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Under-ice plankton abundance and lipid dynamics in a subarctic lake.

A study of the winter ecology of the lower trophic levels in Takvatn.

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Master's thesis in Freshwater ecology
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Abstract

Shortening winters and changing ice and snow cover conditions are examples of the many shifts expected in subarctic lakes due to climate change. Well-documented changes in ice and snow cover conditions highlight the need to understand under-ice ecosystems and the consequences a changing climate brings to the freshwater biota. This study investigated the impact of under-ice environmental conditions and seasonal progression on the plankton community and lipid dynamics in Takvatn, a well-studied subarctic oligotrophic lake in Northern Norway. In particular, this study focused on two actively overwintering copepods, *Cyclops scutifer,* and *Eudiaptomus graciloides*. The two species differed in their life strategies and fatty acid composition; *C. scutifer* overwintered in the C-IV to C-V stage, while *E. graciloides* reproduced under ice-cover. A rapid decrease in lipid content throughout the ice-covered period was observed for both *E. graciloides* (from 60% to 38% DW^{-1}) and *C. scutifer* (from 73% to 33% DW^{-1}). The results indicate the importance of lipid accumulation before ice-cover for the actively overwintering copepods to survive the ice-cover period. In addition, under-ice primary production, which was apparent during the last months of ice-cover, provided a food source for *E. graciloides.* Compared to the previous winter, this winter zooplankton had a higher proportion of lipids to body mass. This suggests the current winter to have favourable conditions and might allow zooplankton to survive harsher/longer periods of ice-cover. Further, *E. graciloides* had large amounts of poly unsaturated fatty acids (in particular Stearidonic acid, 18:4n-3) which decreased rapidly and might be linked to under-ice reproduction in this species. Future changes in ice-cover duration and snow and ice conditions due to climate change effects may play a significant role in the quantity and quality of lipids of an organism. This study contributes to the understanding of plankton and lipid dynamics during the understudied winter period under ice-cover and provides a reference point for future under-ice studies.

1 Introduction

Winter, here defined as the ice-covered period of the year, is an essential but traditionally overlooked season in lake research. The winter season has been assumed to be a period of low biological activity. This, combined with the practical difficulties in doing studies under the ice (Block et al., 2019), has resulted in ecological research mainly focused on the productive summer period. This is surprising considering that half of the world's lakes freeze periodically (Hampton et al., 2017), accounting for more than 50 million lakes (Verpoorter et al., 2014). Yet, in recent decades there has been an increased focus on winter processes in lakes, especially related to impacts of climate change (Benson et al., 2012; Leppäranta, 2015; John J. Magnuson et al., 2000), which is expected to force significant changes in lake ecology (Hobbie et al., 1999).

Lake water temperatures have been rising, especially for lakes in Northern Europe (O'Reilly et al., 2015; P. Schneider & Hook, 2010); in addition, ice-covered lakes are on average warming faster compared to ambient air temperatures (O'Reilly et al., 2015). For lakes, ice-cover is a stable period with reduced mixing of the water column and limited light availability (Leppäranta, 2015). Ice-cover duration has been in decline (J. J. Magnuson et al., 2000). In Müggelsee in northern Germany, the percentage of ice-free winters could increase from 2% to 60% by the end of this century (Livingstonea & Adrianb, 2009). Physical characteristics and ice and snow cover timing are important for several essential biological processes in lakes (Benson et al., 2012; M. V. Moore et al., 2009; Ozersky et al., 2021; Salonen et al., 2009). For example, there is evidence that winter conditions influence the consecutive summer processes (Dokulil et al., 2014; O'Reilly et al., 2015), emphasizing the significance of the winter. For lakes in the high Arctic, changes can be extreme due to Arctic amplification (i.e., faster warming in the arctic)(Serreze & Barry, 2011). The increase in temperature may lead to a regime shift or cascade (e.g., change from perennially ice-covered to annually ice -covered) driven by climate change (Mueller et al., 2009). In addition to ice-on and ice-off timing, the ice and snow conditions play a crucial role in under-ice processes. Rain on snow events are expected to become more common due to climate change (Cohen et al., 2015). This could cause an increase in light transmittance of snow-covered lakes since slush snow transmits

more light than snow cover does (Leppäranta, 2015). There still is a lack of information on high latitude lakes where the ice-cover period is exceptionally long (up to 9 months). The high arctic has low light conditions at the start (polar night) and high at the end of ice-cover (midnight sun) (Berge et al., 2015). The relation between ice quality, primary production and resource availability is currently lacking but vital to understand seasonally ice-covered lakes (Jansen et al., 2021).

1.1 Life under the ice

Life under the ice must adapt to the low light conditions (Bolsenga et al., 1991), low temperatures (Raven & Geider, 1988), lack of mixing, and the absence of oxygen exchange at the surface (Kirillin et al., 2012). A study of annually ice-covered lakes across the world shows that phytoplankton is generally less abundant than during summer (43% chlorophyll a, 15% of phytoplankton biovolume) and zooplankton is at about 25% density relative to summer values (Hampton et al., 2017). In addition to plankton densities, the nutritional content (e.g., lipid composition) differ between summer and winter. Lipid analysis can give insight into an organism's condition and what it has been feeding on (Budge et al., 2006; Dalsgaard et al., 2003; Iverson et al., 2004). Currently, there is a general lack of lipid data in winter compared to summer (Fernandes & McMeans, 2019). Relatively few studies have followed lipid content of phytoplankton and zooplankton during winter (Perga et al., 2021). Although there are a few studies that track lipid contents of primary producers and secondary consumers (zooplankton) during winter (Grosbois et al., 2017; Syväranta & Rautio, 2010).

To cope with the harsher winter conditions, zooplankton can go into a dormant egg stage (Gyllström & Hansson, 2004) or have reduced activity during winter while using previously acquired lipids plus the limited food sources available (i.e., heterotrophs, bacteria, phototrophs) (Grosbois et al., 2017). Many species (especially copepods) accumulate large lipid reserves during the growing season to cope with the less productive periods (Kuosa & Gyllenberg, 1989; Lee et al., 2006). However, copepods and cladocerans have also been observed to grow and reproduce under the ice (Rautio et al., 2011; Rigler et al., 1974). Copepods are often the dominant zooplankton species during ice-cover (Perga et al., 2021), as

cladocerans such as daphnids are frequently observed to go into a dormant resting stage during ice-cover while having no overwintering adults (Carvalho & Wolf, 1989).

Actively overwintering copepods have different life strategies. Calanoid copepods can reproduce under ice-cover (Pasternak, 1999), whereas cyclopoid copepods have been observed to stay active in the C-IV stage (Elgmork & Eie, 1989) and reproduce in July (Primicerio & Klemetsen, 1999). In addition to the differences in timing of reproduction, they also differ in feeding modes, which determine what food sources are available to the organism. The cyclopoid *Cyclops scutifer* is omnivorous but is mainly herbivorous (in the earlier life stages) and has even been successfully bred solely on an algal diet (Pejler, 1983). Many adult cyclopoids select small animal prey such as rotifers and nauplii (Langeland & Reinertsen, 1982). In contrast, filter feeders (e.g., the calanoid copepod *Eudiaptomus graciloides*), which are herbivorous, cannot as readily make use of additional resources such as rotifers, nauplii, etc., which might be more readily available in winter.

1.2 Lipid dynamics

The diet of herbivorous zooplankton consists mainly of phytoplankton in summer. However, in ice-covered lakes with limited light availability, phytoplankton is only available in very low quantities, and previously acquired lipids thus play a vital role in the survival of zooplankton (Grosbois et al., 2017; Perga et al., 2021). In subarctic lakes, zooplankton (notably calanoid and cyclopoid copepods) lipid content has been observed to differ from 20%-60% among seasons, with the highest levels seen in early winter (Syväranta & Rautio, 2010). Copepods can consist of up to 76% lipids of their body mass at the start of ice-cover (Grosbois et al., 2017).

Multiple factors influence zooplankton lipid composition and abundance, mainly food availability and food quality and, to a lesser extent, environmental conditions. The nutritional quality of the food source, particularly the lipid composition is important for the consumer. In particular, the contribution of polyunsaturated fatty acids (PUFA) to the lipid pool is of significance as a high-quality food source for higher trophic levels. Photosynthetic organisms can produce lipids *de novo*, using solar radiation as energy and nutrients to produce carbohydrates. Through consequent biochemical pathways (e.g., desaturation and elongation),

essential fatty acids are produced, which are vital to higher trophic levels (Harwood & Guschina, 2009). However, not all phytoplankton produce the same "quality" fatty acids (FA) (Taipale et al., 2013). The trophic state of a lake influences FA composition, where eutrophic lakes tend to have lower concentrations of highly unsaturated fatty acids (HUFA) compared to oligo-mesotrophic or dystrophic lakes due to differences in community composition (Taipale, et al., 2016). Thus, community assemblage and trophic state are of importance to the lipid composition and quality of higher trophic levels. The availability of PUFA influences the growth rate of zooplankton (Gulati & Demott, 1997), while temperature influences metabolic activity. In addition to environmental factors, biological factors such as the life strategy, for instance, feeding methods and reproduction of zooplankton can affect lipid composition. The role of these biological factors under ice-cover is currently unknown.

1.3 Aim & hypotheses

There is a need for information on plankton dynamics under ice-cover to understand and predict future responses to changing ice- and snow-cover in high latitude lakes (Salonen et al., 2009). For example, what energy source allows zooplankton to survive a long ice-cover period? This is likely highly dependent on environmental conditions such as light availability and available nutrients for primary production and dissolved organic carbon for heterotrophs/ mixotrophs. The aim of this study was to follow the environmental conditions and seasonal differences in plankton community and lipid composition during ice-cover in a subarctic lake. I hypothesized that:

1) A decrease in lipid content of zooplankton during ice-cover with high lipid content at the start compared to the end of ice-cover, with a more rapid reduction of lipids in reproducing zooplankton.

2) A difference in lipid profiles of two actively overwintering zooplankton species due to contrasting life strategies and seasonal changes.

2 Methods

2.1 Sampling site/time

All samples were taken from the subarctic lake Takvatn (Lat: 69.09201, Lon: 19.13962) on an approximately monthly basis during the ice-covered winter period of 2020-2021, including additional sampling prior to and after the ice-covering. Takvatn is an oligotrophic, dimictic lake located 214m a.s.l. in northern Norway with a surface area of 15 km^2 and a maximum depth of 80m. The sampling station used for the present study has a depth of 60m and is located in the southeast part of Takvatn (Figure A1.). The lake typically freezes in November, and ice-off often occurs in early June (Primicerio, 2000). In 2020, ice-on occurred in the first week of December and ice-off in the first week of June 2021. The polar night at Takvatn (i.e., the period when the sun is consistently below the horizon) lasts from November 21st until January 21st.

2.2 Physical and chemical conditions

Snow depth, ice thickness, Secchi depth, and light intensity (starting in February) were measured monthly. Vertical profiles were carried out from 0–60 m using a CTD (SAIV SD-204), providing data on conductivity, temperature, depth, oxygen, and *in situ* chlorophyll fluorescence. Light measurements were performed using LICOR in the field, with a combined above and below ice sensor recording at noon. Discrete water samples were taken just below the ice (0m) and at 58m depth using a Ruttner water sampler. An integrated water sample was taken from 0-10m below the water surface (during open water periods) or bottom of the ice. The integrated water samples were pooled, transferred to black 5L jugs, and kept dark and cool until further processing. Separate samples were taken from just below the ice using a pump and hose to obtain water from the uppermost layer (against the bottom of the ice).

The integrated water samples (0-10m, surface, and bottom water) were filtered through glass fiber filters (Whatman GF/F; nominal pore size 0.7 µm) for analysis of particulate phosphorous and chlorophyll a (chl-a). Particulate organic matter (POM) for FA analysis was filtered through pre-combusted GF/F filters (combusted at 450ºC for 4 h). The volume of the filtered

water ranged from 2–5 L, dependent on the colour of the filters after filtration: i.e., when little colour was visible on the filter (indicating low biomass) more water was filtered to obtain enough biomass for the analysis. All filters were frozen at -20°C except for the samples for FA analysis which were stored at -80°C.

From integrated (0–10 m) and bottom (58m) water samples, a 300ml subsample was taken for the analysis of SiO_2, NO_2/NO_3, PO_4, and NH_4. The sample was filtered through a syringe filter (Whatman 0.7 µm GF/F filter), and collected into acid-washed plastic bottles that were pre-rinsed and then filled with the filtrate and subsequently acidified with 1ml 4N H_2SO_4. Nutrient analyses were performed by the Norwegian Institute for Water Research (NIVA, Oslo, Norway) using standard accredited methods (as described in Kaste et al., 2019). Chl-a concentrations were determined at Akvaplan-NIVA (Tromsø, Norway) through fluorometry (Parsons et al., 1984). Briefly, filters were extracted with acetone (10 ml, 90% acetone) in the dark at -20°C for 12 hours, 3-4ml extract was added to a fluorometer cuvette and measured using a Turner 10-AU-000 fluorometer. Phytoplankton samples for identification were preserved using 1% v/v Lugol's iodine. 50 ml per sample was transferred to an Utermöhl settling chamber and left for 24 hours; the sample was counted using an inverted microscope. A minimum of 200 cells were identified to class level per sample.

2.3 Plankton sampling and analyses

Zooplankton hauls were taken with a 90 µm net from 60-0 and 20-0 m, and phytoplankton hauls with a 20 µm net from 20-0m. All samples were placed in a dark cooler at the site. Zooplankton biomass was measured by filtering a fraction (split using a plankton splitter) of the net haul through a pre-weighed QMA (Whatman quartz fiber filter) and frozen at -20°C until dried at 60°C overnight. Three hauls from 60-0m using a 90µm net were pooled and stored dark at 5°C and sorted to species level the day after; only *C. scutifer* and *E. graciloides* were separated using a stereo microscope at 40x magnification. Living zooplankton were placed in small droplets on a glass petri-dish at room temperature using a glass pipet and subsequently transferred to cryovials (placed on ice), each consisting of about 200 individuals per species; all stages except nauplii were included. Three subsamples were taken for each species and stored at -80°C until FA analysis. POM dry weight was not obtained due to the

very low biomass on the GF/F filters, weighed filters would have large uncertainty, instead µg FA per liter was used. Samples for FA analysis were freeze-dried before transport to Wassercluster Lunz, Austria, for analysis. Samples were stored dark during transport. Zooplankton samples were split into subsamples comprising a known fraction of the total sample, ensuring sufficient biomass for FA analysis. Zooplankton for identification was preserved with 10% formalin to volume on the day of capture and stored at room temperature. After rinsing out the formalin with water, the zooplankton species were identified and counted on stage (Nauplii, C-I to C-III, C-IV to C-V, adult male, adult female, and egg-bearing) under a stereomicroscope.

2.4 Fatty acid extraction

Freeze-dried zooplankton was weighed in a tin cup and added to glass centrifuge tubes. Chloroform (2 ml, or until fully covered) was added to freeze-dried zooplankton and filters (GF/F) containing POM closed under N_2 flow, and left overnight at -80°C to break all membranes.

Samples were stored on ice between all subsequent steps, and vials were always closed under N_2 flow to prevent the oxidation of lipids. Cooled methanol (1ml), cooled chloroform:methanol (1ml) solution (2:1) and cooled NaCl water solution (0.8ml , 0.9%) were added. Samples were sonicated for (10 min) in ice water, vortexed (1 min), and centrifuged (5 min, 3000rpm at 4°C). The lower layer was extracted using the double Pasteur pipette technique, pipettes were rinsed with chloroform (2 ml) in the centrifuge vial. Sonication and subsequent steps were repeated twice more to ensure a high recovery rate. Evaporation of the organic layer followed and was concentrated in chloroform (1.5 ml) and stored at -20°C. 100 µl was added to each of two tin cups and evaporated to dryness, whereafter weighed to obtain lipid weight.

