.2 ± 0.1^{b}	3.6 ± 0.2^{a}
Frontal area						A	B
	18	1.73	5.60	0.56	2.70	-21.0 ± 0.2^{a}	4.9 ± 0.3^{a}
	20	0.89	7.67	0.64	3.73	-19.9 ± 0.2^{b}	4.1 ± 0.1^{b}

Samples were taken in June 2004. The stable isotopes values are mean ± SE. Different lower case letters describe significant difference between stations within each area (Tukey's HSD, $P < 0.05$) and different capital letters indicate significant differences between the two areas (ANOVA, $P < 0.05$).

Stable carbon isotope ratios ($\delta^{13}C$) varied from −21.5‰ at station 8 to −19.9‰ at station 20 (Table II). The ratios differed significantly among stations, both in the RR area (ANOVA $F_{3,8} = 14.63$, $P = 0.001$) and in the frontal area (ANOVA $F_{1,4} = 20.90$, $P = 0.0102$) (Table II). The $\delta^{13}C$ ratios between the RR and the frontal area did not differ significantly (ANOVA $F_{1,4} = 54.54$, $P = 0.010$).

Fatty acid and fatty alcohol compositions

A total of 50 FAs and fatty alcohols were detected, 40 of them with >0.5% in at least one of the samples comprising 98.3–98.7% of the total amount (Table III). The FA compositions in the neutral lipid fractions of all individuals were dominated by a combination of 10 FAs (Table III): 14:0 (comprising 17.8–22.8% of the total FAs), 16:0 (8.1–12.7%), 16:1n7 (4.2–8.1%), 18:1n9 (3.0–6.2%), 22:1n11 (5.9–11.9%), 20:1n9 (3.8–4.9%), 20:5n3 (6–18.9%), 18:4n3 (7–15.9%), 22:6n3 (3.1–4.9%) and 16:4n1 (0.3–4.6%). The sum of dietary-originated FAs was significantly higher (ANOVA $F_{1,16} = 55.85$, $P < 0001$) in the RR area (42.1–44.4%) than in the frontal area at stations 18 and 20 (36.4 and 27.7%, respectively) (Table IV). The fatty alcohol composition was dominated by three fatty alcohols: 22:1n11 (comprising 37.6–53.2% of the total fatty alcohols), 20:1n9 (26.7–33.1%) and 16:0 (9.1–14.2%). The sums of 20:1 and 22:1 alcohols were significantly higher (ANOVA $F_{1,16} = 15.17$, $P = 0.001$) at the stations in the frontal area (82.7–82.9%) than at the stations in the RR area (73.6–82.2%) (Table IV). The sum of relative amount of total fatty alcohols did not differ significantly (ANOVA $F_{1,16} = 2.64$, $P = 0.124$) between the two areas.

To explore relationships between the FA and fatty alcohol compositions of *C. finmarchicus* CV samples from different stations, a multivariate technique (RDA) was used where FA and alcohol relative compositions were used as response variables (Fig. 3). *Calanus finmarchicus*

Table III: Fatty acid and fatty alcohol compositions (mass % of total fatty acid or fatty alcohol, respectively) of neutral lipids of C. finmarchicus CV from stations 4, 8, 10, 12, 18 and 20

