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# Content, composition, and transfer of polyunsaturated fatty acids in an Arctic lake food web

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**Abstract.** Freshwater fish production depends on the production and use of polyunsaturated fatty acids (n-3 and n-6 PUFA) from lower trophic levels. Here, we aimed to identify the main trophic pathways that support PUFA content in different fish species (mean 39.7 mg/g dry weight) used in the subsistence fishery of the Inuit community in Greiner Lake near Cambridge Bay (Nunavut, Canada). We used stable isotope and taxon-specific PUFA stocks, to show that the lake food web was divided into distinctive pelagic and littoral benthic food webs and that different fish species obtained their PUFA from different sources within those food webs. The most concentrated fish in n-3 PUFA was Arctic char (*Salvelinus alpinus*) that obtained nutritionally valuable PUFA compounds by feeding on pelagic zooplankton rich in the essential fatty acids EPA and DHA and on littoral prey with lower PUFA content. The pelagic consumer, lake whitefish (*Coregonus clupeaformis*), that fed on mysids and zooplankton was also rich in n-3 PUFA. The least concentrated in n-3 PUFA was lake trout (*Salvelinus namaycush*) that obtained PUFA from low n-3 PUFA sticklebacks (*Pungitius pungitius*) and macroinvertebrates and from n-3 PUFA-rich littoral mysids. The benthic PUFA were entirely made of n-6 fatty acids and no n-3 PUFA were detected. We further quantified that from the mean daily phytoplankton production of 319 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$, 2.9% was assimilated by zooplankton (9.4 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$) and thereby made available to pelagic fish. The food webs to which fish belonged were supported by PUFA produced in the pelagic and benthic zones but likely complemented by inputs from the watershed. The description of the main PUFA pathways of the Greiner Lake food webs explains for the first time the trophic interactions and underlying mechanisms responsible for the health of the fish community in a high-Arctic lake.

**Key words:** benthic invertebrates; fish; high Arctic; littoral; mysids; omega-3; omega-6; pelagic; PUFA; stable isotopes; trophic structure; zooplankton.

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## Introduction

Canadian Arctic lakes harbor simple and short food webs with few apex predators that include one or a combination of Arctic char (*Salvelinus alpinus*), lake trout (*Salvelinus namaycush*), or lake whitefish (*Coregonus cupleaformis*) (Power et al. 2008). PUFA are important for northern aquatic taxa as energy reserves (Grosbois et al. 2017*b*, Schneider et al. 2017) because they modify cell membrane fluidity (Hazel 1984, Tocher 2003), which is related to better survival in cold environments (Kelly and Kohler 1999). Recently, Gladyshev et al. (2018) demonstrated that high contents of specific PUFA, that is, eicosapentaenoic acid (EPA; 20:5n-3) and docosahexaenoic acid (DHA; 22:6n-3) in fish muscle were associated with important physiological adaptations like swim speed capabilities. Heterotrophs, including fish, are not able to efficiently synthesize α-linolenic acid (ALA; 18:3n-3) and linoleic acid (LA; 18:2n-6) that are the precursors of these physiologically essential n-3 (EPA and DHA, Taipale et al. 2019) and n-6 (arachidonic acid (ARA; 20:4n-6; Arts et al. 2009) PUFA. However, some lineages of fish and marine invertebrates have the ability to synthesize DHA from shorter chained FA, especially in DHA-deficient environments (Kabeya et al. 2018, Ishikawa et al. 2019). While the importance of specific PUFA (EPA and DHA) for fish and humans is recognized, the trophic pathways moving PUFA from the organisms that produce them to consumers that must acquire them through diet is complex and only partially documented (Strandberg et al. 2015, Keva et al. 2019, Thomas et al. 2019). The description of such pathways is necessary for identifying the Arctic taxa responsible for providing the essential ecosystem services represented by PUFA.

PUFA are mainly synthesized by photosynthetic primary producers such as omega-3 ALA and omega-6 LA. Some PUFA, like EPA and DHA, are considered physiologically essential fatty acids (Ruess and Müller-Navarra 2019). Heterotrophic consumers must ingest them to maintain good growth, reproduction, and immune system function as the ratio of bioconversion from ALA and LA is low compared to the more efficient assimilation from diet (Bell and Tocher 2009, Arbex et al. 2015). In lakes, EPA is particularly important for cladoceran growth (Muller-Navarra et al. 2000) and DHA for copepod and fish reproduction (Jónasdóttir 1994, Sargent et al. 1999). Stearidonic acid (SDA, 18:4n-3) is an intermediate molecule in the bioconversion of ALA to EPA and is therefore also important for consumer assimilation (Guil-Guerrero 2007). Major variations in FA composition exist among different algal taxa (Taipale et al. 2013, Strandberg et al. 2015) and the n-3 PUFA, including EPA, DHA, and SDA, are all primarily produced by different algae taxa. As a result, algae such as cryptophytes, diatoms, dinoflagellates are considered high-quality food sources for herbivorous consumers (Taipale et al. 2013, Galloway et al. 2014).

Terrestrial primary producers represent another important carbon source for many freshwater and coastal aquatic systems (Grosbois et al. 2017*a*, Tanentzap et al. 2017). Vascular plants can synthesize the LA and ALA de novo, but do not have the capacity to synthesize EPA or DHA and for food webs are considered poorer sources of essential fatty acids than aquatic primary producers (Alonso and Maroto 2000, Wallis et al. 2002). Moreover, the high levels of recalcitrant lignin and long-chain saturated fatty acids (LC-SAFA) in terrestrial organic matter (Lynd et al. 2002, Taipale et al. 2015*a*) exported from terrestrial biomes to aquatic environments make this export poor in terms of total lipids and n-3 PUFA. Long-chain SAFA can thus be used as biomarkers to trace terrestrial fatty acid consumption by aquatic consumers (Taipale et al. 2015*b*) along with other fatty acid biomarkers such as C18:1n-9 that are commonly found in live terrestrial leaf matter (Torres-Ruiz and Wehr 2010). While terrestrial organic carbon is considered a low-quality food source when compared to eukaryotic phytoplankton (Taipale et al. 2014), climate-driven permafrost thaw is expected to increase its quantity and availability in freshwater food webs (Wauthy et al. 2018) and to initiate a shift from a primary production based food web to a food web based on heterotrophic bacteria production reliant on terrestrial carbon (Forsström et al. 2013, Mariash et al. 2018). As heterotrophic bacteria in freshwater ecosystems are considered devoid of n-3 and n-6 PUFA (Zelles 1999, Wenzel et al. 2012, Taipale et al. 2014), the increasing organic carbon inputs from thawing permafrost may have severe consequences for the synthesis and transfer of PUFA in

Arctic freshwater food webs that will impact the growth and health of resident aquatic organisms. Increased turbidity with permafrost thaw may also reduce water clarity resulting in reductions in primary production.