The remaining total lipid extract was transferred to a glass centrifuge tube, evaporated to dryness, and toluene (1 ml) and H_2SO_4-methanol solution (2 ml, 1%) were added. Afterward, samples were immediately placed in a water bath at 50°C for 16 hours. $KHCO_3$ (2 ml, 2%) and Hexane (5 ml) were added to the tubes, vortexed briefly, and centrifuged (3 min, 1500rpm at 4°C). The upper layer was transferred, hexane (5 ml) was added, and subsequent

steps were repeated. Samples were evaporated to dryness where after extruded from the glass centrifuge vial to a GC-vial and stored at -80°C. FA analysis was performed using a gas chromatograph (TRACE GC THERMO) outfitted with a temperature programmable injector and autosampler; the same temperature profile was applied as stated in Heissenberger et al., (2010).

2.5 Data analysis

Data visualisation was carried out in R version R-4.0.3. All lipid-related data from samples obtained on 27-10-2020 have been removed from further analyses. These were the first samples sorted for FA analysis and took considerably longer to process, which caused samples to warm up. Therefore, the accuracy of these samples cannot be guaranteed since the lipids might have oxidized during sorting.

2.5.1 CTD visualization

Outliers in the CTD data due to sampling error were removed, in March, the CTD sampler hit the sediment and caused an increase in fluorescence and a decrease in oxygen saturation. Only the downcast was selected, and data points were removed when the temperature still reflected the above ice temperature at 0 meters. The interpolation method used for plotting the CTD data is multilevel B-splines (S. Lee et al., 1997), using the MBA package in R (Finley et al., 2017).

2.5.2 Fatty acid data treatment

Changes in lipids over time were assessed using local polynomial regression fitting to indicate the trend of total lipid difference over time with the confidence interval around the line and were made using the GGplot2 package in R (Wickham, 2016). FA were grouped based on saturation and bacterial biomarkers and terrestrial biomarkers, individual FA per group are shown in Table 1. Total lipids and total methylated fatty acids were measured. In this study the focus lies on total FAME, since this includes the sum of all the FA methyl esters, and only covers the FA-containing and saponifiable lipids. In addition, FAME usually accounts for >80% of total lipids and the data appeared less variable and more consistent for both species.

Table 1. Fatty acids groups and biomarkers with the individual fatty acids they contain. Bacterial FA biomarkers were selected based on Kainz et al., (2003). *Terrestrial FA biomarkers were selected based on* Grosbois et al., (2017).

Grouped	**Individual fatty acids**
Saturated fatty acids (SAFA)	C16:0, C17:0, C18:0, C20:0, C22:0, C23:0, C24:0
Monounsaturated fatty acids (MUFA)	C14:1n-5, C15:1n-5, C16:1n-9, C16:1n-7, C17:1n-7, C18:1n-9trans, C18:1n-12, C18:1n-9cis, C18:1n-7, C18:1n-6, C20:1n-9, C22:1n-9, C24:1n-9
Polyunsaturated fatty acids (PUFA)	C18:2n-6trans, C18:2n-6cis (LIN), C18:3n-6, C18:3n-3 (ALA), C18:4n-3, C20:2n-6, C20:3n-6, C20:3n-3, C20:4n-6, C20:4n-3, C22:2n-6, C20:5n-3, C22:3n-3, C22:4n-6, C22:5n-3, C22:6n-3
Bacterial fatty acid biomarkers (BactFA)	iso-15:0, anteiso-15:0, C15:0, iso-16:0, iso-17:0, C17:0, 9,10D16, C18:1n-7, C18:1n-6, 9,10D18
Terrestrial fatty acid biomarkers (TerFA)	C20:0, C22:0, C23:0, C24:0

To visualize seasonal and between species differences, a correspondence analysis was performed on FA compositional data using the EasyCoda (Greenacre, 2018) package in R. The following FA were removed from the analysis: 9,10D16, C20:1n-9, and C19:0 (internal standard); this was done since these columns contained many 0 values and no internal standard was added to the samples. To model the FA as a function of species and sampling date, a canonical correspondence analysis (CCA) was applied using the 'vegan' package in R (Oksanen et al., 2007). The significance of the CCA model was tested by permutation. The same FA were omitted from the CCA as for the CA.

3 Results

3.1 Environmental conditions

Takvatn was ice-covered from the beginning of December until the beginning of June. There was clear ice without snow cover in January, followed by 4.5cm of snow in February. Ice thickness was at its highest in March at 73cm, with a snow depth of 21cm (Table A1., Figure A2.). There was a layer of slush snow on top of the ice in April and May instead of loose snow. The snow layer had disappeared on the 19th of May, and only ice (with frozen slush) remained until ice-off. Underwater light increased rapidly throughout May (up to 600 µmol m^2s^{-1}) and into June, whereas April never received more than 50 µmol m^2s^{-1}. Note that it was overcast on the measurement day in June, resulting in a lower light above/below water (Figure 1). In March and April the lake was still snow-covered, reducing the light transmittance into the water column.

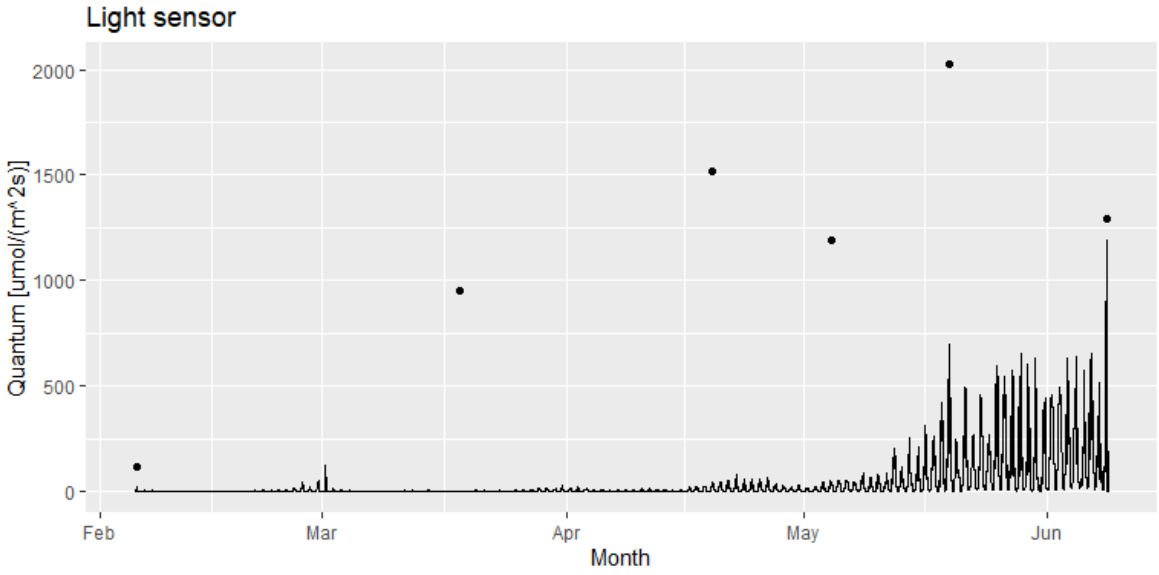

Figure 1. *Light measurements of the submerged light sensor directly below the ice. Dots represent above ice light measurements on the sampling dates.*

In October and November, Takvatn was ice-free and well-mixed (Figure 2 A), with water temperatures around 5Cº throughout the entire water column. The lake was stratified during ice-cover between January and May and mixed in June after ice-off (Figure 2 A). In the middle of ice-cover water temperatures ranged from <1Cº in the upper 35 meters and 2Cº

below. Chlorophyll fluorescence (based on CTD measurements) values were the lowest in February (0.03µg/l) and increased in April and May in the upper 10-0 meters (0.3µg/l) (Figure 2 B). Fluorescence was the highest in late May (0.5 µg/l).

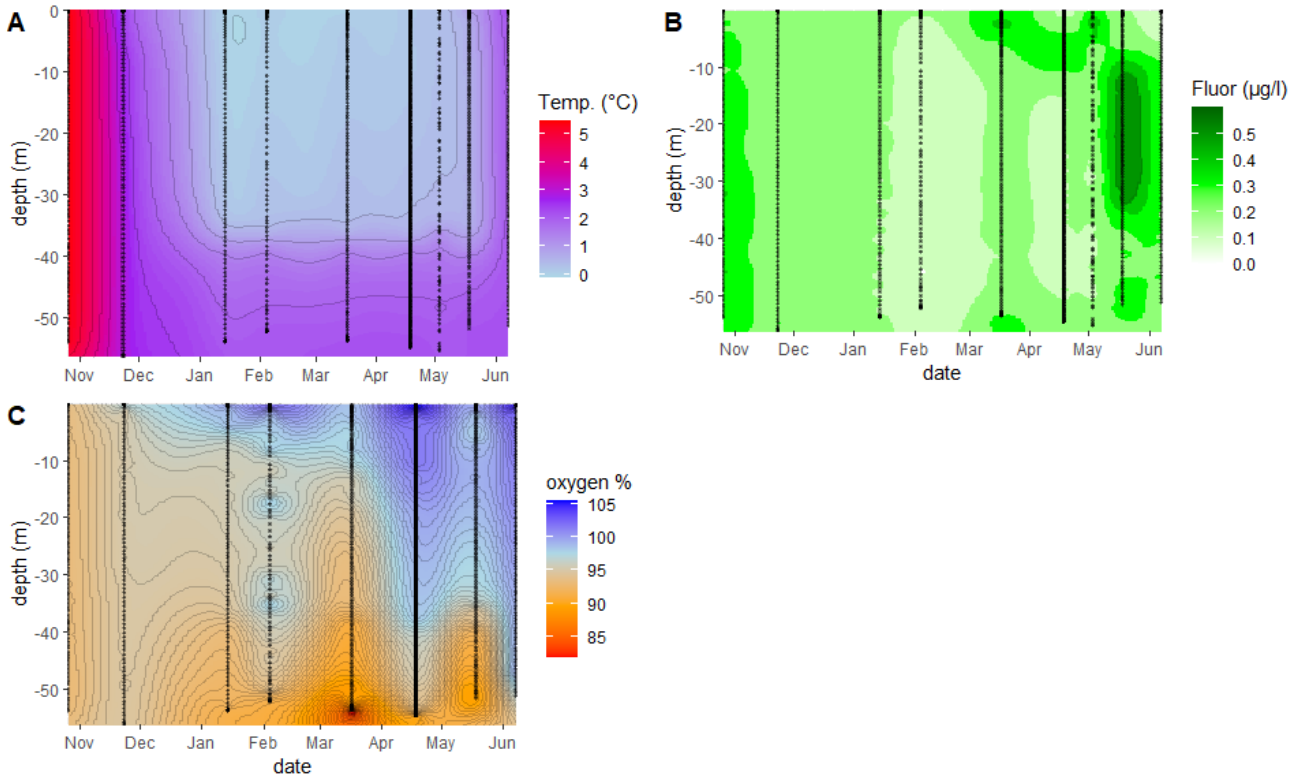

Figure 2. *Vertical CTD cast. A. Temperature profile B. Fluorescence profile C. Oxygen saturation profile. The dotted lines are actual observations while the spaces in between are interpolated, see methods for the interpolation method.*

Oxygen saturation increased from April to June to levels above 100% corresponding with the increase in fluorescence in the upper water column. Oxygen saturation was high (above 85%) in most of the water column except for in March below 50 meters (Figure 2 C).

Nitrite + nitrate values increased slightly during ice-cover from 47 µg/l to 62 µg/l at the end of ice-cover (Figure 3). Ammonium values were highest in January, February, and March (>20 µg/l) and lower during the remainder of the study period. Deep water (58m) showed similar nutrient levels compared to the 0-10 meters, except for nitrate + nitrite and slightly for silicate from March to June where nutrient levels were higher at 58m.

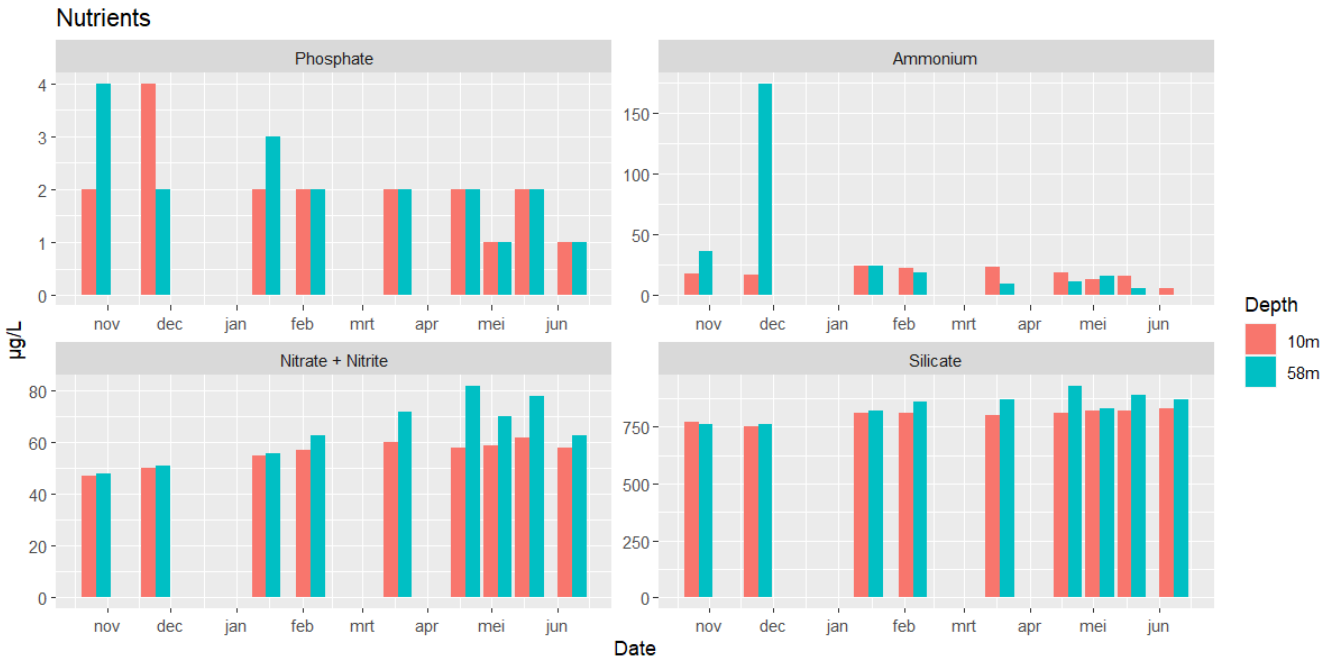

Figure 3. *Nutrient data in Takvatn of the vertical 0-10 meters of the water column and at 58-meter depth, 2 meters above the bottom. Analyzed by Akvaplan NIVA, Oslo.*

Chl-a was detectable in the particulate matter all winter with only minor differences between the integrated 0-10-meter water and right below the ice (0 meters). There was an increase in chl-a content towards May-June when light in the water column returned (Figure 4). Similarly, Ammonium concentrations decreased in June when chl-a increased (Figure 3,4).