Stations	4 ($n = 3$)	8 ($n = 3$)	10 ($n = 3$)	12 ($n = 3$)	18 ($n = 3$)	20 ($n = 3$)
Fatty acids						
14:0	20.1 ± 0.7	18.2 ± 0.1	17.8 ± 0.1	20.9 ± 0.6	18.7 ± 1.1	22.8 ± 1.0
14:1	0.3 ± 0.1	0.6 ± 0.1	0.6 ± 0.0	0.6 ± 0.1	0.6 ± 0.0	1.1 ± 0.1
16:0	8.7 ± 0.2	8.1 ± 0.2	8.3 ± 0.3	9.0 ± 0.1	9.2 ± 0.1	12.7 ± 0.3
16:1n9	0.2 ± 0.0	0.7 ± 0.0	0.6 ± 0.1	0.7 ± 0.1	0.6 ± 0.0	1.0 ± 0.2
16:1n7	6.6 ± 0.5	7.5 ± 0.2	8.1 ± 0.3	4.2 ± 0.2	5.4 ± 0.2	5.9 ± 0.4
16:1n5	0.7 ± 0.1	1.2 ± 0.1	1.2 ± 0.1	1.0 ± 0.1	1.3 ± 0.1	0.9 ± 0.0
16:3n4	0.7 ± 0.1	1.0 ± 0.1	1.1 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.4 ± 0.0
16:4n1	3.6 ± 0.5	3.6 ± 0.1	4.6 ± 0.3	1.4 ± 0.1	2.2 ± 0.2	0.3 ± 0.0
18:0	0.7 ± 0.3	1.4 ± 0.0	1.4 ± 0.1	1.1 ± 0.1	1.2 ± 0.0	1.2 ± 0.0
18:1n9	3.9 ± 0.1	3.3 ± 0.1	3.0 ± 0.1	3.6 ± 0.1	3.8 ± 0.1	6.2 ± 0.3
18:2n6	1.0 ± 0.1	1.1 ± 0.0	0.9 ± 0.0	1.4 ± 0.0	1.0 ± 0.0	1.9 ± 0.1
18:3n3	1.2 ± 0.1	0.9 ± 0.0	0.5 ± 0.2	1.6 ± 0.0	0.8 ± 0.0	1.6 ± 0.0
18:4n3	11.7 ± 1.3	10.4 ± 0.1	7.0 ± 0.8	15.9 ± 0.4	8.1 ± 0.2	7.0 ± 0.7
18:5n3	1.2 ± 0.4	0.2 ± 0.0	0.3 ± 0.0	0.7 ± 0.1	0.3 ± 0.0	1.2 ± 0.4
20:1n11	1.0 ± 0.1	1.1 ± 0.0	1.3 ± 0.0	0.9 ± 0.0	1.2 ± 0.1	1.1 ± 0.1
20:1n9	3.8 ± 0.3	4.6 ± 0.2	4.3 ± 0.2	4.0 ± 0.1	4.9 ± 0.2	4.7 ± 0.4
20:1n7	1.3 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
20:4n6	0.9 ± 0.1	0.8 ± 0.0	0.9 ± 0.1	0.8 ± 0.0	0.6 ± 0.0	0.6 ± 0.0
20:4n3	1.4 ± 0.0	1.2 ± 0.1	0.9 ± 0.0	1.6 ± 0.1	1.3 ± 0.2	1.2 ± 0.1
20:5n3	12.8 ± 1.0	16.3 ± 0.3	18.9 ± 0.6	11.7 ± 0.3	13.7 ± 1.0	6.0 ± 0.2
22:0	0.7 ± 0.1	0.6 ± 0.0	0.5 ± 0.0	0.6 ± 0.1	0.5 ± 0.0	0.5 ± 0.1
22:1n11	7.0 ± 0.2	7.2 ± 0.2	7.1 ± 0.4	5.9 ± 1.0	11.9 ± 0.1	9.5 ± 1.0
22:1n9	0.6 ± 0.1	1.3 ± 0.4	1.7 ± 0.0	1.9 ± 0.1	2.4 ± 0.1	1.8 ± 0.1
22:5n3	0.7 ± 0.0	0.7 ± 0.0	0.7 ± 0.1	0.5 ± 0.0	0.6 ± 0.0	0.4 ± 0.0
22:6n3	3.3 ± 0.3	3.3 ± 0.0	3.1 ± 0.1	4.9 ± 0.8	4.4 ± 0.2	3.4 ± 0.1
Minor components	6.0 ± 0.2	4.9 ± 0.1	5.1 ± 0.3	4.6 ± 0.2	4.5 ± 0.1	6.6 ± 0.1
Sum of dietary FAs	42.1 ± 0.8	44.3 ± 0.9	44.4 ± 1.0	42.2 ± 0.9	36.4 ± 0.8	27.7 ± 0.5
Sum of 20:1 and 22:1	13.7 ± 0.6	14.2 ± 0.7	14.5 ± 0.7	12.7 ± 0.8	20.5 ± 1.1	17.1 ± 0.8
Fatty alcohol						
14:0	0.4 ± 0.1	3.4 ± 0.1	3.6 ± 0.4	2.0 ± 0.1	2.0 ± 0.1	1.6 ± 0.1
16:0	14.2 ± 0.3	12.8 ± 0.2	12.5 ± 0.2	10.0 ± 0.2	9.7 ± 0.3	9.1 ± 0.6
16:1n7	7.9 ± 1.4	5.7 ± 0.1	6.2 ± 0.5	2.5 ± 0.2	2.6 ± 0.1	2.3 ± 0.3
18:1n9	3.9 ± 0.1	3.1 ± 0.1	3.7 ± 0.8	3.3 ± 0.1	2.8 ± 0.0	4.2 ± 0.4
20:1n9	31.1 ± 1.5	32.2 ± 0.5	31.2 ± 0.9	33.1 ± 0.6	26.7 ± 0.8	27.0 ± 2.4
22:1n11	37.6 ± 1.5	39.5 ± 0.4	39.8 ± 1.4	46.0 ± 0.6	53.2 ± 0.9	52.1 ± 1.5
22:1n9	4.9 ± 0.1	3.2 ± 0.1	3.1 ± 0.2	3.2 ± 0.2	3.1 ± 0.1	3.6 ± 0.0
Sum of 20:1 and 22:1	73.6 ± 5.0	75.0 ± 5.5	74.1 ± 5.6	82.2 ± 6.3	82.9 ± 7.2	82.7 ± 7.0
Ratio 20:1/22:1	0.7	0.8	0.7	0.7	0.5	0.5
% of FAlcA of total moites	37.3 ± 0.6	42.3 ± 0.2	40.9 ± 0.2	40.7 ± 0.9	42.3 ± 0.6	41.3 ± 0.8