To estimate the transfer of PUFA from primary producers to fish, the estimation of production rates at all lower trophic levels is required. Knowing the rate of primary production allows for estimates of PUFA synthesis and availability to the rest of the lake food web. While photosynthetic organisms in Arctic lakes include pelagic and benthic cyanobacteria, eukaryotic algae, and ciliated protists (Bonilla et al. 2009, Ayala-Borda et al. 2021), only eukaryotic algae have been found to produce essential PUFA (Bell and Tocher 2009). In many Arctic water bodies, they are most abundant in benthic microbial mats due to the combination of high water transparency, low nutrient concentration in water, and nutrient access in sediments that benefit benthic primary production and undermine pelagic primary production (Vadeboncoeur et al. 2003, Karlsson et al. 2009). Although heterotrophic bacteria may use PUFA to build lipidic membranes (Russell and Nichols 1999), they do not store lipids (e.g., triacylglycerols) like eukaryotes cells, which results in low or no PUFA content in newly produced bacterial biomasses (Taipale et al. 2014). Nevertheless, heterotrophic bacteria still play an essential role in making terrestrial carbon available to the higher food web (Guillemette et al. 2016). Zooplankton production is a critical measure of ecosystem function as it contributes to determining the amount of energy and organic matter, including PUFA, made available to fish (Blanchard et al. 2012). Zooplankton production is rarely estimated in aquatic ecosystems as traditional methods are fastidious and time-consuming (Yebra et al. 2017). New enzymatic methods, however, have made zooplankton production measures accessible (Sastri and Dower 2006, Sastri et al. 2013) and allow for more accurate estimation of PUFA transfer along the food web.

The objective of this study was to investigate the content, composition, and transfer of PUFA in a high-Arctic lake food web from pelagic and littoral (benthic) algal producers to fish via zooplankton and benthic macroinvertebrates during the time of warmest lake temperatures (about 10°C) in early August. The chosen period occurs in the mid-point of three-month open-water period and was assumed to co-occur with the peak summer production period. Another objective was to provide baseline data on the uptake of terrestrial fatty acids in an Arctic aquatic food web prior to the predicted increasing Arctic permafrost thaw expected to result in increased concentrations of these compounds in the organic diet pool sustaining aquatic production (Wauthy et al. 2018, Grosbois et al. 2020). The study was carried out in Greiner Lake, located approximately 5 km from the Inuit community of Cambridge Bay. The lake provides important ecosystem services to the local Inuit community, including a subsistence fishery and drinkable freshwater. Fish are an important part of the traditional Inuit diet (Stewart 2005, Tian et al. 2011), providing both essential sources of proteins and the nutrients necessary for good health, such as vitamin D and polyunsaturated fatty acids (n-3 and n-6 PUFA) (Kuhnlein et al. 2006, Bendik et al. 2014, Deckelbaum and Calder 2015). The high fish production capabilities of the lake and of the region have been known for a long time and are reflected in the Inuinnaqtun (local Inuit language) name "*Ekaluktutiak*" for Cambridge Bay which translates as "a good fishing place." As whole-lake production of new biomass in Arctic lakes is usually dominated by benthic sources (Ask et al. 2009), we hypothesized that benthic algae would be an important source of PUFA (including EPA and DHA), which in turn would be made available to fish via their feeding on benthic macroinvertebrates. Further, we hypothesized that fish feeding on benthic prey would contain higher levels of PUFA, EPA, and DHA than fish feeding primarily on zooplankton. The estimated trophic stocks and pathways of essential fatty acids passing from pelagic and benthic primary producers through invertebrate consumers to fish were based on a combination of methods including stable isotope and fatty acid analyses, and taxon-specific production estimation techniques.

## Methods

### *Study site*

Greiner Lake (69°10′35.72″N, 104°55′54.87″W) has a surface area of 41.2 $km^2$ and lies on a recently deglaciated high-Arctic landscape near

Cambridge Bay, Nunavut, Canada (Fig. 1). The soil of the area is characterized by a continuous permafrost layer (Zhang et al. 2008) covered by one of two tundra types: a dry tundra with patchy vegetation composed of dominant prostrate shrubs (<5 cm tall, e.g., *Dryas* and *Salix arctica*) graminoids, forbs, and lichens, and a moist tundra dominated by sedges and dwarf shrubs (<40 cm tall) with a well-developed moss layer and barren patches (Team et al. 2003). Greiner Lake is relatively shallow with a maximum depth of 12 m and an average depth of 5 m (Johnson 1962). There are 6296 lakes and ponds within its watershed and Greiner Lake discharges to the Dease Strait via its main outlet, Freshwater Creek. Historically, the open-water season began at the end of July and ended in mid-September (Johnson 1962). Recent observations (2016–2019) indicate that the open-water period can vary considerably from year to year and has increased, with ice now disappearing totally by mid-July and reforming in mid-September to early October (J. Wagner, Polar Knowledge Canada, Cambridge Bay, *personal communication*). The ice can form to a thickness of >2 meters (2.15 m in June 2015). Maximum water temperatures in this cold monomictic lake are about 10°C as recorded for 3–4 weeks between end of July and mid-August (see Appendix S1: Figs. S1, S2). Greiner Lake shows characteristics typical of an oligotrophic Arctic freshwater lake, with an August chlorophyll *a* concentration of 2.6 ± 0.3 µg/L, total nitrogen concentration of 467.7 µg/L, total phosphorous about 6.6 ± 1.0 µg/L and dissolved organic carbon of 4.5 ± 0.8 mg/L. The lake sits on limestone bedrock and has a pH of 7.9 ± 0.1 and Secchi depth of 3.7 ± 0.2 m. Reported background physico-biochemical data are means ± SE for early August measurements from 2017, 2018, and 2019.