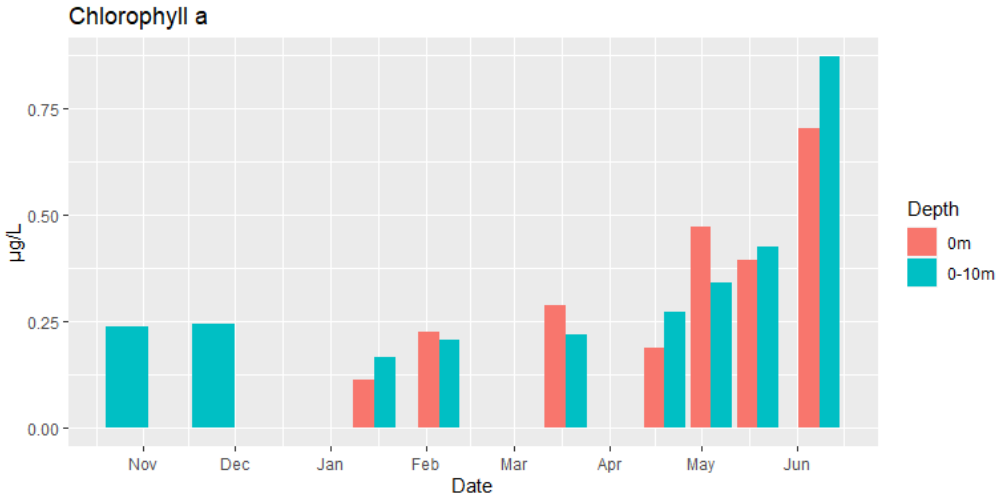

Figure 4. *Chlorophyll-a values in µg/L In October and November, no surface samples were taken since there was no ice-cover and the lake surface waters were well-mixed. 0m: surface samples were taken directly below the ice.*

3.2 Plankton dynamics

Phytoplankton was present during the whole ice-cover period, and cryptophytes were present in high numbers. Chlorophytes and cyanobacteria increased from April to June (Figure 5). Dinoflagellates, chlorophytes, and cyanobacteria were notably higher in the 0m samples from April to June. There are large size differences between the classes; thus, these abundance data are not a good representation of the relative biomass or biovolume of the various phytoplankton classes observed.

Figure 5. *Phytoplankton composition in numbers per liter, Samples were taken at 0 meters: just below ice and integrated 0-10 meters.*

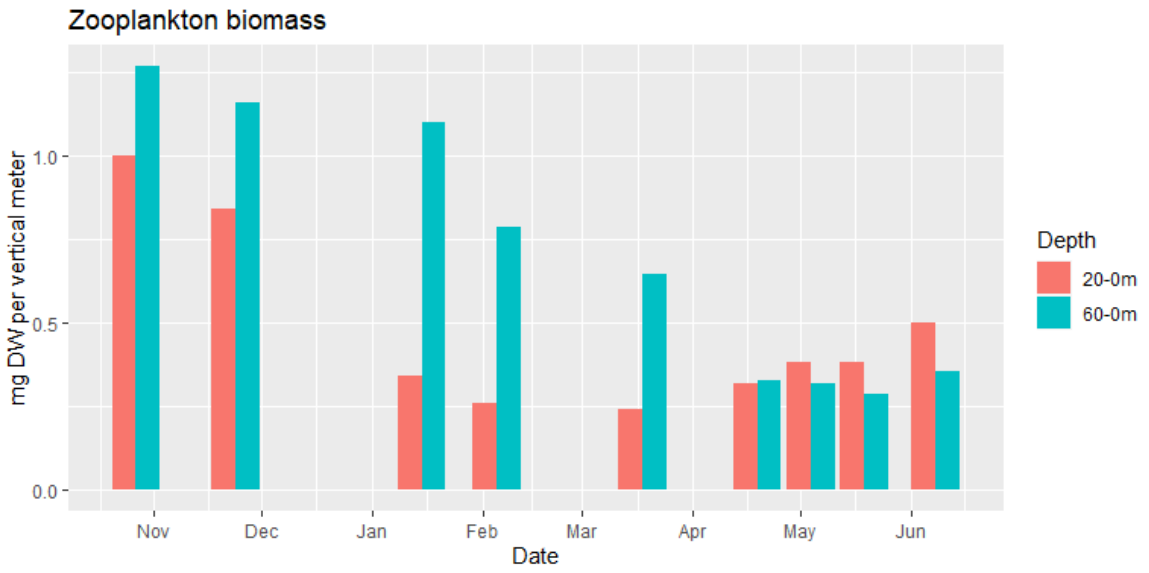

Figure 6. *Zooplankton biomass in Takvatn, in mg/ liter. Samples were taken at two different depths, 60-0 meters, and 20-0 meters. Values have been standardized by dividing the samples by 60 or 20 corresponding to sample depth.*

Zooplankton biomass declined during the ice-covered period. From January to March there was more biomass per vertical meter from 60-0 meters in the water column compared to the upper 20 meters of the water column (Figure 6). In April, there was an increase in zooplankton biomass in the upper 20 meters compared to the 60-0 meter, with an overall slight increase in June.

The abundance of *E. graciloides* and *C. scutifer* declined during the ice-covered period. In addition, the zooplankton biomass per vertical meter (in mg dw*m^{-1}) declined (Figure 6), corresponding with the loss of biomass as seen in a decrease in lipid contents (Figure 10) as well as in individuals per vertical meter (Figure 7). For *E. graciloides*, some females carrying an egg sack were observed as early as January. The number of females with eggs increased strongly in February and March (Figure 7). Males were present, and spermatophores attached to females were occasionally observed in the same period. C-IV to C-V stages were also present during ice-cover, and occasionally C-I to C-III stages were observed, but only sporadically and with negligible abundances. From January to February the highest abundance of zooplankton was recorded below 20-meter depth, which was also illustrated by

the zooplankton biomass (Figure 6). Both species were observed with orange coloured lipid droplets during winter.

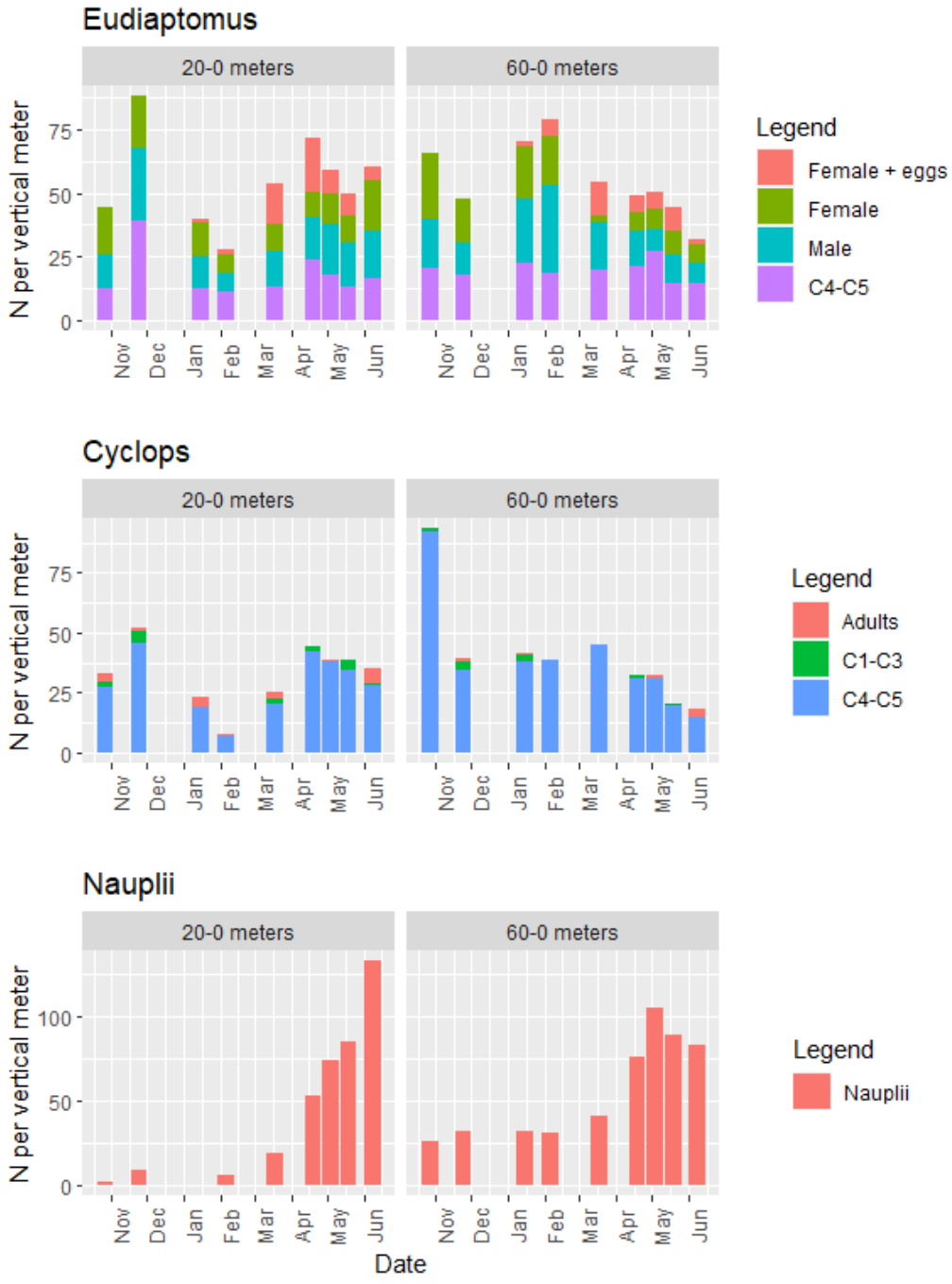

Figure 7. *E. graciloides development stages. ''Female + eggs'' includes only females that carried an egg sack, while ''Female'' are the females without eggs. C. scutifer development stages. The top grey bars indicate the sampling depth. The y-axis indicates the number of individuals per liter water pulled through the net.*

C. scutifer was mainly present in the C-IV to C-V stage throughout the winter. Very small numbers of adults and C-I to C-III stages were observed. The C-IV to C-V stages decreased throughout the ice-covered period in the 60-0 meter net hauls, while this less pronounced in the 20-0 meter hauls, with the lowest numbers observed in January and February. Nauplii occurred in large numbers with an increase in March when *E. graciloides* started to release eggs. Nauplii mainly stayed in the upper 20-0 meters.

3.3 Lipid dynamics and fatty acid composition

Total lipid content decreased during the ice-covered period for both *E. graciloides* (from 60% to 38%) and *C. scutifer* (from 73% to 33%). All groups of FAs (SAFA, MUFA, PUFA) declined during the ice-cover period in both species, but they stabilized in *E. graciloides* (Figure 8) during May and June. FA content of POM increased towards May and June. Relatively seen, the PUFAs decreased most in *E. graciloides.* Towards the end of ice-cover starting in May, the abundance changed towards a higher contribution of SAFA and less PUFA for *C. scutifer* (Figure 9). This was not observed for *E. graciloides*, where relative FA composition remained more consistent with only a small decrease in % PUFA and a slight increase in % MUFA and % SAFA towards the end of ice-cover. POM lipids were highly variable. Still, a relative downward trend of % SAFA and a relative increase of % PUFA and % MUFA was observed towards the end of the ice-covered period.

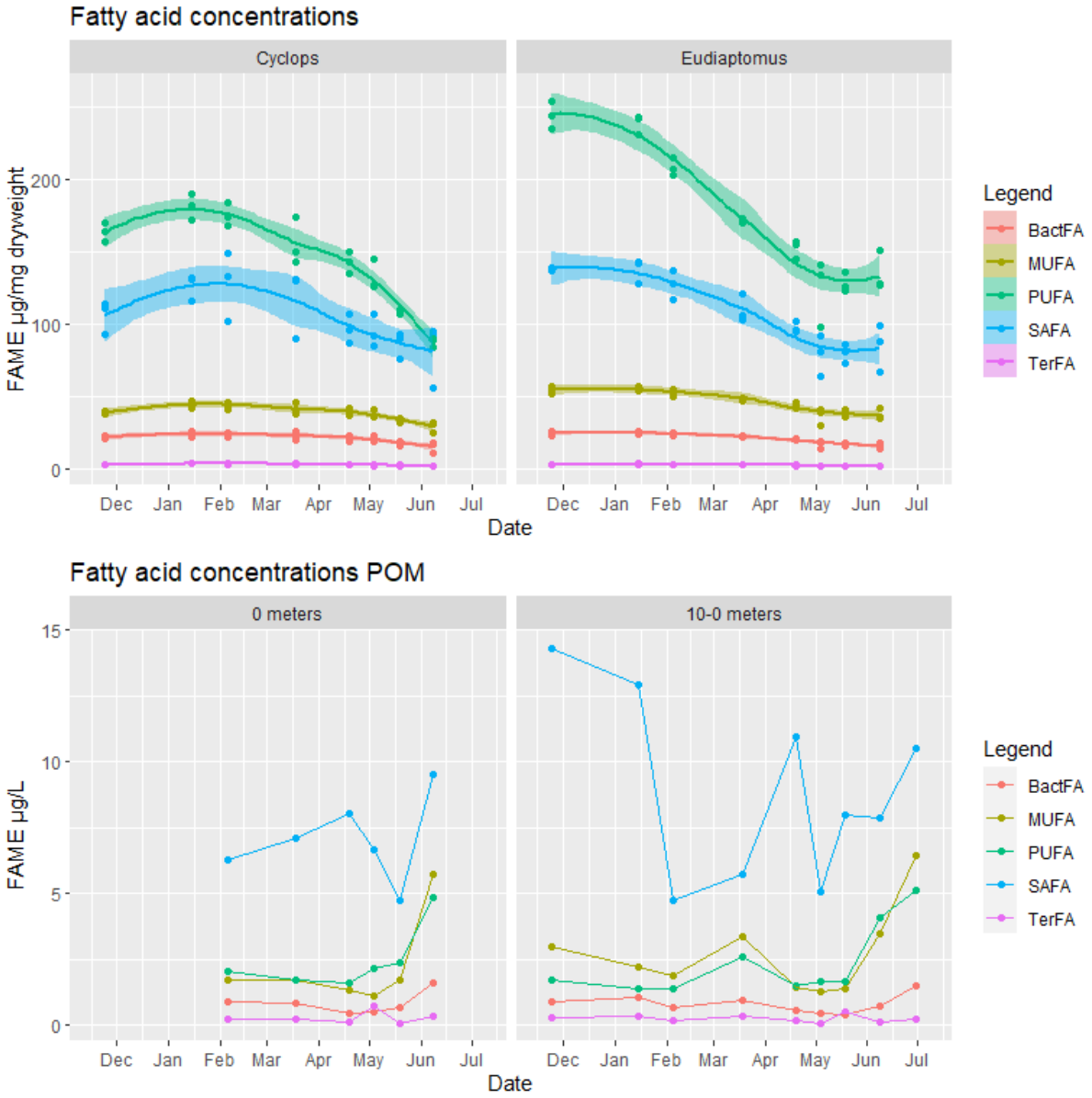

Figure 8. *Grouped fatty acid data for zooplankton and POM. Y-axis shows the fatty acids in µg/mg dry weight for zooplankton and µg/l for POM (seston). BactFA= Bacterial fatty acid biomarkers, MUFA= monounsaturated fatty acids, PUFA= polyunsaturated fatty acids, SAFA= saturated fatty acids, TerFA= terrestrial fatty acid biomarkers. Note that measurements were only taken at the dots and the lines are a generalization to visualize the pattern over time.*

Within the PUFA's, Stearidonic acid, 18:4n-3 (SA) was particularly high in *E. graciloides* at the start of ice-cover (77.8±3.6 µg/mg dry weight^{-1}, 17.31±0.3 % of total FAME) and rapidly declined with the lowest value on 4-5-2021 (29.6±5.8 µg/mg dry weight^{-1}) and slightly higher in June (37.3±4.4 µg/mg dry weight^{-1}) (Figure A3.).