Samples were taken in June 2004. Each sample composed of ~10 individuals. Values are mean ± SE.

Table IV: Selected fatty acids and alcohol (derived from Fig. 3), sum of dietary fatty acids, sum of 20:1 and 22:1 fatty acids and alcohols as well as sum of % of total fatty alcohols and the alcohol ratio of C. finmarchicus were individually tested (ANOVA, $P < 0.05$) between the two area i.e. Reykjanes Ridge and the Frontal area

	$F_{1,16}$	*P*-value
Fatty acids		
16:1n7	2.77	0.115
16:3n4	16.67	<0.001
16:4n1	11.53	0.004
20:1n9	9.68	0.007
20:5n3	9.74	0.006
22:1n11	32.03	<0.001
22:1n9	7.64	0.014
Sum of dietary FA	55.85	<0.001
Sum of 20:1 and 22:1	83.79	<0.001
Fatty alcohols		
22:1n11	44.64	<0.001
Sum of 20:1 and 22:1	15.17	0.001
Ratio 20:1n9/22:1n11	72.73	<0.001
% of FAlcA	2.64	0.124

from different stations were significantly different in FA and fatty alcohol compositions (Monte Carlo $F = 16.5$, $P = 0.002$) and 87.8% of the total variability in their compositions was explained by different stations from which they were caught.

The main gradient along axis 1 which explains 50.3% of the total variance in the data set, divided the *C. finmarchicus* from the different stations into two groups based on similarities (Fig. 3), where animals from RR stations in the north (Stns 4, 8 and 10) made one group and the stations in the frontal area (Stns 18 and 20) made another, while the values at station 12 (closest to the frontal region of the RR stations) were intermediate (Fig. 3). The phytoplankton-originated FAs (for example, 20:5n3, 16:3n4, 16:4n1, 16:1n7) and the FAs and alcohols biosynthesized *de novo* by *C. finmarchicus* (the FAs: 22:1n11, 22:1n9, 20:1n9 and the alcohol: 22:1n11) were important distinguishing factors between these groups. *Calanus finmarchicus* from the RR stations had relatively high amounts of the phytoplankton-originated FAs and low amounts of the *Calanus* originated FAs and alcohols compared with the stations in the frontal area where the reverse was true. These FAs and alcohols were tested further statistically for differences between the RR and the frontal area (Table IV). The relative amounts of all of them (except 16:1n7) were significantly different between the two areas (ANOVA, $P < 0.05$). Axis 2 in the RDA explained 20.4% of the variance in the data set.

DISCUSSION

The present study defined two main groups of stations based on FA and alcohol compositions and stable nitrogen isotope values of *C. finmarchicus* CV, i.e. this grouping explaining 50% of the total variance in the data set: the stations in the RR area (Stns 4, 8 and 10) constituted one group, station 12, was a single intermediate, whereas the stations in the frontal area (Stns 18 and 20) made up another group. The most important FAs and alcohols in distinguishing the grouping were significantly different between the two areas. Further, the stable nitrogen isotope values were also significantly different between the two areas.

The explanations for these findings may partly be related to the current pattern southwest of Iceland (Fig. 1). There is a south-westward current along the eastern flank of the RR (Pollard *et al.*, 2004; Knutsen *et al.*, 2005) which is weak at the surface and stronger deeper down. The major source of the deeper one is in the Norwegian Sea. Therefore, there could be significant advection of *C. finmarchicus* at depth, south-westward along the RR which may explain the grouping of the stations in the RR area. Conversely, the water masses (both in the upper waters and at depth) at the stations in the frontal area originate in the west, thus suggesting that the population in the frontal region may originate from a different area than the RR one. Furthermore, the temperature and salinity properties at the core of the LSW, which originate in the Labrador Sea and are found at about 1500 m depth in the study area, indicate the same grouping of stations (H. Søiland, Institute of Marine Research, personal communication; Søiland *et al.*, 2008). These deep flows may therefore be important in explaining the distribution of *C. finmarchicus* as they stay in a state of dormancy at great depths during a major part of the year (Gislason and Astthorsson, 2000; Heath *et al.*, 2004).