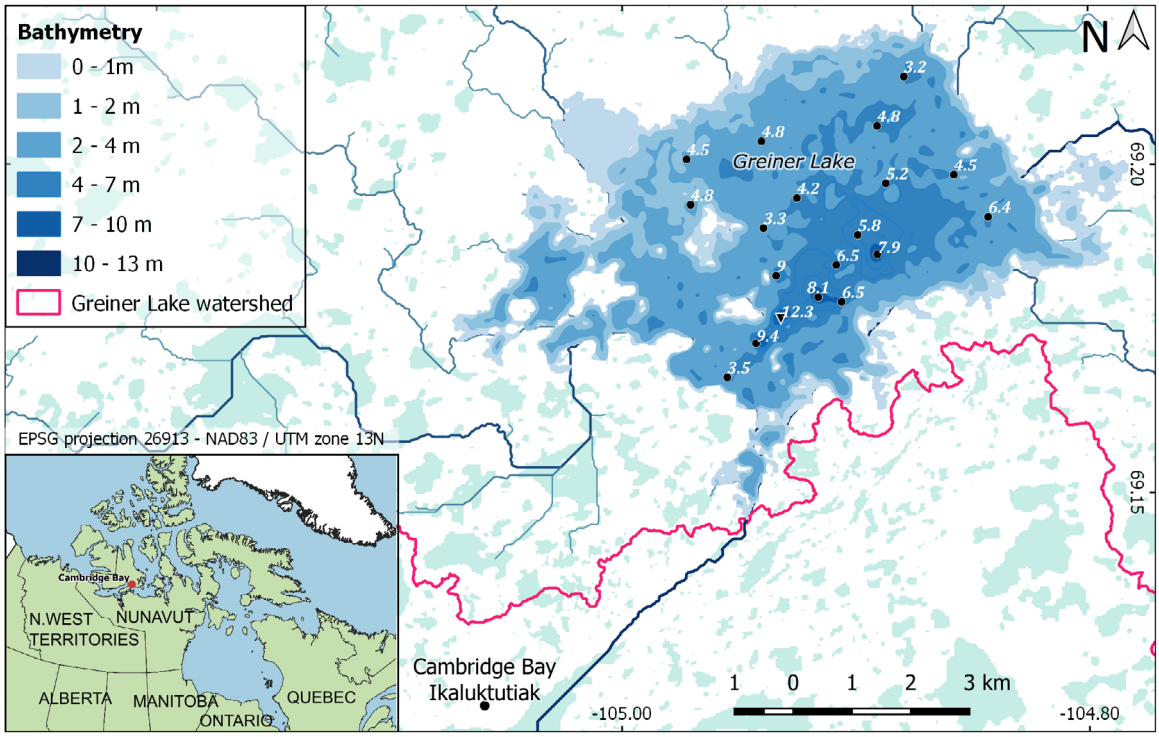


Fig. 1. Map of Greiner Lake near Cambridge Bay (Nunavut, Canada). The bathymetry is based on depth estimations from satellite imaginary (Ponomarenko et al. 2019), spot measures from Johnson (1962), and our echosounder transects and other depth measures collected in 2018 and 2019. The black dot represents the deepest site measured (12.3 m). Littoral zone (0–2 m) makes 39% of the total lake area.

In the absence of vascular plants in the inshore zone and the presence of photosynthetically available radiation (PAR, 400–700 nm) in deep water (euphotic zone 9.9 m), it is not meaningful to use the traditional southern latitude definition of the littoral zone as the lake area where at least 1% of incoming PAR reaches the bottom and allows macrophytes to grow (Peters and Lodge 2009). Here, we follow the definition from Bégin et al. (2021) who showed how the ice boundary between littoral and pelagic had a structural impact on communities. In Greiner Lake, shallow waters to 2 m depth freeze to the sediments in winter and are characterized by rocks and boulders covered with an approximately 0.5 cm thick layer of coherent benthic microbial mats. The softer sediments that dominate the deeper parts of the lake are mostly absent from this littoral zone due to ice scouring that removes them. Using the 2 m depth contour, the littoral zone accounts for 39% of the lake area (Fig. 1). All samplings were completed during the first two weeks of August. Stable isotope samples and fatty acids for macroinvertebrates and terrestrial plants were obtained in 2017 while the rest of the fatty acid samples were collected in 2018. Pelagic primary production was measured in 2017 and 2018, benthic primary production in 2017, and zooplankton production in 2017, 2018, and 2019. During sampling, water temperatures varied between 9.4 and 12.3°C (2017–2019) and the lake was entirely mixed as a combination of shallow depths, cold air temperatures, and constant wind prevents thermal stratification during the short open-water season.

### *Pelagic sampling*

Lake water was collected with a 2-L Limnos sampler (Limnos, Turku, Finland) from the surface (0 m) and at depths of 4 and 8 m from the deepest point of the lake and mixed to provide one integrated sample of the water column. Aliquots of water (each about 1000 mL) were then filtered on pre-combusted and pre-weighed GF/F filters, and the resulting seston samples were stored at −20°C for one week until freeze-drying for weight and fatty acid analyses.

Zooplankton (bulk community) were collected from the deepest point of the lake with a zooplankton net (30 cm diameter, 500 μm) towed vertically from about 8 m to the surface for stable isotope and fatty acid analyses. A 20 L sample representing the integrated lake water column (0–8 m) was sieved (50 μm), and the collected individuals were identified with an inverted microscope (Axio Observer A1, Zeiss, Jena, Germany, x50-100) using Utermöhl chambers. Individuals were measured with an optical camera (AxioCam ERC 5S; Zeiss) coupled to microscope software (AxioVision; Zeiss). The zooplankton community was dominated by *Leptodiaptomus sicilis* (41% of the zooplankton biomass), *Limnocalanus macrurus* (34%), the *Daphnia pulex* species complex (21%), and *Cyclops scutifer* (4%).

The fish community was composed of Arctic char *(Salvelinus alpinus)*, lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), least cisco (*Coregonus sardinella*), and nine-spined sticklebacks (*Pungitius pungitius*). The Arctic char in this study were considered lake resident based on coloring and given that the sampling took place before the return of the anadromous fish to the lake in late August and September. Lacustrine status was confirmed by referencing $\delta^{13}C$ values (see Trophic structure of the Greiner Lake food web section) to the range of $\delta^{13}C$ values reported for lacustrine Arctic char across the Canadian Arctic (e.g., Gantner et al. 2010, van der Velden et al. 2013). Fish were sampled at multiple sites using multi-mesh (12–140 mm bar mesh) monofilament sinking benthic gillnets set in 0–5 m depths for 12-h overnight sets. Captured fish were measured (fork length, mm) and weighed (g) before examination of stomach contents. A piece of white dorsal muscle tissue was sampled from each individual posterior to the dorsal fin and above the lateral line for stable isotope and fatty acid analyses and immediately frozen, first at −20°C for some days when in the North and thereafter at −80°C. The stomach was removed and contents determined (Hyslop 1980), with diet composition (%) calculated based on the presence/absence of prey in the non-empty fish stomachs.

### *Benthic, littoral, and watershed sampling*

Benthic microbial mats were collected from stones in the littoral zone at a depth of 0.5 m. Stones were gently scraped over a standard area (0.79 $cm^2$) with an electronic toothbrush ($d$ = 10 mm), and collected material was frozen in plastic tubes and later analyzed for dry

weight, stable isotope, and fatty acid composition ($n$ = 3 replicates per analyses).

The littoral zoobenthos was dominated by tadpole shrimps (*Lepidurus arcticus*), opossum shrimps (mysids), amphipods (gammarids), oligochaetes, chironomids, and water mites. They and littoral mysids were collected with a dip net from the littoral zone, and individuals were either directly sorted in the field or within 3 h after returning to the lab. Nine-spine sticklebacks were collected in the littoral zone using an electro-fisher (Smith-Root, LR-24; Smith-Root, Vancouver, Washington, USA) and dipnets.