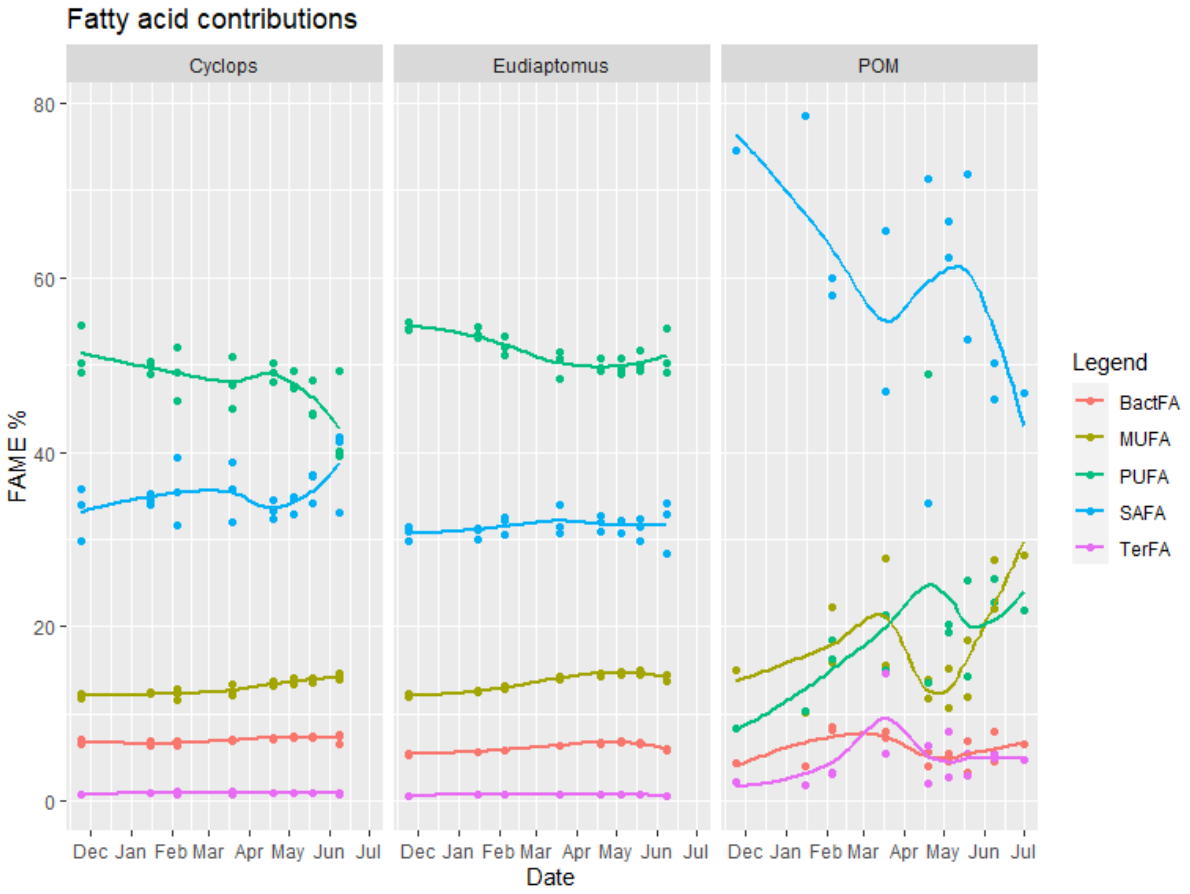

Figure 9. *Composition of grouped fatty acids and biomarkers for C. scutifer, E. graciloides, and POM (seston), 0m and 0-10m pom samples were pooled since thy behaved similarly.*

There was a large difference between total lipids and total FA within *C. scutifer* (Figure 10). In January and February, *C. scutifer* had a higher total lipid content and then quickly declined, while in *E. graciloides* total lipids followed the same pattern as total FAME. Both total FAME and total lipids declined during ice-cover and remained stable from May to June in *E. graciloides* while they kept declining in *C. scutifer*.

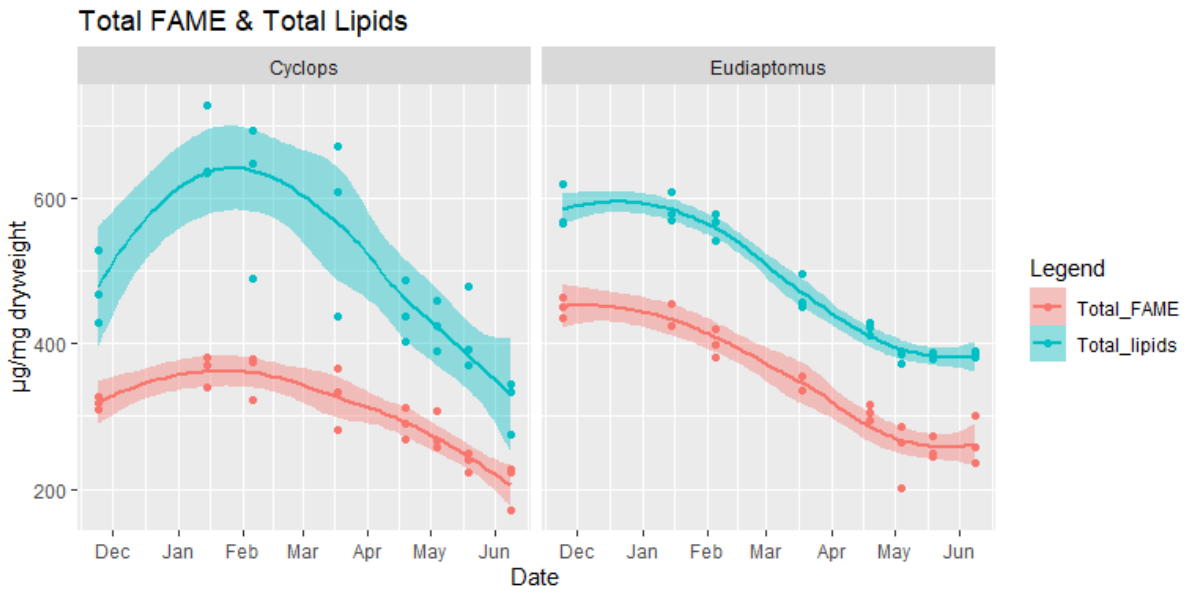

Figure 10. *Difference in total fatty acids methyl esters (FAME) and total lipids.*

Based on the correspondence analysis (CA), *E. graciloides* and *C. scutifer* differed in their FA composition, with separation of the two species along the first axis (Figure 11). Seasonal changes in FA composition were also apparent based on the separation of sampling dates along second axis (Figure 11). While *E. graciloides* contained more C18:3n-3, C18:1n-9cis, C18:2n-6cis and C18:4n-3, *C. scutifer* was characterized by longer chain FA; C20:4n-3, C22:5n3 and C22:1n-9. There was a shift for both species toward more SAFA and MUFA (C16:1n-9, C17:1n-7, C16:0, C23:0, C18:0 and C18:1n-6) towards the end of the ice-covered period. The first two dimensions (axes) display 83% of the total inertia in the data set. Based on permutation test on CCA results of the same data presented in Figure 12, there is a significant difference between species (P-value 0.001) as well as a significant seasonal effect (P-value 0.001).

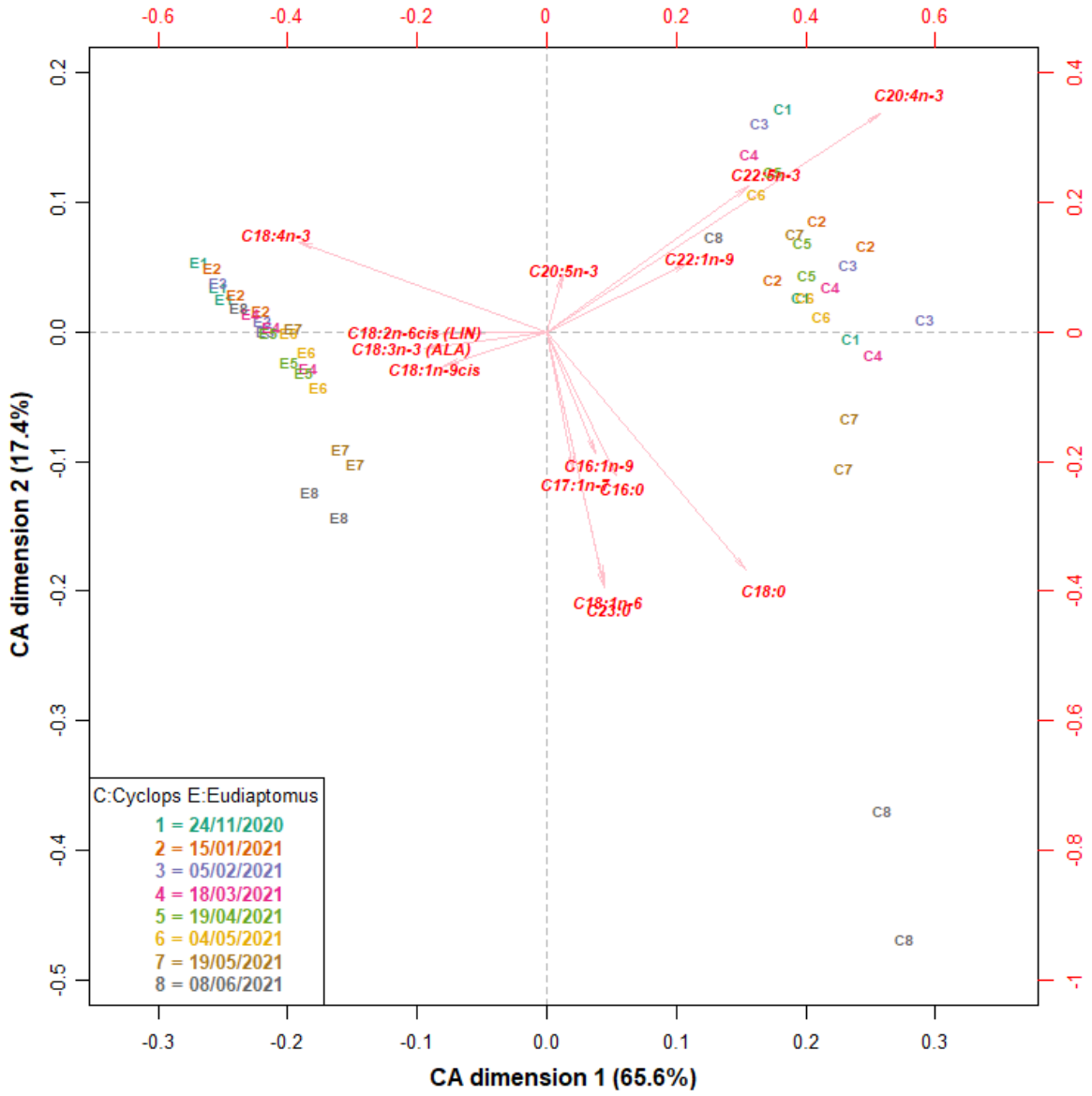

Figure 11. *Correspondence analysis of the fatty acid profiles of E. graciloides, C. scutifer. The first dimension (axis) contributes to 65.6% and the second dimension to 17.4% of the inertia. FA labels are shown when they contribute more to the inertia than expected if all FA were equal, except for C20:5n-3 which was added manually.*

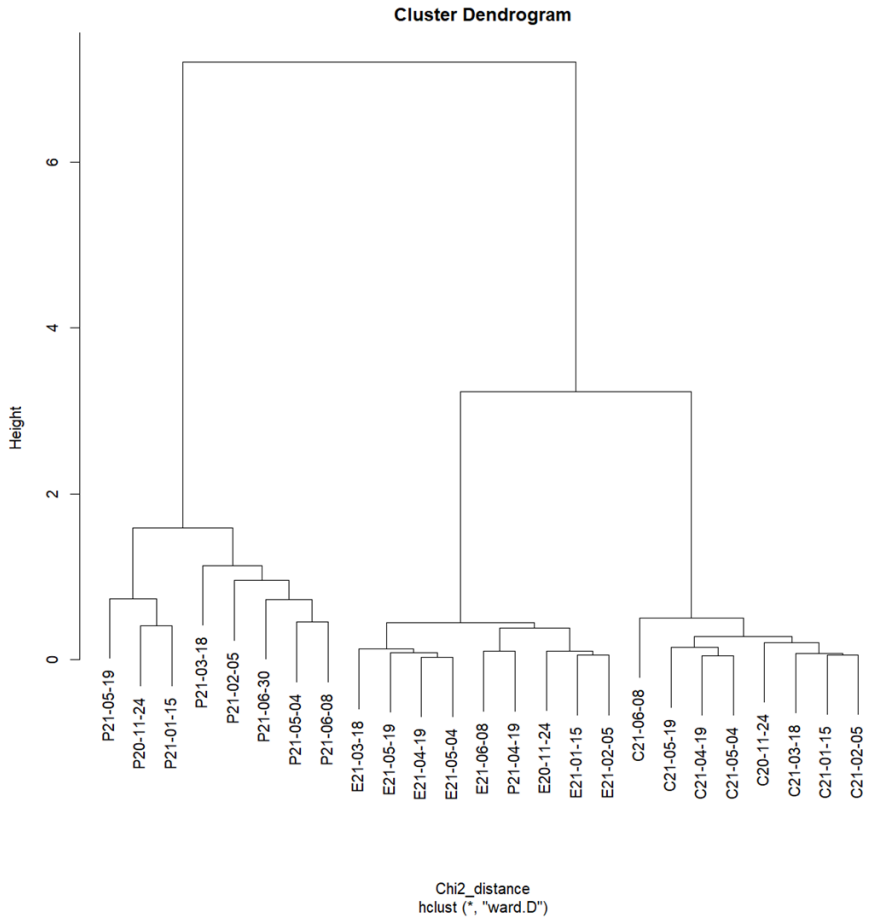

Figure 12. *Cluster dendrogram visualizing the difference between species and dates from different samples. Mean values per date were used. E: E. graciloides, C: C. scutifer, P: Particulate organic matter.*

Results of hierarchical clustering highlighted differences in FA composition between POM and zooplankton (Figure 12). Particulate matter and phytoplankton biomass were low throughout the study period, leading to low amounts of material on the filters and high variation between sampling dates. Based on a permutation test for a CCA on the FA data, species/POM were significantly different (P-value 0.001), whereas the seasonal trend was not (P-value 0.157).

Based on the CA, a seasonal pattern within the FA composition of *C. scutifer* was observed (Figure 13). In January, February, and March, *C. scutifer* tended to have a higher proportion C18:4n-3 and C20:4n-3 compared to other dates, as well as increased C18:0. Towards April and May there was a relative increase in C20:5n-3 and C22:6n-3. The last samples in May

and June had relative higher contributions of C18:1n-12, C16:1n-9, C16:0. C17:1n-7, C23:0 and C18:1n-6. There is a significant seasonal effect (P= 0.006) as seen in a permutation test of a CCA of the same data shown in Figure 13.