In the frontal area, there is probably a prevailing bloom situation, likely of dinoflagellates or/and *Phaeocystis* as indicated by the relatively higher amounts of FAs characteristic of these phytoplankton groups (C18, C22 PUFAS). Further supporting this is the proportion of used nitrogen and silicate (~1.7:1, respectively) indicating that other phytoplankton groups than diatom have been growing as well, because nitrogen and silicate are equally used (1:1) by spring diatoms (Henson *et al.*, 2006a; Olafsdottir, 2006) There is always a certain fraction of regenerated nitrogen (ammonium) used in primary production making the real fraction of non-diatoms probably even higher than the 1.7:1 proportion indicates. On the other hand, in the north, a subsurface maximum (~20–50 m) was observed. This

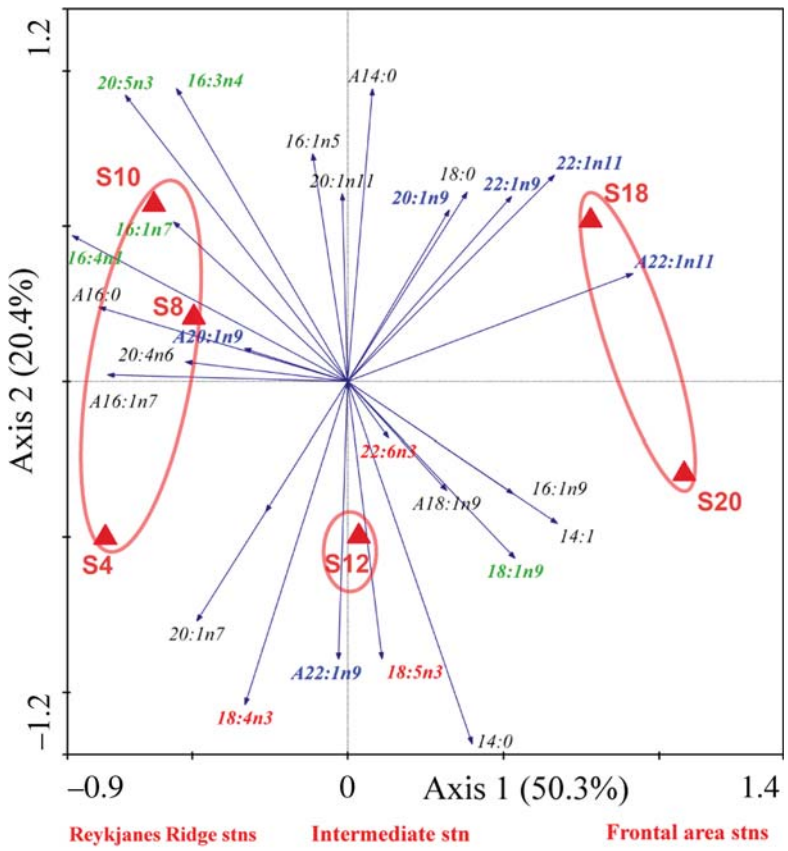

Fig. 3. Redundancy analysis (RDA) plot based on fatty acid and fatty alcohols values of *C. finmarchcius* CV from stations 4, 8, 10, 12, 18 and 20. Triangles indicate mean values of the respective station. The *C. finmarchcius* from each station were applied as dummy variable (environmental variable) and its fatty acids as response variables. The fraction of unconstrained variance accounted for by each axis is given in bracket. Samples were taken in June 2004. Red, dinoflagellate trophic marker; green, diatom trophic marker; blue, *Calanus* trophic marker synthesised *de novo*. The circles around the stations indicate the grouping of stations.

is probably the end or post diatom bloom as deduced by the higher amounts of diatom FAs in the *C. finmarchicus* in the RR area. The spring bloom in the offshore waters south of Iceland generally starts in late April, then culminates in mid-May and finally declines in June (Gudmundsson, 1998; Henson *et al.*, 2006b). It may take 2 weeks for *C. finmarchicus* to exchange 22% of their lipids (Graeve *et al.*, 2005), thus indicating recent diatom feeding in the northern area.