To investigate terrestrial carbon and terrestrial PUFA sources, soils, plants (sedge, shrub, moss), and bird (largely goose) feces were collected for stable isotope analysis as potential terrestrial inputs from the surrounding landscape. Only plants were analyzed for fatty acid content as other terrestrial samples were assumed not to be a significant source of fatty acids for the aquatic food web, that is, bird feces were very degraded, soil is very poor in fatty acid content, and moss were very scarce on the watershed. In the laboratory, all food web samples were kept frozen until freeze-dried for stable isotope and fatty acid analyses.

### *Stable isotope and fatty acid analyses*

Biological samples for stable isotope analyses were freeze-dried, ground, and encapsulated in tin cups prior to being analyzed at the NHRC stable isotope laboratory in Saskatoon. Samples were combusted to $N_2$ and $CO_2$ for stable isotope analyses with a Carlo Erba NA1500 elemental analyzer prior to introduction to an Elementar (Elementar GmBH, Langenselbold, Germany) Isoprime IRMS via an open split. Calibrated in-house reference materials BWBIII and PRCGel (BWB III: $\delta^{13}C = -20.0‰$, $\delta^{15}N = -14.1‰$ and PRCGel: $\delta^{13}C = -13.6‰$, $\delta^{15}N = -4.7‰$) were used to normalize results to VPDB (Craig 1957) and atmospheric nitrogen (Mariotti 1983) for carbon and nitrogen stable isotopes, respectively. Precisions (1σ) for both $\delta^{13}C$ and $\delta^{15}N$ values were based on replicates of in-house references and samples and were ±0.1‰ for both C and N.

Freeze-dried biological samples were run for fatty acid analyses. Fatty acids were extracted and methylated using methods developed in our laboratory, modified from Grosbois et al. (2017*b*). First, a mixture of methanol/toluene and acetyl chloride (4/1/0.125) was added to the samples with internal standard (nonadecanoic acid; C19:0), available from Sigma-Aldrich, Saint-Louis, Michigan, USA, N5252). After centrifugation, they were incubated at 90°C for 20 min. Trans-esterified fatty acids were extracted with hexane and submitted to gas chromatography–mass spectrometry (GC-MS) for identification and quantification using calibration curves. FAME were quantified from the peak area of the most abundant ion out of the four ions recorded ($m/z$ 74, 79, 81, and 87). The chromatographic areas of seven different concentrations of individual fatty acids from a standard mix were measured to obtain standard linear models. Standards included a FAME mix (37 components 10 mg/mL, Supelco, 47885-U), a bacterial acid methyl ester (BAME) mix (Sigma-Aldrich, 47080-U), methyl palmitoleate (Fluka, 76176), trans-11-vaccenic methyl ester (Sigma-Aldrich, 46905-U), methyl stearidonate (Fluka, 43959), and 9(Z)-eicosenoic acid methyl ester (Cedarlane, 20-2001-1). The model coefficient of determination ($r^2$) was >0.99 for each individual standard curve. Fatty acids were quantified using the general expression: $C_x = C_s.\ (A_x/A_s)$ where $C$ refers to the amount of fatty acid, $A$ to the chromatographic area, $x$ to any specific fatty acid, and s to the internal standard such as in Rodríguez-Ruiz et al. (1998) or Levitan et al. (2015). Agilent 7890 A chromatograph (Agilent Technologies, Santa Clara, California, USA) with an Agilent 5975 C mass spectrometer with a triple-axis detector and an Agilent J&W DB-23 column (60 m length, 0.25 mm inner diameter, 0.15 μm film thickness) was used for the measures.

To estimate the phytoplankton $\delta^{13}C$ composition, analyses were carried out on specific algal fatty acids, that is, SDA (18:4n-3), eicosenoic acid (20:1n-9), EPA (20:5n-3), DHA (22:6n-3) (Barberá et al. 2011, Taipale et al. 2015*b*) that were recovered from the bulk seston samples previously analyzed for FA composition (Pace et al. 2007, Berggren et al. 2014). The $\delta^{13}C$ values of algal-specific FAME were calculated as an average of the specific algal fatty acid $\delta^{13}C$ from all seston samples and corrected by the derivatization reagent (methanol) following the formula provided in Bec et al. (2011): $\delta^{13}C\text{-FA} = ((n + 1) \times \delta^{13}C\text{-FAME} - \delta^{13}C\text{-MeOH})/n$, where $\delta^{13}C$-FAME

and $\delta^{13}$C-MeOH are measured $\delta^{13}$C values of fatty acids and methanol during methylation, $\delta^{13}$C-FA is the $\delta^{13}$C value prior to methylation, and $n$ is the number of carbon atoms in the (non-methylated) FA. We assumed a lipid fractionation of 3.8‰ between the FA $\delta^{13}$C values corrected by the derivatization reagent and the $\delta^{13}$C value of algal biomass (Berggren et al. 2014).

*Biomass and production calculations.*—Phytoplankton and benthic algal biomasses were estimated as seston and benthic mat dry weight. Integrated lake water (0–8 m) was filtered on pre-combusted and pre-weighed GF/F filters (1000–2000 ml, three replicates) to collect seston samples. GF/F filters were then freeze-dried and weighted again on a micro-balance (XP26 DeltaRange, Mettler Toledo, Greifensee, Switzerland). Benthic mat samples (three replicates) were collected from littoral zone stones with an electronic toothbrush ($d$ = 10 mm, surface = 0.79 cm$^2$) and freeze-dried before weighing on a micro-balance. The biomass of the zooplankton community was estimated from the identification of species and length-dry weight regressions following Malley (1989), Grosbois and Rautio (2018), and Doubek and Lehman (2011).

To estimate the relative importance of pelagic and benthic primary production supporting the upper food web, primary productivity was estimated as in Rautio and Vincent (2006). In brief, lake water (20 mL, <50 μm to remove potential grazers) and benthic disks of algal mats ($d$ = 10 mm, collected from littoral rocks and placed in 20-mL glass vials with GF/F filtrated lake water) were spiked with 50 μL (pelagic) or 25 μL (benthic) of $^{14}$C-bicarbonate and incubated for 1.5–2 h just below the surface to keep them at lake temperature. Incubation was carried out in a Rae box that applies a gradient of light intensities (100%, 50%, 8%, 3%, 1%, 0% of incident solar radiation) that represent the downward irradiance (E) in water. Total water column phytoplankton productivity (mg C·m$^{-2}$·h$^{-1}$) was estimated from the pelagic photosynthetic rate to irradiance (P-E) curves obtained from the Rae box and applied to the light gradient in the lake, measured with a Li-Cor PAR sensor (LiCOR, Lincoln, Nebraska, USA). Littoral benthic algae productivity was estimated from the benthic P-E curves and applied to surface light irradiance. Daily primary production rates (mg C·m$^{-2}$·d$^{-1}$) were estimated using the photosynthetic rates estimated at the incubation time and the percentage of light received at each hour of the day at the Greiner Lake geographical position. To be able to compare the algal sources available to support the higher trophic levels, the pelagic production rates were calculated to a 5 m deep water column, that is, the mean lake depth while littoral benthic production was calculated to mats at 1 m depth, that is, the mean of depth of the littoral zone. All production was standardized per m$^2$.