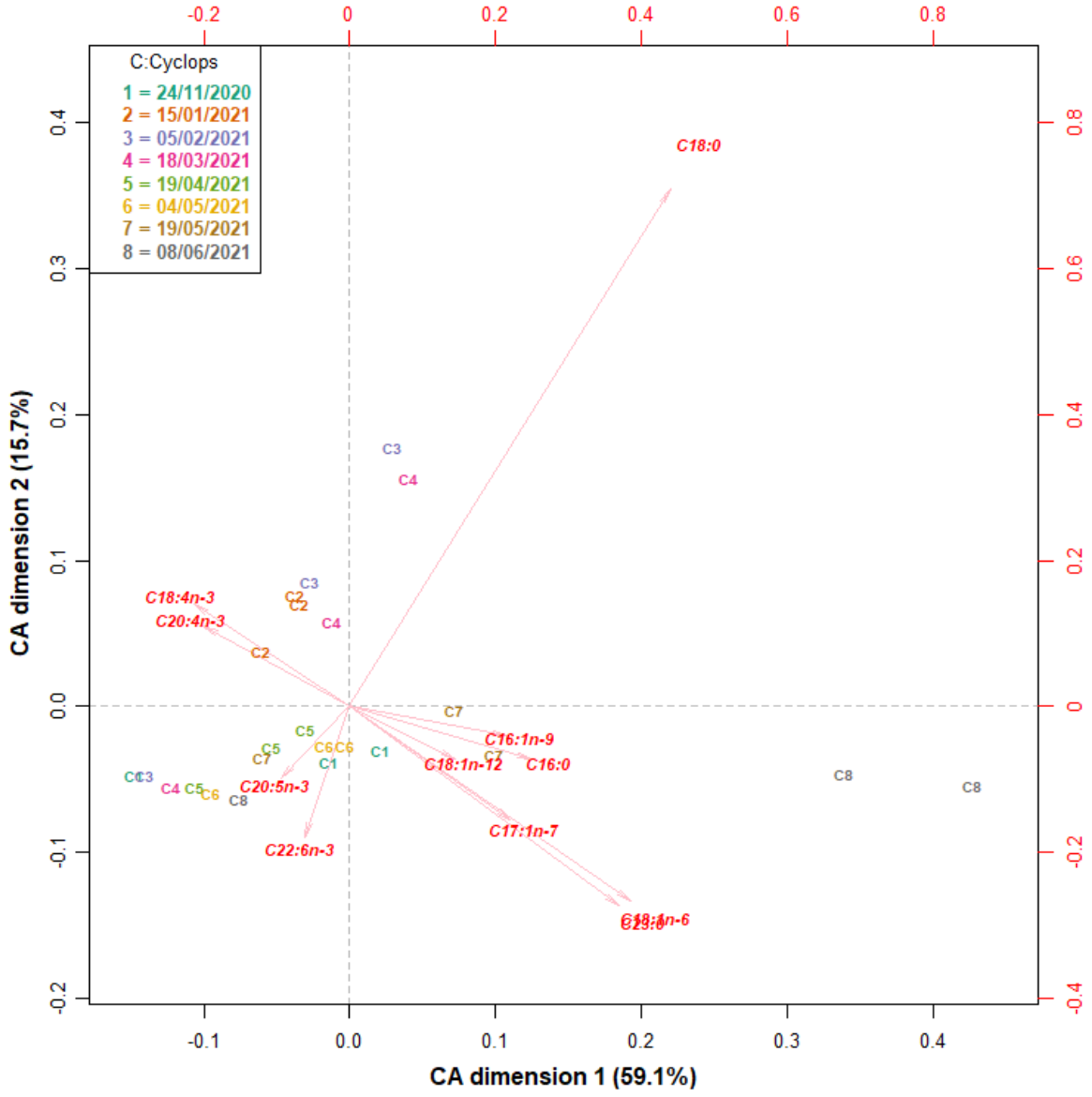

Figure 13. *Correspondence analysis of the fatty acid profile of C. scutifer, dates are in different colours, and numbered fatty acids are shown in red. FA labels are shown when they contribute more to the inertia than expected if all FA were equal, except for C20:5n-3 which was added manually.*

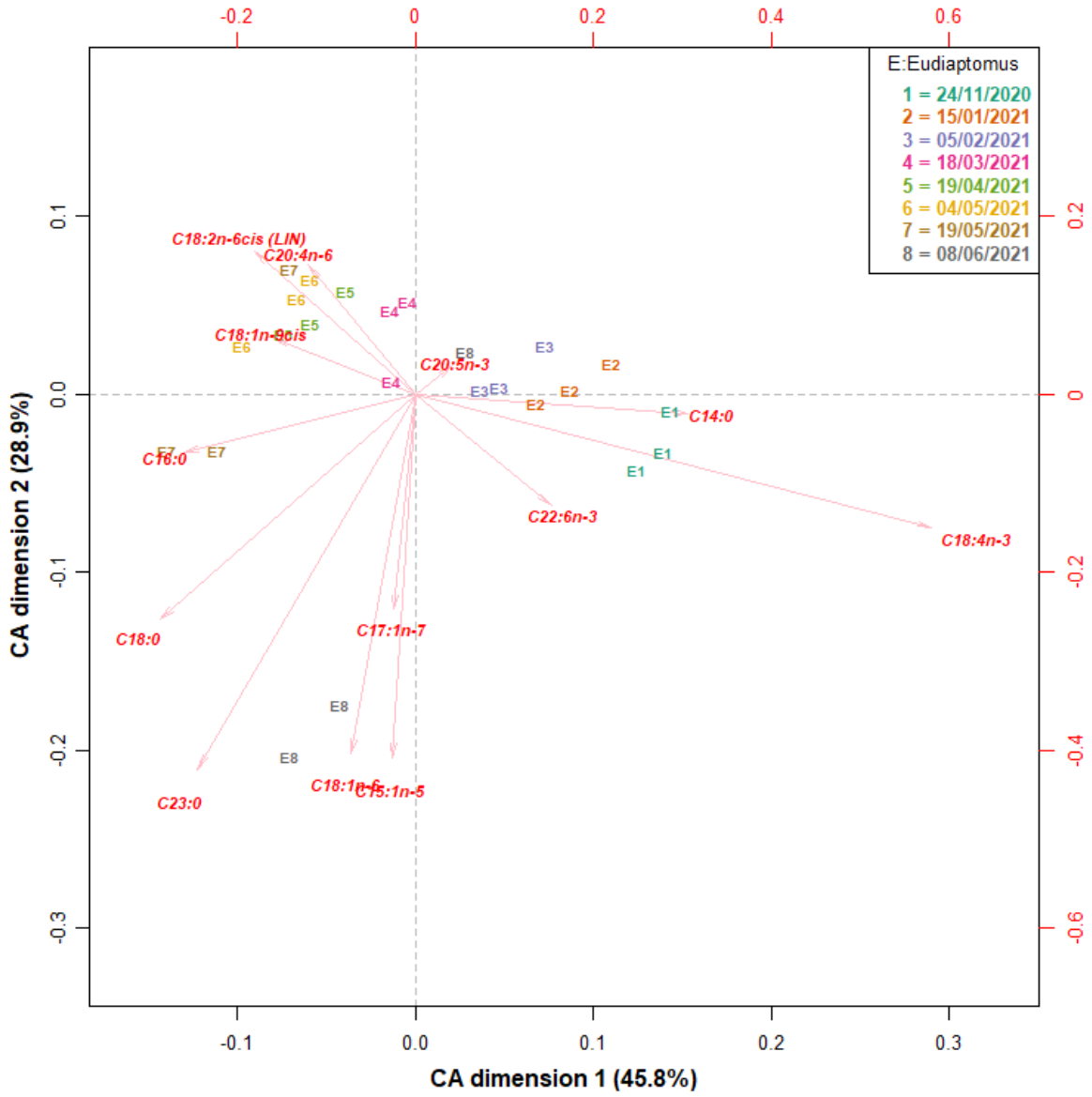

Figure 14. *Correspondence analysis of the fatty acid profile of E. graciloides, dates are in different colours and numbers. FA labels are shown when they contribute more to the inertia than expected if all FA were equal, except for C20:5n-3 which was added manually.*

E. graciloides exhibited a similar seasonal pattern as *C. scutifer (Figure 14).* However, compared to *C. scutifer*, *E. graciloides* had less variability within the triplicate subsamples. The seasonal pattern is more pronounced, with an anti-clockwise rotation starting in November, from more PUFA towards more MUFA and SAFA. Sampling dates showed a season pattern and had a significant effect (P= 0.001), as seen in a permutation test of a CCA.

4 Discussion

This study illustrates important ecosystem processes during the ice-cover period. The high lipid storage at the start and reduced lipid content at the end of winter reveals the importance of previously acquired lipids. The difference in lipid dynamics between *C. scutifer* and *E. graciloides* (i.e., steeper decline in PUFA in *E. graciloides*) reflects differences in their life history and overwintering strategies. Contrary to the hypothesis, the reproducing *E. graciloides* did not have a larger decrease in total lipids compared to *C. scutifer* although did exhibit a large decrease in total FAME. FA composition differed between species and exhibited seasonal changes throughout the study period. Seasonal changes in lipid content and composition suggested that *C. scutifer* was feeding actively during the early ice-cover period, while *E. graciloides* was feeding actively during the late ice-cover period.

4.1 Plankton dynamics

In the current study, zooplankton biomass declined during ice-cover due to a combination of lipid depletion and a decrease in abundance. In general zooplankton biomass was lower during winter months (Hampton et al., 2017). Zooplankton biomass was lower compared to a previous study in Takvatn, where biomass was measured from July to September (Dahl-Hansen, 1995). In shallow lakes in temperate regions, zooplankton and phytoplankton dynamics are dependent on their biomass during autumn and winter conditions (Dokulil & Herzig, 2009), this might be the case for larger lakes as well. However, it should be noted that the results from our net hauls can only be considered to be semi-quantitative due to uncertainty regarding the true volume of water sampled.

E. graciloides reproduced under the ice during March-June which was visible by the increased number of females with egg sacks followed by an increase in nauplii when hatched. This corresponds with a previous study in Takvatn (Primicerio & Klemetsen, 1999), however the reproductive period of *E. graciloides* in the current study was earlier compared to previous studies in other lakes, e.g. in Lake Glubkoe, Russia where the reproductive peak occurred in mid-May (Pasternak, 1999). In another study in the Schöhsee in Northern Germany, females were observed with eggs as early as January however it was not reported

whether the lake was ice-covered during this period (Santer et al., 2000). In deep lakes, multiple zooplankton species reproduce after winter to ensure the nauplii are able to take advantage of the high food availability during the spring bloom (Rivier, 2005). The reproductive period is likely highly dependent on environmental conditions (Vanderploeg et al., 1992) and the availability of phytoplankton, as also previously seen in Takvatn (Abdurhman Kelil, 2007). In the current study, the release of Nauplii coincided with the increase in chl-a. In contrast to *E. graciloides*, *C. scutifer* was predominantly present in the C-IV to C-V stage, which is consistent with previous observations from Takvatn, where reproduction has been reported to occur during late June - July in Takvatn (Primicerio, 2000).

Zooplankton biomass and community data show lower zooplankton abundance in the coldest water <1Cº (30-0m) compared to deeper warmer water 2-3Cº (30-60m). This is surprising since staying in the colder waters could keep metabolic costs down during overwintering (Koussoroplis et al., 2014). A possible explanation for the movement to deeper warmer water could be predator avoidance, since zooplankton had brightly coloured lipids combined with little food availability in the upper water column it might be beneficial to escape predation in deeper darker waters. During the sorting of zooplankton it was observed that *E. graciloides* and *C. scutifer* (to a lesser degree) had brightly orange coloured lipid droplets, which has also been observed for zooplankton under ice in other northern regions, including Russia (Pasternak, 1999) and Canada (Grosbois et al., 2017), which has been suggested to be linked to metabolism and reproduction (T. Schneider et al., 2016).

Phytoplankton was present at very low abundances during winter, although these low abundances may also in part reflect high grazing pressure from the active overwintering zooplankton. A potential grazing effect might be expected to be particularly pronounced during late ice-cover when increased light availability could have supported high primary production and where nauplii abundance in the upper water column was increasing rapidly. Chl-a values are low but comparable with other oligotrophic subarctic lakes (just before and after ice-off) (Forsström et al., 2005), and under-ice in high latitude lakes (Hampton et al., 2017). Summer chlorophyll fluorescence values measured by CTD in Takvatn reach 1 µg/l in late July (Lyche Solheim et al., 2019). In a subarctic oligotrophic lake in Sweden, microalgae

were found at abundances reaching 11 million cells per liter (Rodhe, 1953), considerably higher than found in Takvatn. In Takvatn highest abundances were found in cryptophytes which contain large proportions of PUFA's, however cryptophytes are very small and might not contribute substantially to the total POM pool. Cold oligotrophic lakes are often dominated by flagellates (crysophytes and dinoflagellates) in the open water season (Forsström et al., 2005; Trifonova, 1998). In Takvatn dinoflagellates and cyanobacteria were present during winter and were higher in April to May directly below the ice, suggesting favourable conditions, e.g., due to higher light intensity and/or convective mixing that could retain cells in the upper water column. Some phytoplankton taxa might benefit from a milder and shorter winter, with a better-mixed water column while this could be disadvantageous to mixotrophic plankton, in contrast a severe winter favours motile taxa and limits phototrophic taxa (Özkundakci et al., 2016). Contrary to expectations, bacterial FA were low and relatively stable during the ice-covered period, with an increase in June coinciding with ice-off and mixing. The increase in terrestrial FA biomarkers coincided with melting of snow/ice and increased river inputs, which in this region typically occurs during May-June (Poste et al., 2021). There was no evidence of significant uptake of terrestrial FA in zooplankton, this could be since terrestrial input is of poor quality and they simply avoid it (Taipale et al., 2016). Takvatn is also an oligotrophic lake with relatively low inputs of both particulate and dissolved terrestrial material, which likely reduces the potential importance of bacterial production and heterotrophy/mixotrophy during winter compared to e.g., a brown-water lake that receives substantial inputs of terrestrial organic matter.

4.2 Lipid dynamics

Lipids are essential in aquatic food webs, for the transfer of energy between organisms, as an efficient way to store energy (+- 39 kJ g^{-1}) compared to proteins and carbohydrates (+- 17-18 kJ g^{-1}) and are used as building blocks e.g. in cell membranes (Arts et al., 2009). Total lipids were determined by weighing, but large variability between replicates raised some concern about the reliability of this technique in our dataset. In Canadian lakes, fall and early winter has been found to be essential times for the accumulation of lipids in zooplankton species (Grosbois et al., 2017; Mariash et al., 2016). This is seen in Takvatn as well, where *C. scutifer* had the highest total lipid content in February (up to 73% of dry weight) when Takvatn is

already ice-covered. *E. graciloides* highest total lipid percentage was at 60% of dry weight in November. Grosbois et al., (2017) report up to 76% lipids in copepods under ice-cover in January in Lake Simoncouche, which supposedly play an important role in survival under ice-cover. Total lipids decreased down to 33% for *C. scutifer* in June and 38% for *E. graciloides* indicating the high importance of previously acquired lipids. In Lake Simoncouche, *C. scutifer* had up to 50% total lipid content of their biomass in January compared to only 21% in May (Grosbois et al., 2017). Takvatn is located much farther north compared to Lake Simoncouche, this could cause more light availability during late winter if snow/ice-cover conditions allow. This could explain why *C. scutifer* needs a larger storage of lipids but does not indicate as to why it does not decrease to the same level or lower at the end of ice-cover. It is likely that the lipid content at the end of winter can be highly variable depending on environmental conditions and food availability throughout the ice-cover period. Total lipid content of bulk zooplankton (combined *E. graciloides, C. scutifer*) was lower at the end of ice-cover (early June) of 2019-2020 (128.9 µg/mg dry weight) compared to 2020-2021 (274.9 µg/mg dry weight) in Takvatn (unpublished data). Snow cover was higher in 2019-2020, likely leading to less primary production at the end of the ice-cover season. Accordingly, the zooplankton lipid content (as % of dw) was less than half of the values found in late ice-cover (June 2021). However, a long-term study would be necessary to shed more light on the intricacies of zooplankton lipid content and environmental conditions during ice-cover.

Zooplankton starvation experiments show that calanoid zooplankton rapidly use storage lipids, nearly depleting them entirely within 10 days (Koussoroplis et al., 2014) and (Burns, 1988) show that zooplankton did not survive for more than 25 days without a food source at 15Cº. However, most starvation experiments were performed at higher temperatures and cannot be compared to the winter water temperatures in this study. In addition, the zooplankton did not have time to store up lipids as zooplankton under natural conditions typically do before ice-cover. Starvation experiments under more realistic winter conditions could provide important insight into how zooplankton condition before ice-cover is likely to affect survival. As under ice temperatures in Takvatn were much lower (< 3Cº) this likely caused a decreased metabolic costs, as starvation tolerance was found to be inversely related to temperature (Borchers & Hutchings, 1986). However, it is unlikely they could survive the

whole ice-cover period without a food source, even with a decreased metabolic cost. This is illustrated by a starvation experiment where calanoid copepods kept at 4C^{o} did not survive more than 73 days (out of 163 days of ice-cover) solely on previously acquired lipids (Grosbois et al., 2017).