Significantly lower relative amounts of dietary FAs were observed in *C. finmarchicus* in the frontal area than in the RR area, conversely the sums of the relative values of the C20:1 and C22:1 FAs were significantly higher in the frontal area compared with the RR area. The higher relative amounts of the high energy, long-chain FAs C20:1 and C22:1 and lower relative amounts of dietary FAs have been explained by the preferred utilization of dietary acids under unfavourable conditions, i.e. dormancy (Falk-Petersen *et al.*, 1987; Kattner and Krause, 1989). This may indicate that the population in the frontal area surfaced later than the population in the RR area and therefore the seasonal development was less advanced in the frontal area, which is opposite to what one would expect based on the latitudinal progress of spring and summer. The population structure of *C. finmarchicus* in the area may also provide some evidence for this interpretation, as the populations were in a more advanced stage of development in the RR area with most of the animals being at stages CIV and CV, i.e. probably from the G1 generation, than in the south where the population in the upper 50 m were dominated by females and no young stages were found indicating the animals belonged mainly to the G0 generation (unpublished data; Gislason *et al.*, 2008).

The sum of relative amounts of fatty alcohols in *C. finmarchicus* did not differ significantly between the two areas, indicating similar relative amounts of wax esters in *C. finmarchicus* within the study area. *Calanus finmarchicus* accumulates wax esters when food is particularly abundant, preparing for diapause (Lee *et al.*, 2006).

If it is assumed that *C. finmarchicus* in the frontal area surfaced later than *C. finmarchicus* in the RR area, one would expect *C. finmarchicus* in the frontal area to have lower relative amounts of wax esters i.e. if belonging to the same generation. However, the previously mentioned suggestion of G0 generation in the frontal area and G1 generation in the RR area could explain these similar relative amounts of wax esters. Also, the alcohol ratios C20:1 relative to C22:1 were significantly lower in the frontal area (~0.5) compared to the RR area (~0.7–0.8). Higher relative amounts of the C22:1 alcohols have been observed in winter animals (Sargent and Falk-Petersen, 1988; Kattner and Krause, 1989), supporting the theory of later ascent in the frontal area. Further favouring this is a long-time annual study of *C. finmarchicus* in the North Atlantic, where it is evident that the study area is close to a boundary where the mean annual abundance of *C. finmarchicus* was reached either in mid-season (east side of the study area) or in late season (west side of the study area, reaching to the Labrador Sea) (Planque and Batten, 2000). Hence, the probability of inter annual variability could support the hypothesis of a more advanced population in the RR area than the frontal area this year.

In this context, it may further be noted that the stable nitrogen isotope values ($\delta^{15}N$) were significantly higher in the frontal area than the RR area, which might indicate higher trophic position of the frontal area populations with feeding on the heterotrophic microbial food web. However, the pelagic-POM baseline is also somewhat variable depending on the seasonal progression of the phytoplankton community with respective uptake of nitrogen forms by different taxa (Søreide *et al.*, 2006a). Compared to the G0 overwintered generation, the G1 generation of *C. finmarchicus* has been found to be depleted in $\delta^{15}N$, due to their feeding on new primary production (Saage *et al.*, 2008). However, no trend was observed in $\delta^{13}C$ values, indicating that phytoplankton was the main carbon source in the whole study area.

In general, the stable nitrogen isotope values were low in the study area (~52–60°N) compared with other areas (Fry, 1988; Vizzini and Mazzola, 2003; Mincks *et al.*, 2008; Søreide *et al.*, 2008; Laakmann *et al.*, 2009). Low values in the area were also observed in the study by Petursdottir *et al.* (Petursdottir *et al.*, 2008) and Mahaffey et al. (Mahaffey *et al.*, 2003) (area further south). Reasons for the oceanic low ^{15}N signals may be nitrogen fixation by N_2-fixing organisms (e.g. the cyanobacterium *Trichodesmium*) or phytoplankton growth based on regenerated nitrogen (Altabet, 1988; Rees *et al.*, 2006). Studies performed near the Azores (48°N) argue for nitrogen fixation there (Mahaffey *et al.*, 2003; Álvares and Álvares-Salgado, 2007). Clearly, more interdisciplinary studies on nitrogen and N_2 fixation are needed for interpretation of the low values presented here for oceanic zooplankton.

Taken together, the relatively great differences in FA and fatty alcohol compositions of *C. finmarchicus* between the RR and frontal areas shown in the present study suggest a different developmental pattern and/or populations of *C. finmarchicus* in the two regions. The explanation for these findings could be related to the current patterns in the area, especially deep water currents that may be important for the advection of animals to the region from different source areas.

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