The bacterial production rate was measured following the [$^3$H]-leucine incorporation method of Kirchman (1993). Triplicate aliquots of 1.5 mL water samples and two TCA-killed blanks were incubated with 40 nmol/L [$^3$H]-leucine for 3 h at lake temperature. All productivity samples were later mixed with a scintillation cocktail and measured for $^{14}$C or $^3$H activity using a Perkin Elmer scintillation counter. Average blank-corrected rates of leucine uptake were converted to rates of C production assuming the standard conversion factor of 1.55 kg C/mol leu multiplied by an isotopic dilution factor of 2.

The zooplankton production rate was measured following Sastri et al. (2013) from the standing lake activity and the turnover rate of the chitobiase enzyme that molting organisms release in the water. Two replicates of 500 mL lake water were sieved (50 μm) to remove zooplankton that could produce new chitobiase molecules and placed in previously bleached- and acid-washed Nalgene bottles. Bottles were incubated for 6 d and a 20 mL aliquot was collected every 24 h and immediately filtered (<0.2 μm) to prevent any bacterial degradation of the enzyme. Due to the lower temperatures and the slower turnover rate of the chitobiase enzyme in Greiner Lake, the incubation time was extended to 6 d from the 1.5-d experiments used in north temperate lakes by Sastri et al. (2013). Aliquots were kept at 4°C and spectrofluorometric analyses were carried out within 20 d as suggested in St-Gelais et al. (2017). Water from each aliquot was incubated for one hour with methylumbelliferyl-β-d-*N*-acetyl glucosaminide (MBF-NAG) that binds to the chitobiase enzyme. Chitobiase degradation rates were determined with sample fluorescence (excitation: 360 nm; emission: 450 nm) using a Cary Eclipse

fluorescence spectrophotometer (Agilent, Santa Clara, California, USA) against an MBF standard.

### *Statistical analyses*

Multivariate PERMANOVAs were used to test for differences in stable isotope signatures and FA contents among taxa in PRIMER v.7.0.13 with PERMANOVA+ (Anderson et al. 2008). PERMANOVA pairwise comparisons were applied to test for differences in the $\delta^{13}C$ and $\delta^{15}N$ values among food web components and in FA contents between two specific taxa. To limit the number of comparisons, groups were formed based on the stable isotope value clustering ($\delta^{13}C$ and $\delta^{15}N$, see Appendix S1: Fig. S3). A Wilcoxon test was applied to test differences between $\delta^{13}C$ values of pelagic vs. littoral species. Principal component analysis (PCA) was performed on fatty acid percentage data to visualize the relative dominance of different FA categories in each taxon and its sources using the dudi.pca function from ade4 package in R (Dray and Dufour 2007). PERMANOVAs were utilized to compare fatty acid compositions among food web components. Fatty acid percentages were gathered in groups (PUFA, MUFA, SAFA, n-3, n-6, terrestrial, algal, bacterial) to better understand taxa fatty acid composition. PCA calculations were based on a correlation matrix and Euclidean distances. A linear relationship among variables was verified with bi-plots, and the data set was scaled before analysis. The principal component number was chosen following the rule and calculations provided in Karlis et al. (2003) and loadings corresponded to the scaled data set. All analyses were performed in the R software (R Development Core Team 2015).

## Results

### *Trophic structure of the Greiner Lake food web*

The structure of the Greiner Lake food web was well defined by the $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 2A). The $\delta^{15}N$ values of the top fish consumers, that is, Arctic char, lake trout, lake whitefish, and least cisco (10.8 ± 1.1‰, mean ± SD), differed significantly (PERMANOVA, $F_{3,130} = 379.1$, $P = 0.001$) from invertebrates, that is, zooplankton, mysids, amphipods, *L. arcticus*, chironomids, and oligochaetes (6.3 ± 1.1‰) and from benthic microbial mats and potential allochthonous inputs, that is, soils, mosses, terrestrial plants, and bird feces (1.4 ± 1.0). Sticklebacks had intermediate $\delta^{15}N$ values (7.0 ± 1.3‰) whose mean did not significantly differ from macroinvertebrates (PERMANOVA pairwise, $t = 1.59$, $P = 0.134$) but did differ significantly from other species of fish (PERMANOVA pairwise, $t = 10.86$, $P = 0.001$). The $\delta^{13}C$ values showed that the Greiner Lake food web was divided into two main food webs and that carbon sources differed among fish species (Fig. 2A). The $\delta^{13}C$ values of Arctic char, lake trout, and sticklebacks (respectively −25.9 ± 1.9, −25.1 ± 0.7, −24.6 ± 1.7‰) did not differ ($P > 0.05$) from the $\delta^{13}C$ values of macroinvertebrates (−25.6 ± 1.8‰). Stickleback $\delta^{13}C$ values were not different from lake trout $\delta^{13}C$ ($t = 1.00$, $P = 0.31$). The different diet sources were supported by the presence of sticklebacks, amphipods, and zooplankton in the stomachs of Arctic char and by the presence of sticklebacks, amphipods, and mysids in the stomachs of lake trout (Fig. 2B). Least cisco (−29.7 ± 1.3‰) and lake whitefish $\delta^{13}C$ (−30.6 ± 1.1‰) did not differ ($P > 0.05$) from zooplankton (−31.2 ± 1.1‰) indicating a direct consumer-prey trophic link. The link was further confirmed by the presence of zooplankton in the stomachs of both species, with lake whitefish also having consumed mysids (Fig. 2B). Least cisco, lake whitefish, zooplankton, and phytoplankton $\delta^{13}C$ values differed significantly from the $\delta^{13}C$ values of Arctic char, lake trout, sticklebacks, macroinvertebrates, benthic mats, and terrestrial material (Wilcoxon test, $w = 4217.5$, $P < 0.001$), showing a clear division in the Greiner Lake food web between pelagic and littoral species.