The present study indicates that zooplankton are likely actively feeding at least during part of the 5-month ice-cover period in Takvatn. This can be seen by the increase in total lipids until January for *E. graciloides* and February for *C. scutifer*. *C. scutifer* might feed on microzooplankton after the autumn bloom and thus stores up lipids for a longer period. In addition, at the end of the ice-covered period the decline in lipid reserves in *E. graciloides* stopped, indicating that the uptake of energy met metabolic needs. *E. graciloides* possibly fed on a resource that *C. scutifer* cannot utilize since calanoid copepods are filter feeders and can feed selectively (Ger et al., 2011). In contrast, *C. scutifer* has a raptorial feeding strategy in the later stages (from C-IV onwards), in addition, not all cyclopoids can digest every algae species (Fryer, 1957). Another possibility is that *C. scutifer* starts to metabolize newly obtained lipids quickly at the end of ice-cover and thus still declines. Rotifers could be an important food source for *C. scutifer* under ice-cover although there was no observed increase in bacterial FA, which would be expected if *C. scutifer* fed on rotifers (Desvilettes et al., 1997; Nichols et al., 1996). However, rotifer abundance was not quantified in this study. Changes in ice-on timing due to climate change might be especially important for *C. scutifer* while ice and snow conditions at the end of ice-cover might have a larger effect on *E. graciloides*. As seen in the respective lipid accumulation or feeding periods. Expectations in subsequent months are an increase in lipids, though, these open water months were not sampled. The current study also shows that there is primary production under ice-cover at the end of winter, which at Takvatn is a period with many hours of daylight and with the midnight sun present from the 18th of May. With such a high light availability above ice per day and nutrients not being limited, the role of ice and snow on the lake plays a crucial role in primary production (Hampton et al., 2017). In addition, in winter there is less competition from other zooplankton species combined with an efficient way to utilize low phytoplankton biomass might help these species to survive under ice-cover.

4.3 FA composition

FA content of POM is low in Takvatn during winter compared to other ice-covered lakes, this is not surprising as it is an oligotrophic lake with little light availability in winter. FA concentrations (µg/l) in Takvatn were lower than observed in Lake Simoncouche (Grosbois et al., 2017). Cryptophytes and chlorophytes are high in ALA and SA (Brett et al., 2009; Jónasdóttir, 2019), cryptopythes have been proven to be a highly suitable food for *Eudiaptomus* with regard to reproduction (Von Elert & Stampfl, 2000). While cryptophytes were present in large numbers during the whole ice-cover duration chlorophytes were not. In early May there was a large increase in PUFA in the POM, this coincided with increased light availability, phytoplankton abundance and chl-a. The lack of apparent drawdown of nutrients in May suggests that phytoplankton are not likely nutrient limited at this point. In May-June POM FA increase, e.g., EPA and DHA which are present in large quantities in diatoms and cryptophytes. This is in reflected in the FA composition of *E. graciloides* which increases in PUFA's from late May to June. In contrast, *C. scutifer* still declines in PUFA indicating a possible lack of food availability. There is no clear indication that zooplankton replenishes its lipids with heterotrophs and/or mixotrophs as no observable increase in bacterial biomarkers was observed. This could be due to Takvatn being a clear water lake resulting in little organic carbon in the water column for bacterial production. However, phytoplankton is present in low abundances during winter, and they may replenish some of their energy by utilizing this food source.

At the start of ice-cover large lipid reserves were observed with high concentrations of PUFA's. MUFA and SAFA are the major groups for storage lipids, whereas long chain poly unsaturated fatty acids (LCPUFA) are mainly incorporated into cell structural lipids (Arts et al., 2009). However, storage of LCPUFA might be of importance in *E. graciloides* for reproduction under late ice-cover. Contradictingly, our results show the opposite with higher contribution of LCPUFA in *C. scutifer*. The higher trophic position of *C. scutifer* may be of more importance here, possibly causing an increase (Persson & Vrede, 2006). However, in absolute values *E. graciloides* has more PUFA. The PUFA content especially omega-3 and 6 are of importance to higher trophic levels and there is currently an availability shortage of omega-3 LCPUFA's to meet the recommended human intake (Hamilton et al., 2020). It is

important to understand where and when these LCPUFA's are produced and transferred in the food web. The omega-3 FA play important physiological roles in all vertebrates and impact neural signalling and influence memory, learning, mood and visual acuity (Pilecky et al., 2021).

The high PUFA content with a quick decrease in *E. graciloides* corresponds with an increase in females carrying and releasing eggs. The very high values of SA (18:4n-3) up to 17.3±0.3 % of total FAME and 77.8±3.6 µg/mg dry weight in *E. graciloides* showed a steep decline during ice-cover, with an increase towards the end when primary production increased. The SA values of *E. graciloides* are higher compared to the adult calanoid copepod *L. minutes* (19.0 µg/mg dry weight) previously reported at the start of ice-cover (Grosbois et al., 2017). Similar concentrations of 18:4n-3 in *Eudiaptomus* have been observed in subarctic (between 14.5-18.7% of total FAME in September (Hiltunen et al., 2016). Boreal lakes had much lower values of 18:4n-3 and thus might be related to lipid accumulation before ice-cover or differences in food availability in the subarctic. It is possible that SA is used to bioconvert to longer chained omega-3 FA, since SA is a precursor for the longer chained essential FA EPA and DHA (Guil‐Guerrero, 2007). Through bio conversion SA can be elongated (adding carbon atoms) and desaturated (removal of hydrogen atoms) increasing the number of double bonds (Arts et al., 2009). However, bioconversion is energetically costly, often limited and might only play a small role. Another possibility for the high amounts of SA could be due to reproductive costs and investment in eggs. It is likely that *Eudiaptomus* highly invests PUFA (possibly mainly SA) and MUFA into egg production, as seen in Daphnia (Arts et al., 2009). During egg production dietary and/or storage lipids are converted to phospholipids. The phospholipids eventually become part of the egg yolk (Arts et al., 2009). *E. graciloides* total FAME closely followed total lipids.

In general the C-V and C-VI stages of *C. scutifer* feed primarily on rotifers and nauplii (J. W. Moore, 1978). *C. scutifer* is known to reproduce late June in Takkvatn, thus might use the spring bloom to invest in reproduction (Primicerio & Klemetsen, 1999). *C. scutifer* had higher total lipids compared to total FAME. *C. scutifer* possibly has more wax esters containing fatty alcohols and thus resulting in a difference between the two. This is commonly observed for

copepods in marine systems (Sargent & Falk-Petersen, 1988) and cold water adapted organisms (Arts et al., 2009). In zooplankton, the most variable component is the storage lipids, mostly triacylglycerols and wax esters (Arts & Wainman, 1999). Storage lipids are often quickly metabolized when an organism is starved (Koussoroplis et al., 2014; Taipale et al., 2021) this could result in the observed decline in total lipids if the difference is caused by non-saponifiable lipids. To gain more information on this difference further research is required, for example a separation of lipid classes will give insight whether there is a difference in storage lipids between the species.

4.4 Conclusion & future perspectives

The results of the present study indicate that winter conditions play an important role in zooplankton lipid content and composition, this is in agreement with other studies (Grosbois et al., 2017; Hébert et al., 2021). Especially ice and snow cover can limit primary production. The two actively overwintering copepods in Takvatn have different life strategies, where the release of nauplii of *E. graciloides* coincides with increased under-ice primary production under late ice-cover, *C. scutifer* does not. This may play a role in species abundance in future scenarios. The ice-cover period is predicted to be shorter in the future (Sharma et al., 2016) which can shift phytoplankton and zooplankton communities. In Takvatn a shorter ice-cover period, as well as expected increases in the frequency of rain-on-snow events (Hisdal et al., 2021) will most likely result in higher lipid concentrations in both species, where the light limitation at the end of ice-cover is especially important for the herbivorous *E. graciloides*. Knowledge of the importance of abiotic factors as well as the life strategies of winter-active species is vital to predict future changes (Hurst, 2007).

The expectations with an increase in temperature is a rapid increase in primary production (Karlsson et al., 2005). It's been suggested that the biomass production of phytoplankton is related to the length of the ice-free season, more so than weather conditions and thermal stability (Forsström et al., 2005). In addition, trophic mismatch might occur due to earlier offset of spring phytoplankton blooms, this effect might be especially strong in lakes with ice-cover (Peeters et al., 2007). A decrease in the thermal niche availability of cold water adapted fish species is already observed (Santiago et al., 2016) and thought to further decrease with

climate warming (Cline et al., 2013; John J. Magnuson et al., 1990). This could lead to a change in the community structure for phyto and zooplankton, where the cold water adapted zooplankton (*C. scutifer* and *E. graciloides*) may eventually be outcompeted by species adapted to warmer waters. This is also the case for higher trophic levels such as fish where some winter specialists (e.g., salmonids) actively feed during the winter (Shuter et al., 2012).

Besides changes in the community structure due to changes in winter conditions, changes in the quality of the lipids (FA composition) are likely due to other ongoing changes to the lake ecosystem. Climate change could cause more nutrients to enter lake systems (Rouse et al., 1997). Oligotrophic systems have higher concentrations of HUFA's compared to eutrophic systems (Taipale, et al., 2016), however the overall biomass of HUFA's could increase in an eutrophic lake with an increase in lipids overall. Overall, it is important to understand the current conditions under ice and to understand how the community composition and lipid composition might change in future decades. Zooplankton are the base of the pelagic food web and an important source of energy and lipids to higher trophic levels (including fish and humans), and changes in abundance, lipid content and lipid composition can have a broad range of consequences for lake ecosystems.

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6 Appendix

6.1 Map of study location

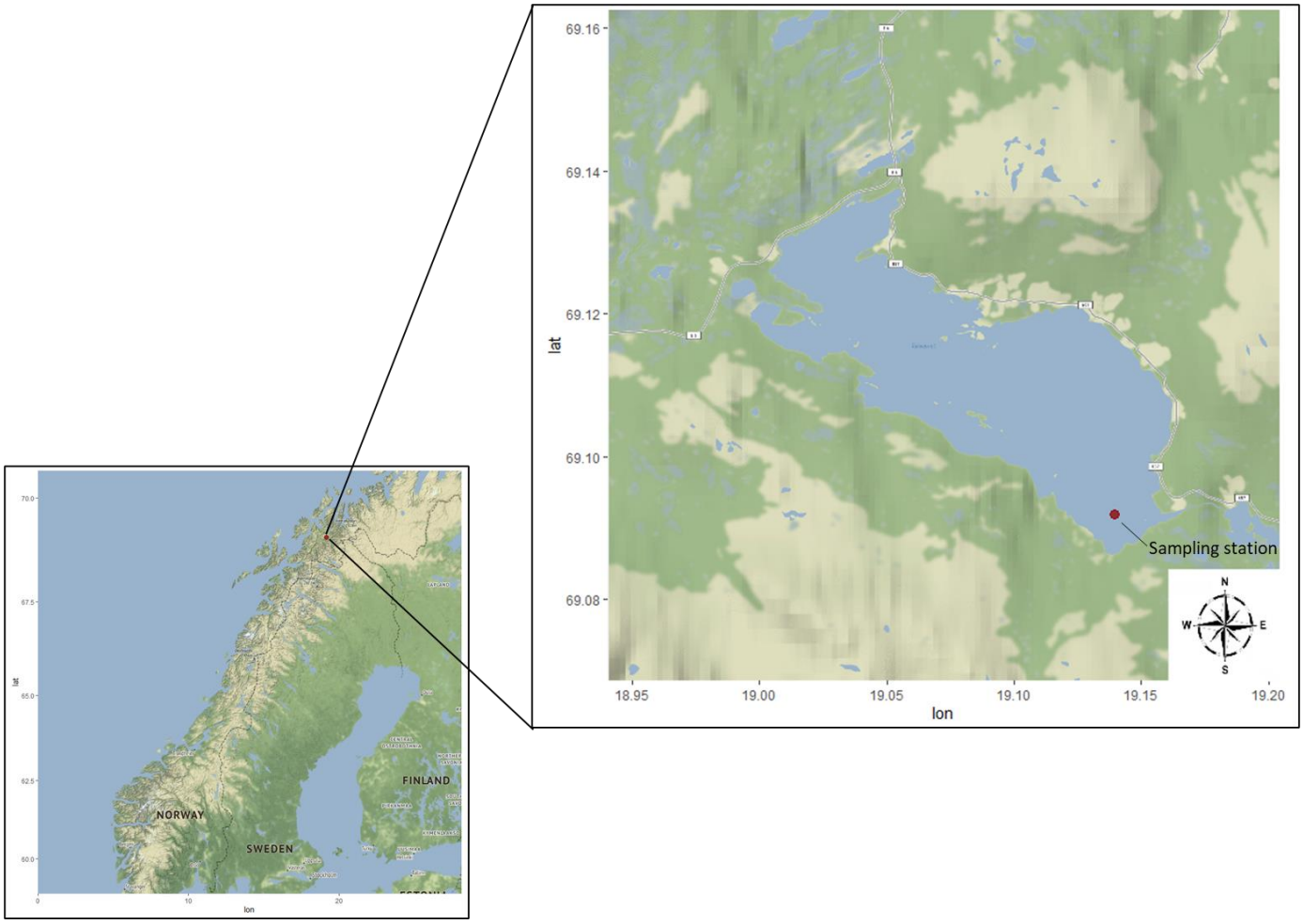

Figure A1. *Map of Takvatn, red dot indicates sampling location (Lat: 69.09201, Lon: 19.13962)*

6.2 Physical conditions

Table A1. *Observed physical conditions for each sampling date.*

Date	Secchi depth (m)	Snow depth (cm)	Ice thickness (cm)	Conditions
27-10-2020	11,5	-	-	Open water
24-11-2020	10,5	-	-	Open water
15-01-2021	14	0-0,5	42,5	Clear ice
05-02-2021	11	4,5	62,5	Dry snow
18-03-2021	10	21	73	Dry snow
19-04-2021	11,5	8	65	Slush, small hard layer on top
04-05-2021	10,5	4,2	69	Thick frozen slush (20cm)
19-05-2021	18	0	56	Dry ice, sharp point at the top.
08-06-2021	15	-	-	Open water at the sampling site.