### *Fatty acid content and composition in pelagic, benthic, and terrestrial samples*

Fatty acid content varied among taxa ($F_{13,92} = 20.836$, $P = 0.001$). Arctic char was the most concentrated top consumer fish in total, polyunsaturated (n-3 and n-6 FA), and n-3 fatty acids with 44.2 ± 26.6, 10.7 ± 5.7, and 6.5 ± 3.2 μg fatty acids mg/dry weight (μg FA/mg DW; mean ± SD; Fig. 3), respectively. Total fatty acid, PUFA, and n-3 FA contents, respectively, were as follows: 35.2 ± 36.0, 9.3 ± 8.4, and 6.0 ± 5.3 for lake whitefish; and 26.9 ± 15.9, 3.7 ± 1.9, and 2.1 ± 1.5 for lake trout. The essential fatty acids

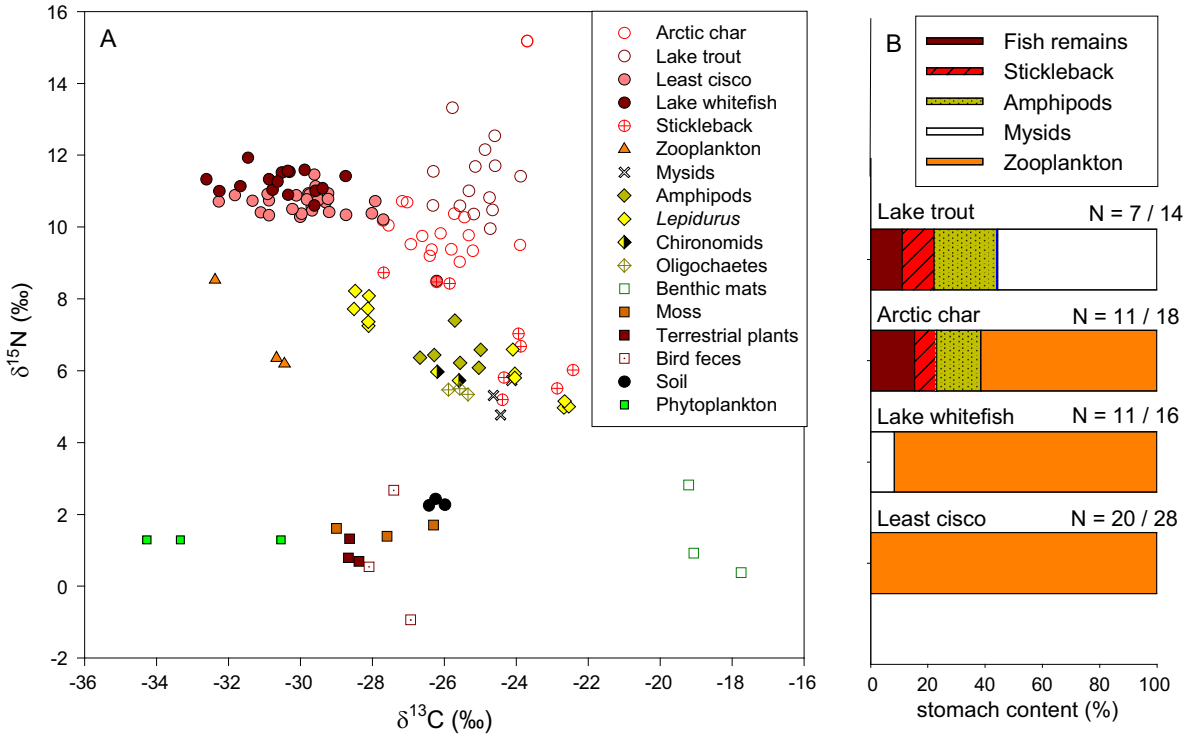


Fig. 2. (A) Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) for the Greiner Lake food web showing the trophic structure from benthic, pelagic, and terrestrial producers through pelagic and benthic primary consumers to resident fish species. The pelagic food web dominates the left side of the bi-plot and the benthic/littoral food web dominates the right side. Phytoplankton $\delta^{15}N$ values are assumed to equal the mean $\delta^{15}N$ values of other primary producers (terrestrial plant, moss, and benthic mat). (B) Fish diet composition (%) based on identification of items in non-empty fish stomachs. N = number of stomachs examined/total number of stomachs.

EPA and DHA were the most concentrated in Arctic char (4.2 ± 1.6), followed by lake whitefish (3.6 ± 2.8) and by lake trout (1.7 ± 1.1). However, no significant differences in PUFA (PERMANOVA, $F_{2,36} = 1.50$, $P = 0.23$) or EPA-DHA ($F_{2,36} = 1.98$, $P = 0.14$) were found among the top consumer fish species.

Overall, mysids had the highest contents of total fatty acids (716.1 ± 30.9 μg FA/mg DW) followed by zooplankton (351.5 ± 107.3 μg FA/mg DW). However, zooplankton samples were more concentrated in polyunsaturated, n-3 fatty acids, and EPA + DHA with 126.9 ± 43.4, 106.2 ± 42.9, and 94.8 ± 45.5 μg FA/mg DW, respectively, compared to 111.9 ± 8.8, 70.2 ± 3.3, and 49.6 ± 1.8 μg FA/mg DW for mysids (Fig. 3). Differences in mysids and zooplankton PUFA and n-3 FA contents were not significant (pairwise tests PERMANOVA, $P \geq 0.05$). Benthic macroinvertebrates had intermediate total fatty acid contents, with amphipods having averages (μg of total FA/mg DW) of 348.1 ± 283.8, *L. arcticus* (259.8 ± 68.7), water mites (258.2 ± 20.3), chironomids (167.7 ± 61.0), and oligochaetes (139.7 ± 43.2). Amphipod PUFA and n-3 FA contents, respectively, were 48.7 ± 37.5 and 23.4 ± 19.8 μg/mg DW, followed by water mites, chironomids, *L. arcticus*, and oligochaetes (Tables 1, 2; Fig. 3). Mysids, zooplankton, and macroinvertebrates were significantly more concentrated in total, polyunsaturated and n-3 FA than top consumer fish (Arctic char, lake trout, lake whitefish, $P \geq 0.05$). Sticklebacks that had a similar trophic level to macroinvertebrates and zooplankton (see $\delta^{15}N$ in Fig. 2) also had similar fatty acid contents, with 40.6 ± 22.3, 3.4 ± 2.6 and 2.8 ± 2.7, respectively, for total, polyunsaturated and n-3 FA.

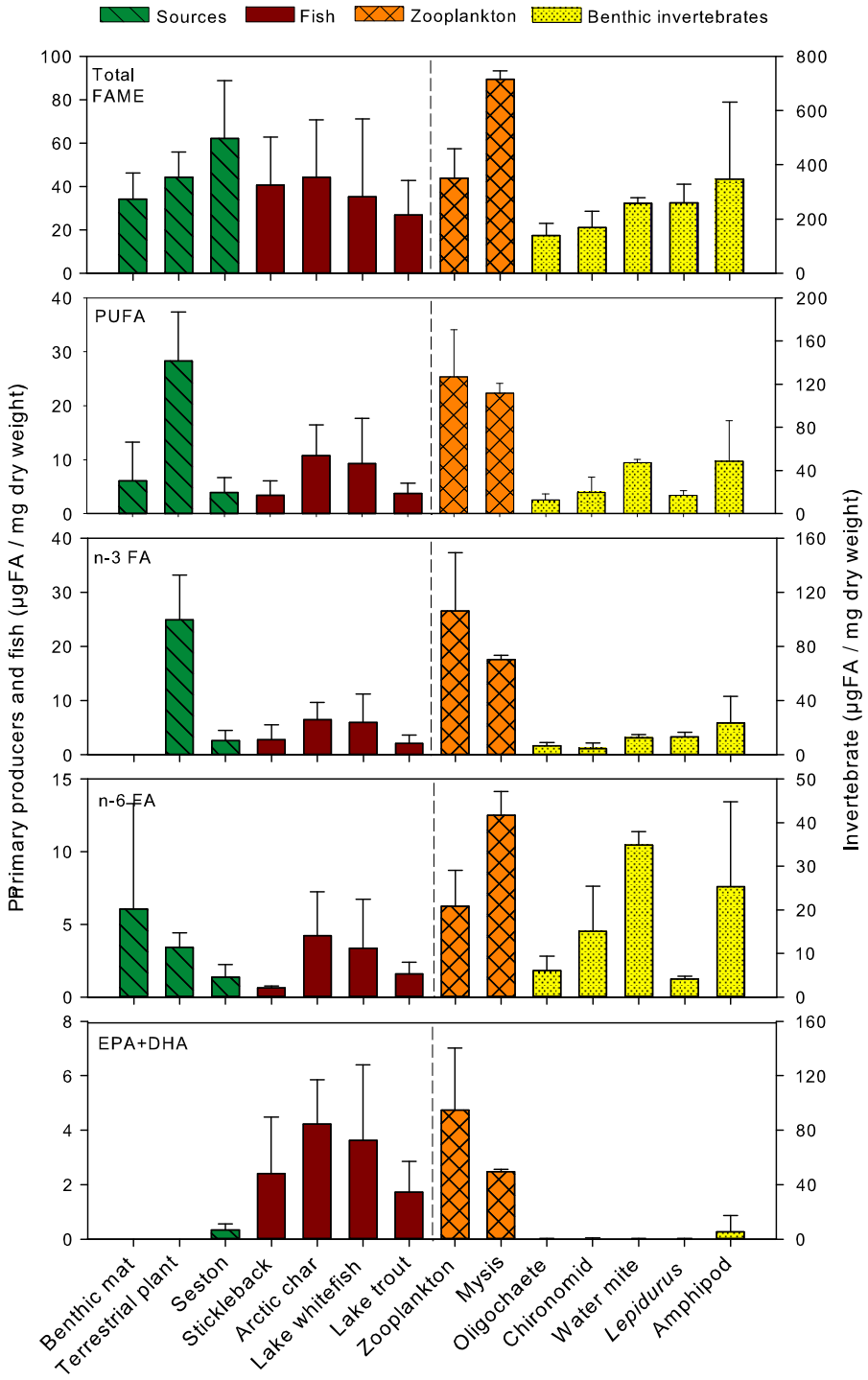


Fig. 3. Total, polyunsaturated, n-3, n-6, and EPA + DHA fatty acid contents in the Greiner Lake food web. Data are shown for fish (open bars), benthic invertebrates (dotted bars), pelagic and littoral zooplankton (doubled hatched bars), potential autochthonous food sources, and potential allochthonous inputs to the lake (hatched bars). Error bars are standard deviation (SD) of the mean. Notice the different scales of the *y*-axes with low concentrations shown on the left and high concentrations on the right of the dashed line.

Seston was more concentrated in total FA (62.2 ± 26.8 μg FA/mg DW), PUFA (4.0 ± 2.7), and n-3 FA (2.6 ± 2.0) than benthic mats with 34.2 ± 12.1 in total FA, of which 6.1 ± 7.2 was PUFA and 0.0 ± 0.0 μg/mg DW was n-3 FA. Contents of terrestrial vascular plants in total FA, PUFA, and n-3 FA were 44.2 ± 11.8, 28.3 ± 9.0, and 24.9 ± 8.3 μg FA/mg DW, respectively. The essential fatty acids EPA and DHA were present in seston (0.34 ± 0.23) but not in the benthic mats. Terrestrial vascular plants were dominated by C18 PUFA (Table 2).

Fatty acid composition differed by food web component ($F_{7,92}$ = 10.77, $P$ = 0.001, Fig. 4). Fish FA compositions (lake whitefish, Arctic char, and lake trout) differed significantly among each other (pairwise PERMANOVA comparisons, $P < 0.05$). The FA composition of zooplankton significantly differed from macroinvertebrates (pairwise PERMANOVA comparison, $P$ = 0.001). Zooplankton samples were characterized by a high proportion of n-3 PUFA and were the most concentrated among organisms in terms of EPA + DHA. Mysids were best characterized by n-6 PUFA and monounsaturated fatty acids (MUFA) (Fig. 4).

Among fish, lake whitefish had the greatest percentage of PUFA (28.1%), followed by Arctic char (26.6%), stickleback (14.3%), and lake trout (14.2%). Among benthic macroinvertebrates, water mites had the greatest percentage of PUFA (18.4%), followed by amphipods (14.7%), chironomids (11.4%), oligochaetes (9.0%), and *L. arcticus* (6.7%). Zooplankton had 36.2% and mysids 15.6% PUFA. Benthic mats had a higher percentage of PUFA (14.6%) than seston (6.1%). Terrestrial plants had 63.4% PUFA composed of C18 molecules, mainly C18:3n-3 (Table 2).

Fish had medium percentages of C20:5n-3 + C22:6n-3 (EPA + DHA), with lake whitefish and Arctic char having the highest percentages (12.8% and 12.4%, respectively) and lake trout the lowest percentage (6.5%). The greatest percentage of EPA + DHA was found in zooplankton (26.0%), followed by Mysis (6.9%), amphipods (1.5%), chironomids (0.2%), oligochaetes (0.2%), *L. arcticus* (0.1%), and water mites (0.1%). Seston contained 0.7% of EPA + DHA and benthic mats 0%.

Long-chain SAFA as terrestrial biomarkers were very low in fish (lake trout 0%, sticklebacks 0%, Arctic char 0.02%, lake whitefish 0.02%). Among benthic macroinvertebrates, LC-SAFA were measured in oligochaetes (1.0%), water mites (1.5%) *L. arcticus* (1.2%), chironomids (0.7%), and amphipods (1.0%). The highest percentage was measured in zooplankton (3.2%). LC-SAFA were measured in seston (0.2%) and in benthic mats (0.04%). They also had a low prevalence in plants (0.3%) that were dominated by fatty acid C18:1n-9 (15.7%) and 18-C PUFA (11.7%) (Table 2), which is common to live terrestrial leaf matter (Torres-Ruiz and Wehr 2010).