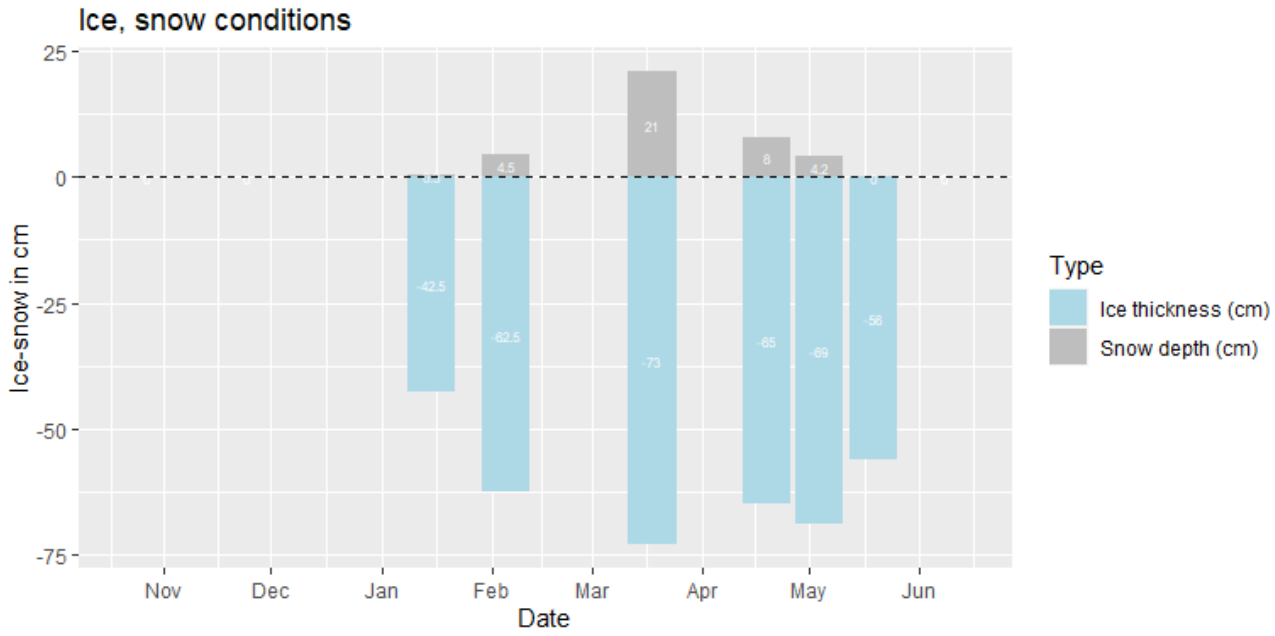

Figure A2. *Ice and snow depth, the dotted line represents the surface of the ice.*

6.3 Individual PUFA's

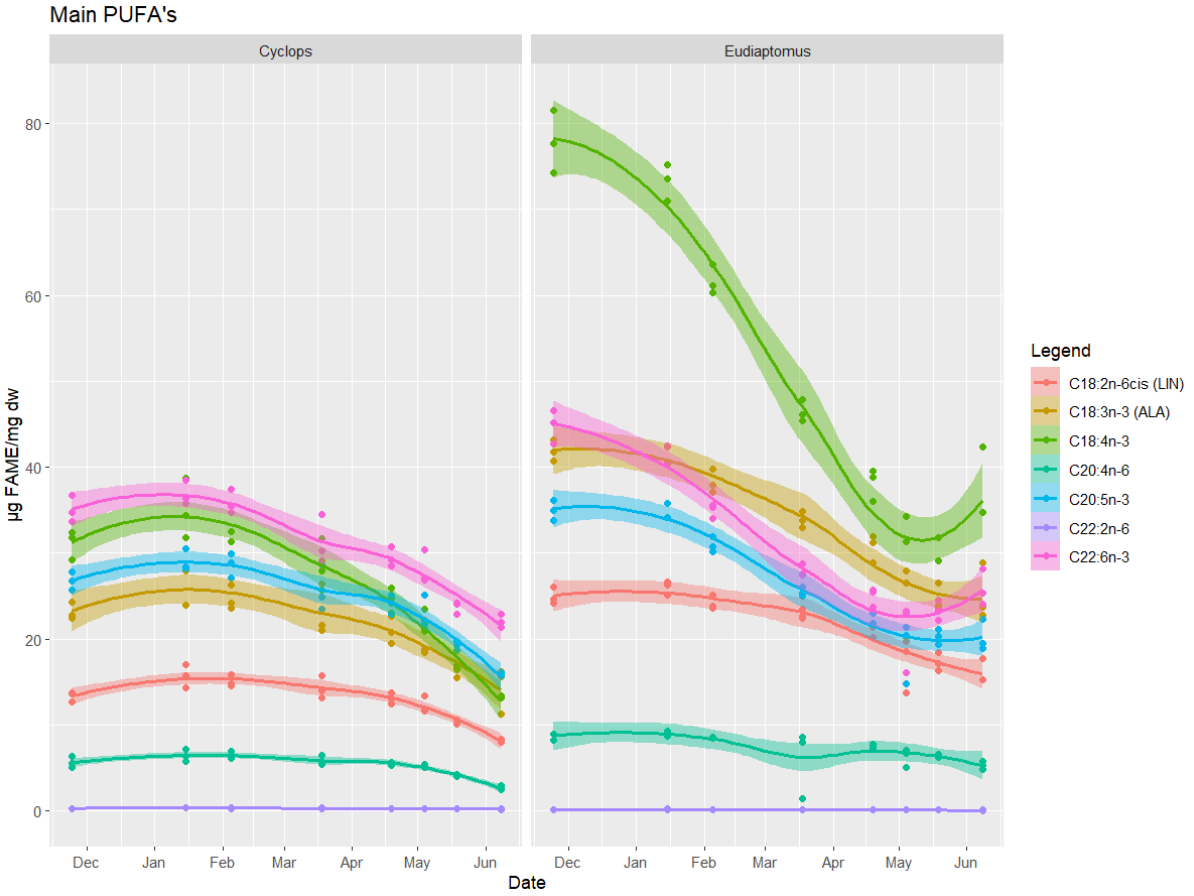

Figure A3. *Y-axis shows the fatty acids in µg/mg dry weight for zooplankton. Note that measurements were only taken at the dots and the lines are a generalization to visualize the pattern over time.*

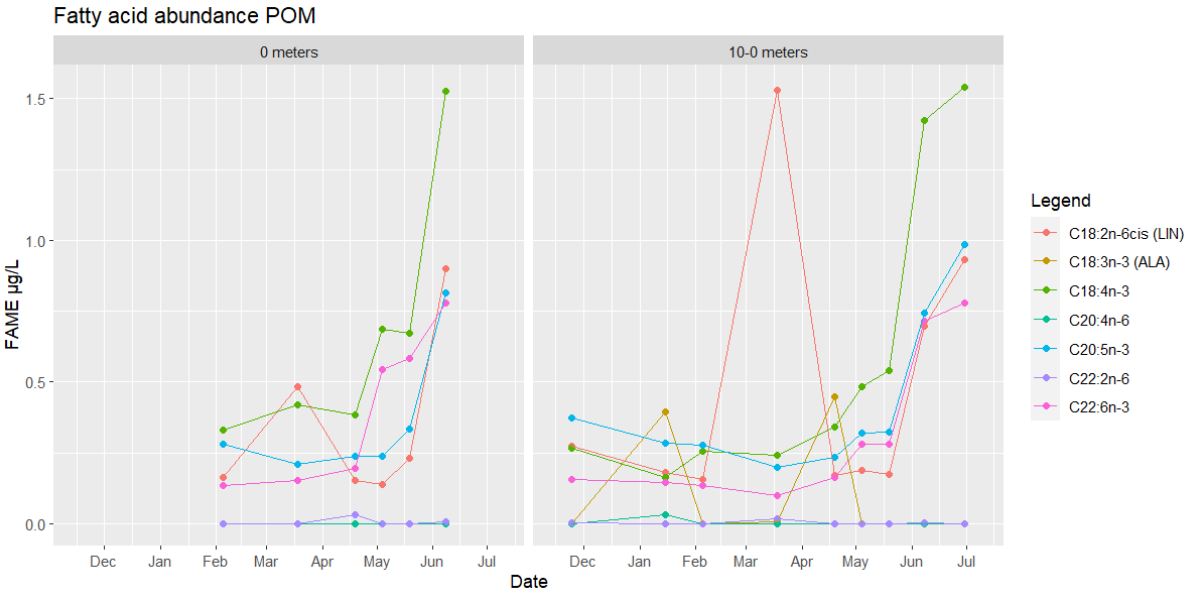

Figure A4. *Y-axis shows the fatty acids in µg/L of water filtered. Note that measurements were only taken at the dots and the lines are a generalization to visualize the pattern over time.*

6.4 Fatty acid composition data

Table A3. *Fatty acid concentrations in % of total FA, except for total lipids which is depicted in µg mg DW^{-1}, mean ± standard deviation, n= number of subsamples. n.d.= not detected.*

Date	24-11-2020	24-11-2020	24-11-2020	15-1-2021	15-1-2021	15-1-2021
Species	C. scutifer	E. graciloides	POM	C. scutifer	E. graciloides	POM
Sub samples	3	3	1	3	3	1
Total_lipids	474.96±23.32	584.27±11.49	NaN±NaN	666.6±32.04	585.54±1.08	NaN±NaN
C14:0	10.14±0.33	12.85±0.16	2.22	9.53±0.33	12.11±0.26	3.06
iso-15:0	1.48±0.09	1.24±0.01	0.81	1.36±0.03	1.28±0.02	0.13
anteiso-15:0	0.78±0.02	0.78±0.01	0.42	0.78±0.02	0.79±0.01	0.36
C14:1n-5	0.09±0.01	0.08±0.02	0.08	0.09±0.01	0.07±0.01	0.06
C15:0	0.83±0.02	0.6±0.01	0.47	0.79±0.01	0.63±0	0.44
iso-16:0	0.78±0.24	0.4±0.08	0.17	0.64±0.05	0.51±0	0.25
C15:1n-5	0.11±0.09	0.03±0.01	n.d.	0.02±0.01	0±0.01	n.d.
C16:0	15.49±1.61	13.16±0.44	25.74	15.23±1.09	13.35±0.17	29.21
iso-17:0	0.32±0.02	0.3±0	0.54	0.33±0.01	0.31±0	0.18
C16:1n-9	0.44±0.08	0.37±0.01	0.53	0.6±0.1	0.4±0.02	0.83
C16:1n-7	4.04±0.14	4.39±0.03	7.22	4.1±0.11	4.65±0.03	3.05
C17:0	0.34±0.02	0.32±0.02	0.36	0.41±0.04	0.35±0.02	0.36
9,10D16	n.d.	0.05±0.09	n.d.	n.d.	n.d.	n.d.
C17:1n-7	0.13±0.09	0.05±0	n.d.	0.05±0.02	0.03±0	n.d.
C18:0	5±1.2	2.73±0.32	43.93	7.05±0.82	3.32±0.7	43
C18:1n-9trans	0.13±0.02	0.11±0.01	0.11	0.18±0.01	0.13±0.02	n.d.
C18:1n-12	0.03±0.05	0.02±0.03	0.28	n.d.	0.03±0	0.21
C18:1n-9cis	3.48±0.2	4.84±0.17	2.27	3.74±0.15	5±0.01	3.63
C18:1n-7	1.71±0.27	1.47±0.04	0.94	2.14±0.3	1.61±0.03	2.29
C18:1n-6	0.49±0.35	0.14±0.07	0.74	0.1±0.01	0.05±0	n.d.

C19:0	0.59±0.15	0.36±0.03	0.31	0.45±0.14	0.27±0.01	1.07
C18:2n-6trans	n.d.	0±0.01	n.d.	n.d.	0.01±0.01	0.05
9,10D18	0.09±0.01	0.13±0	n.d.	0.08±0	0.12±0	0.09
C18:2n-6cis (LIN)	4.18±0.21	5.56±0.07	1.44	4.32±0.14	5.85±0.07	1.24
C20:0	0.43±0.02	0.39±0.01	0.59	0.55±0.02	0.43±0.02	0.51
C18:3n-6	0.29±0.02	0.63±0.02	0.17	0.36±0.1	0.64±0.01	0.08
C20:1n-9	n.d.	n.d.	2.92	n.d.	n.d.	n.d.
C18:3n-3 (ALA)	7.26±0.2	9.32±0.03	n.d.	7.31±0.27	9.39±0.09	3.23
C21:0	0.03±0.05	0.01±0.02	0.03	0.12±0.09	0.03±0	0.28
C18:4n-3	9.77±0.64	17.31±0.3	1.4	9.6±0.5	16.45±0.29	2.46
C20:2n-6	0.55±0.04	0.44±0	0.11	0.57±0.01	0.47±0.01	0.08
C22:0	0.21±0.01	0.2±0.01	0.41	0.26±0.03	0.23±0.01	0.27
C20:3n-6	0.2±0.01	0.1±0	0.69	0.2±0.02	0.11±0	n.d.
C22:1n-9	0.72±0.04	0.06±0.01	0.03	0.7±0.06	0.06±0	n.d.
C20:3n-3	0.21±0.03	0.11±0.01	1.81	0.22±0.02	0.13±0	0.18
C20:4n-6	1.77±0.25	1.94±0.1	0	1.78±0.19	2.04±0.02	n.d.
C23:0	0.02±0.03	0.02±0.03	0.07	0.05±0.02	0.03±0.01	0.03
C20:4n-3	4.93±0.36	0.51±0.03	0.12	4.66±0.45	0.55±0.05	0.22
C22:2n-6	0.1±0	0.04±0	0.02	0.1±0.01	0.04±0.01	n.d.
C24:0	0.11±0.01	0.06±0.01	0.38	0.13±0.01	0.07±0.01	0.26
C20:5n-3	8.4±0.49	7.79±0.04	1.82	8±0.34	7.91±0.11	1.58
C24:1n-9	0.69±0.04	0.48±0.02	n.d.	0.72±0.02	0.54±0.01	0.1
C22:3n-3	0.28±0.04	0.14±0.01	n.d.	0.3±0.03	0.15±0.01	n.d.
C22:4n-6	n.d.	0±0.01	n.d.	n.d.	n.d.	n.d.
C22:5n-3	2.36±0.15	0.48±0.01	0.09	2.23±0.17	0.47±0.01	0.12
C22:6n-3	11.01±0.72	9.96±0.15	0.76	10.15±0.35	9.4±0.14	1.11

Date	5-2-2021	5-2-2021	5-2-2021	18-3-2021	18-3-2021	18-3-2021	19-4-2021	19-4-2021	19-4-2021
Species	C. scutifer	E. graciloides	POM	C.scutifer	E. graciloides	POM	Cyclops	E. graciloides	POM
Sub samples	3	3	2	3	3	2	3	3	2
Total_lipids	610.18±24.49	561.94±20.22	NaN±NaN	571.92±24.38	467.77±8	NaN±NaN	442.46±34.03	420.4±32.79	NaN±NaN
C14:0	10.44±0.74	12.3±0.12	4.3±0.75	10.6±0.56	11.76±0.35	3.52±0.03	10.15±0.31	11.05±0.12	6.73±5.61
iso-15:0	1.47±0.1	1.37±0.04	1.93±0.72	1.51±0.09	1.48±0.04	1.86±0.3	1.58±0.02	1.52±0.03	1.42±0.14
anteiso-15:0	0.86±0.05	0.82±0.01	0.79±0.13	0.88±0.04	0.89±0.01	0.67±0.07	0.88±0.03	0.91±0.01	0.63±0.19
C14:1n-5	0.1±0	0.07±0.01	0.07±0.09	0.11±0.01	0.08±0	0.06±0.09	0.09±0.02	0.08±0	0.11±0.07
C15:0	0.84±0.04	0.64±0	1.22±0.16	0.89±0.02	0.66±0	1.27±0.01	0.91±0.02	0.68±0.02	0.48±0.13
iso-16:0	0.63±0.03	0.53±0.01	0.22±0.02	0.83±0.09	0.62±0.04	0.39±0.09	0.81±0.1	0.64±0.02	0.31±0.16
C15:1n-5	0.01±0.02	n.d.	n.d.	0.01±0.02	n.d.	n.d.	0.02±0.01	0.01±0	0.09±0.12
C16:0	14.94±1.11	13.76±0.21	25.78±0.89	15.51±0.92	14.52±0.51	23.34±3.97	15.54±0.37	15.07±0.47	17.96±3.05
iso-17:0	0.34±0.04	0.31±0.02	1.57±1.04	0.35±0.03	0.37±0	1.03±0.01	0.38±0.01	0.38±0	0.67±0.6
C16:1n-9	0.55±0.09	0.39±0.02	1.82±0.39	0.55±0.08	0.4±0.04	1.43±0.08	0.59±0.07	0.45±0.04	0.54±0.23
C16:1n-7	4.28±0.32	4.81±0.06	8.39±1.76	4.45±0.29	5.12±0.05	4.1±0.98	4.76±0.16	5.2±0.06	4.39±0.38
C17:0	0.42±0.04	0.36±0.02	0.57±0.05	0.42±0.03	0.41±0.01	0.67±0.03	0.44±0	0.44±0	0.35±0.08
9,10D16	n.d.	0.01±0.02	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
C17:1n-7	0.03±0.02	0.03±0	n.d.	0.04±0.03	0.03±0.01	n.d.	0.04±0	0.03±0	0.08±0.11
C18:0	7.31±3.3	3.64±0.82	24.27±3	7.05±3.06	3.82±1	24.26±9.96	4.97±0.86	3.68±0.56	25.66±28.86
C18:1n-9trans	0.17±0.04	0.14±0.02	0.11±0.16	0.17±0.01	0.16±0.01	0.8±0.68	0.18±0.01	0.18±0.01	0.16±0.05
C18:1n-12	n.d.	0.01±0.02	0.58±0.37	0.03±0.05	0.02±0.02	0.41±0.57	0.02±0.02	0.03±0.03	0.18±0.25
C18:1n-9cis	3.57±0.31	5.19±0.18	3.34±0.76	3.79±0.23	5.69±0.12	11.07±5.73	4.03±0.1	5.77±0.13	4.37±1.97
C18:1n-7	1.91±0.06	1.67±0.03	1.34±0.25	1.92±0.12	1.82±0.06	1.49±0.33	2.06±0.03	1.93±0	0.78±1.09
C18:1n-6	0.09±0.01	0.05±0	0.66±0.93	0.1±0.01	0.05±0	n.d.	0.11±0.01	0.06±0.01	0.21±0.29
C19:0	0.42±0.03	0.26±0	0.73±0.22	0.3±0.19	0.22±0.01	0.7±0.12	0.44±0.04	0.24±0.02	0.59±0.07
C18:2n-6trans	0.01±0.02	0.01±0.01	n.d.	0.01±0.01	0±0.01	0.18±0.25	0.02±0.01	0±0.01	n.d.
9,10D18	0.07±0.01	0.11±0	n.d.	0.07±0.01	0.1±0	0±0	0.07±0	0.09±0	0.09±0.12

C18:2n-6cis (LIN)	4.22±0.3	6.04±0.17	1.78±0.26	4.41±0.26	6.68±0.06	8.72±5.91	4.53±0.12	6.9±0.1	3.77±3.37
C20:0	0.56±0.09	0.44±0.01	0.67±0.1	0.55±0.08	0.46±0.02	0.9±0.05	0.5±0.01	0.42±0.01	0.42±0.14
C18:3n-6	0.28±0.03	0.64±0.01	0.22±0.01	0.28±0.01	0.65±0.01	0.07±0.09	0.29±0.01	0.63±0.01	0.32±0.27
C20:1n-9	n.d.	n.d.	2.77±0.2	n.d.	n.d.	2.28±0.19	n.d.	n.d.	1.61±2.27
C18:3n-3 (ALA)	6.91±0.65	9.55±0.13	n.d.	7.07±0.54	9.91±0.14	0.03±0.04	7.23±0.04	10.02±0.22	4.71±6.66
C21:0	0.06±0.01	0.03±0.01	n.d.	0.07±0	0.03±0	0.07±0.1	0.09±0.01	0.04±0	n.d.
C18:4n-3	9.18±0.58	15.4±0.33	3.17±0.02	8.75±0.4	13.59±0.13	2.95±1.31	8.47±0.15	12.47±0.24	8.62±7.33
C20:2n-6	0.57±0.04	0.47±0.01	n.d.	0.59±0.04	0.51±0.01	0.25±0.1	0.63±0.03	0.51±0.01	0.27±0.23
C22:0	0.27±0.02	0.24±0.01	0.75±0.23	0.28±0.03	0.27±0.01	0.45±0.63	0.27±0.01	0.28±0.01	0.27±0.1
C20:3n-6	0.22±0.01	0.07±0	3.09±0.26	0.21±0.01	0.08±0	0.37±0.52	0.22±0	0.08±0	0.36±0.37
C22:1n-9	0.74±0.02	0.06±0	n.d.	0.71±0.04	0.07±0	0.03±0.04	0.74±0.03	0.06±0	0.06±0.01
C20:3n-3	0.22±0.01	0.14±0	4.78±2.8	0.21±0.03	0.15±0	2.81±0.61	0.23±0.02	0.15±0.01	1.89±2.52
C20:4n-6	1.82±0.18	2.14±0.11	n.d.	1.8±0.19	1.78±1.2	n.d.	1.91±0.08	2.44±0.08	0.85±1.21
C23:0	0.04±0.05	0.04±0.01	n.d.	0.04±0.04	0.02±0.03	0.09±0.13	0.19±0.11	0.07±0.02	0.19±0.27
C20:4n-3	4.81±0.13	0.52±0.03	n.d.	4.45±0.27	0.57±0.01	n.d.	4.56±0.09	0.51±0.02	0.23±0.19
C22:2n-6	0.1±0	0.04±0	n.d.	0.09±0	0.05±0	0.07±0.1	0.1±0.01	0.05±0	0.13±0.18
C24:0	0.12±0.03	0.07±0	0.67±0.12	0.13±0.01	0.08±0	0.9±0.1	0.13±0.01	0.09±0	0.16±0.14
C20:5n-3	7.99±0.39	7.73±0.16	2.85±0.46	7.89±0.47	7.45±0.11	1.68±0.19	8.31±0.24	7.43±0.1	4.51±3.56
C24:1n-9	0.75±0.05	0.55±0.02	n.d.	0.78±0.04	0.67±0.01	n.d.	0.87±0.04	0.73±0.01	0.3±0.42
C22:3n-3	0.29±0.02	0.15±0	n.d.	0.26±0.02	0.16±0	n.d.	0.29±0.02	0.15±0.01	0.1±0.01
C22:4n-6	n.d.	n.d.	n.d.	0.02±0.03	n.d.	n.d.	n.d.	n.d.	n.d.
C22:5n-3	2.39±0.11	0.43±0.01	0.17±0.07	2.18±0.12	0.43±0.01	0.03±0.05	2.19±0.07	0.38±0.02	0.21±0.13
C22:6n-3	10.03±0.71	8.75±0.24	1.39±0.25	9.62±0.67	8.16±0.05	1.04±0.38	10.18±0.37	8.18±0.21	5.26±5.16

Date	4-5-2021	4-5-2021	4-5-2021	19-5-2021	19-5-2021	19-5-2021	8-6-2021	8-6-2021	8-6-2021	30-6-2021
Species	C. scutifer	E. graciloides	POM	C. scutifer	E. graciloides	POM	C. scutifer	E. graciloides	POM	POM
Sub samples	3	3	2	3	3	1	3	3	2	1
Total_lipids	423.93±23.03	382.73±15.75	NaN±NaN	413.45±28.07	382.33±21.21	NaN±NaN	317.8±31.8	384.16±11.33	NaN±NaN	NaN±NaN
C14:0	10.29±0.22	10.84±0.12	4.46±0.54	9.68±0.24	9.31±0.85	5.75±3.43	9.02±0.78	10.63±0.45	8.08±0.14	10.38
iso-15:0	1.7±0.04	1.61±0.07	1.45±0.13	1.71±0.19	1.55±0.1	1.2±0.69	1.79±0.43	1.34±0.17	1.03±0.18	1.37
anteiso-15:0	0.9±0.02	0.93±0.02	0.43±0.12	0.84±0.04	0.85±0	0.4±0.18	0.77±0.03	0.76±0.01	0.82±0.32	0.73
C14:1n-5	0.09±0.01	0.08±0	0.04±0.05	0.09±0.01	0.06±0.01	0.11±0.04	0.08±0.01	0.06±0	0.13±0.01	0.2
C15:0	0.87±0.03	0.68±0.01	0.51±0.23	0.89±0.03	0.67±0.01	0.48±0.1	0.7±0.05	0.6±0.03	1.06±0.59	0.75
iso-16:0	0.84±0.17	0.65±0.02	0.1±0.14	0.87±0.1	0.52±0.12	0.08±0.11	0.6±0.05	0.47±0.08	0.25±0.08	0.17
C15:1n-5	0.02±0.02	n.d.	n.d.	0.01±0.03	n.d.	n.d.	0.05±0.04	0.11±0.09	n.d.	n.d.
C16:0	15.86±0.47	15.07±0.3	19.43±0.07	17.06±0.79	15.5±0.33	19.43±2.85	18.54±2.36	14.79±1.22	18.95±2.05	22.07
iso-17:0	0.38±0.02	0.38±0	0.89±0.14	0.36±0.03	0.36±0.01	0.8±0.22	0.27±0.04	0.26±0.02	0.62±0.15	0.76
C16:1n-9	0.62±0.11	0.43±0.05	0.66±0.17	0.77±0.25	0.5±0.14	0.67±0.12	1.1±0.56	0.51±0.16	2.23±1.76	0.64
C16:1n-7	4.85±0.2	5.28±0.07	5.24±1.6	4.89±0.05	5.3±0.2	5.8±0.95	4.18±0.75	4.7±0.14	7.15±0.45	11.84
C17:0	0.44±0.01	0.43±0.02	0.44±0.03	0.46±0.03	0.47±0.01	0.43±0.15	0.43±0.01	0.4±0.03	0.47±0.2	0.31
9,10D16	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	0.17±0.24	n.d.
C17:1n-7	0.04±0.01	0.02±0	0±0	0.05±0.02	0.03±0.03	0±0	0.25±0.26	0.12±0.07	n.d.	n.d.
C18:0	5.27±0.92	3.66±0.47	34.94±0.63	6.49±1.19	4.19±0.75	33.06±17.7	8.24±3.08	4.06±1.15	17.68±6.26	11.43
C18:1n-9trans	0.18±0.01	0.18±0.02	n.d.	0.22±0.01	0.18±0.02	0.08±0.11	0.17±0.05	0.13±0.02	0.12±0.07	0.12
C18:1n-12	0.01±0.01	0.03±0.03	n.d.	n.d.	0.06±0.05	0.08±0.11	0.09±0.07	0.01±0.02	0.76±1.08	n.d.
C18:1n-9cis	4.09±0.18	5.81±0.09	2.92±0.5	4.04±0.13	5.85±0.2	3.24±1.12	4.28±0.5	5.81±0.44	7.19±1.62	7
C18:1n-7	2.09±0.03	1.99±0.04	1.25±0.21	1.98±0.25	1.95±0.1	1.18±0.24	1.74±0.33	1.62±0.19	1.39±0.12	1.58

C18:1n-6	0.1±0.01	0.07±0.02	0±0	0.14±0.07	0.14±0.08	0.61±0.87	0.8±0.64	0.28±0.19	0.3±0.43	0.85
C19:0	0.43±0.04	0.25±0.03	0.62±0.12	0.57±0.15	0.28±0.05	0.63±0.19	0.81±0.29	0.46±0.1	0.67±0.02	0.87
C18:2n-6trans	0.01±0.01	0.01±0.01	n.d.	0.01±0.02	0.01±0.01	n.d.	n.d.	n.d.	0.12±0.17	n.d.
9,10D18	0.08±0.01	0.1±0.01	n.d.	0.11±0.02	0.12±0.01	n.d.	0.11±0.02	0.16±0.01	n.d.	n.d.
C18:2n-6cis (LIN)	4.45±0.14	6.95±0.09	1.91±0.69	4.39±0.13	6.77±0.24	2.11±0.72	4.04±0.59	6.1±0.32	4.51±0.06	4.19
C20:0	0.51±0.01	0.4±0.02	0.49±0.07	0.55±0.01	0.4±0.02	0.47±0.03	0.45±0.01	0.3±0.02	0.45±0.04	0.44
C18:3n-6	0.29±0.01	0.64±0.02	0.22±0.04	0.29±0.01	0.61±0.02	0.27±0.12	0.25±0.04	0.52±0.02	0.31±0	0.42
C20:1n-9	0±0	0±0	2.83±0.87	0±0	0±0	3.53±1.03	0±0	0±0	5.6±0.73	6.03
C18:3n-3 (ALA)	7.18±0.18	9.98±0.14	n.d.	6.85±0.47	9.68±0.07	n.d.	6.92±0.25	9.48±0.25	n.d.	n.d.
C21:0	0.09±0.01	0.04±0.01	n.d.	0.07±0.06	0.03±0.01	n.d.	0.06±0.01	0.02±0.03	n.d.	n.d.
C18:4n-3	7.91±0.27	11.83±0.26	6.46±0.6	6.98±0.38	11.76±0.16	6.21±1.9	6.53±1.04	14.07±0.61	8.35±1.2	6.86
C20:2n-6	0.63±0.03	0.52±0.01	0.06±0.09	0.62±0.03	0.52±0.03	0.03±0.04	0.5±0.09	0.44±0.03	0.06±0.08	n.d.
C22:0	0.27±0	0.27±0	3.18±4.5	0.28±0.02	0.28±0.01	1.9±2.46	0.24±0.02	0.2±0.01	0.17±0.24	0.21
C20:3n-6	0.22±0	0.11±0.03	0.38±0.54	0.24±0.03	0.08±0	0.57±0.16	0.18±0.02	0.09±0.02	0.13±0.18	0.39
C22:1n-9	0.72±0.05	0.08±0.01	n.d.	0.69±0.07	0.06±0.01	0±0	0.59±0.13	0.04±0.01	0.02±0.02	n.d.
C20:3n-3	0.23±0.01	0.14±0	3.27±0.47	0.29±0.03	0.14±0.01	3.21±1.62	0.27±0.02	0.13±0.02	2.17±0.26	2.57
C20:4n-6	1.88±0.1	2.52±0.03	n.d.	1.73±0.06	2.53±0.15	n.d.	1.33±0.38	2.02±0.18	n.d.	n.d.
C23:0	0.28±0.19	0.08±0.11	n.d.	0.46±0.37	0.19±0.16	n.d.	0.62±0.54	0.26±0.2	0.06±0.08	n.d.
C20:4n-3	4.35±0.18	0.56±0	0.18±0.25	3.9±0.26	0.5±0.03	0.06±0.09	2.74±0.55	0.41±0.03	0.23±0.02	n.d.
C22:2n-6	0.1±0.01	0.05±0	n.d.	0.12±0	0.05±0.01	n.d.	0.1±0.02	0.02±0.03	0.03±0	n.d.
C24:0	0.13±0.01	0.1±0.01	0.3±0.15	0.15±0.02	0.1±0.01	0.26±0.02	0.13±0.02	0.06±0.01	0.51±0.23	0.32
C20:5n-3	8.33±0.23	7.55±0.21	2.98±1.08	8.08±0.22	7.95±0.33	3.11±0.57	7.78±1.24	7.66±0.48	4.1±0.54	4.1
C24:1n-9	0.87±0.05	0.77±0.03	n.d.	0.96±0.09	0.75±0.05	n.d.	0.94±0.17	0.65±0.05	n.d.	n.d.
C22:3n-3	0.27±0.01	0.15±0.01	n.d.	0.25±0.05	0.14±0.01	n.d.	0.17±0.03	0.11±0.03	n.d.	n.d.
C22:4n-6	n.d.	n.d.	n.d.	n.d.	0.01±0.01	n.d.	0.03±0.02	n.d.	0.02±0.03	n.d.
C22:5n-3	1.98±0.14	0.43±0.01	0.17±0.05	1.85±0.15	0.36±0.02	0.04±0.06	1.31±0.27	0.33±0.02	0.16±0.01	0.14
C22:6n-3	10.17±0.28	8.3±0.36	4.18±1.28	10±0.68	9.15±0.34	4.23±2.63	10.81±1.5	9.8±0.78	3.93±0.52	3.24