### *Productivity and biomass in plankton and benthos*

The production rates of different food web components yielded an energy pyramid ranked from high algal production to lower heterotrophic productivity (Table 3, Fig. 5). Benthic mats from the rocky littoral zone of the lake produced 120.4 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ and phytoplankton in seston produced 318.9 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ when standardized with the lake mean depth (Table 3). Bacteria and zooplankton communities produced 188 and 9.4 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$, respectively, when standardized to 5 m mean depth (Table 3).

When standardized by volume ($m^3$), phytoplankton produced 63.8 mg $C{\cdot}m^{-3}{\cdot}d^{-1}$ at the surface, bacteria produced 37.6 mg $C{\cdot}m^{-3}{\cdot}d^{-1}$ and zooplankton communities 1.9 mg $C{\cdot}m^{-3}{\cdot}d^{-1}$ (Fig. 5). Phytoplankton and benthic algal biomasses were estimated as seston and benthos dry weight. The DW were 2341 mg/$m^3$ and 147,662 mg/$m^2$, respectively, for seston and benthos (Fig. 5).

## Discussion

Our study described the species composition, interactions, and the nutritional quality of the trophic components of the Greiner Lake food web. We quantified contents and composition of PUFA in key organisms of the lake food web which, when combined with the identification of trophic relationships using stable isotopes, led to the identification of the main trophic pathways of PUFA from pelagic, benthic, and terrestrial producers to top predators in the lake. To our knowledge, no other study has provided such information for an Arctic lake before. We showed that different fish species in the lake were supported either by

Table 1. Mean (±*SD*) fatty acid content (μg·mg·dry weight$^{-1}$) in the different food web components (fish, mysid, zooplankton and seston) of Greiner Lake.

| Fatty acid (μg·mg·dry weight$^{-1}$) | Arctic char | Lake whitefish | Lake trout | Stickleback | Mysid | Zooplankton | Seston |
|---|---|---|---|---|---|---|---|
| *n* | 21 | 13 | 3 | 3 | 2 | 12 | 8 |
| Length (mm) | 424 ± 54 | 272 ± 99 | 528 ± 83 | 61 ± 8 | | | |
| Weight (g) | 771 ± 319 | 312 ± 332 | 1412 ± 449 | 1.7 ± 0.6 | | | |
| Total FA | 44.2 ± 26.7 | 35.2 ± 36.0 | 26.9 ± 15.9 | 40.6 ± 22.3 | 716.11 | 349.0 ± 106.7 | 62.1 ± 26.7 |
| PUFA | 10.7 ± 5.7 | 9.3 ± 8.36 | 3.72 ± 1.94 | 3.41 ± 2.64 | 111.85 | 126.9 ± 43.4 | 3.95 ± 2.72 |
| n−3 FA | 6.52 ± 3.18 | 5.96 ± 5.25 | 2.13 ± 1.47 | 2.8 ± 2.71 | 70.21 | 106.2 ± 42.8 | 2.59 ± 1.95 |
| n−6 FA | 4.22 ± 3.03 | 3.34 ± 3.37 | 1.59 ± 0.78 | 0.61 ± 0.14 | 41.64 | 20.77 ± 8.32 | 1.36 ± 0.88 |
| EPA+DHA | 4.23 ± 1.62 | 3.62 ± 2.78 | 1.72 ± 1.14 | 2.4 ± 2.08 | 49.61 | 94.8 ± 45.5 | 0.34 ± 0.23 |
| MUFA | 18.8 ± 13.9 | 13.2 ± 18.1 | 14.8 ± 12.1 | 17.5 ± 14.7 | 455.5 | 58.6 ± 24.2 | 25.8 ± 16.8 |
| SAFA | 14.57 ± 7.7 | 12.6 ± 10.2 | 8.25 ± 1.92 | 19.2 ± 9.1 | 145.34 | 154.4 ± 67.7 | 31.6 ± 13.7 |
| C14:0 | 1.52 ± 0.97 | 1.14 ± 1.6 | 0.41 ± 0.21 | 2.17 ± 1.56 | 17.66 | 25.2 ± 11.1 | 8.36 ± 5.09 |
| C14:1n−5 | 0.01 ± 0.04 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.06 ± 0.11 | 0.37 | 0.41 ± 1.02 | 0.07 ± 0.04 |
| C15:0 | 0.06 ± 0.11 | 0.07 ± 0.14 | 0.00 ± 0.00 | 0.00 ± 0.00 | 1.9 | 1.61 ± 1.29 | 0.52 ± 0.37 |
| C15:1n−5 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.06 ± 0.11 | 0.00 | 0.15 ± 0.15 | 0.03 ± 0.05 |
| C16:0 | 10.9 ± 5.8 | 9.64 ± 7.79 | 6.45 ± 1.74 | 16.3 ± 8.6 | 117.23 | 112.8 ± 53.2 | 15.8 ± 6.6 |
| C16:1n−7 | 10.9 ± 8.4 | 8.1 ± 11.61 | 9.62 ± 9.22 | 16.8 ± 14.1 | 351.19 | 18.3 ± 21.7 | 15.9 ± 10.2 |
| C17:0 | 0.07 ± 0.13 | 0.02 ± 0.06 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.89 | 1.54 ± 1.25 | 0.11 ± 0.08 |
| C17:1n−7 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.12 | 0.12 ± 0.12 | 0.02 ± 0.03 |
| C18:0 | 2.04 ± 0.97 | 1.71 ± 0.93 | 1.39 ± 0.26 | 0.71 ± 1.24 | 7.4 | 10.1 ± 6.8 | 6.56 ± 3.32 |
| C18:1n−7 | 0.18 ± 0.24 | 0.23 ± 0.19 | 0.14 ± 0.13 | 0.06 ± 0.11 | 0.00 | 9.3 ± 7.6 | 5.09 ± 6.92 |
| C18:1n−9 | 7.75 ± 5.94 | 4.88 ± 6.51 | 5.06 ± 2.99 | 0.51 ± 0.44 | 100.37 | 24.7 ± 9.3 | 3.84 ± 2.92 |
| C18:2n−6 | 2.64 ± 2.48 | 0.61 ± 0.82 | 0.79 ± 0.7 | 0.06 ± 0.11 | 26.02 | 4.28 ± 6.16 | 1.14 ± 0.81 |
| C18:3n−3 | 1.34 ± 1.16 | 1.1 ± 0.91 | 0.34 ± 0.41 | 0.4 ± 0.69 | 14.61 | 2.6 ± 4.05 | 1.11 ± 0.91 |
| C18:3n−6 | 0.76 ± 0.65 | 1.83 ± 1.97 | 0.46 ± 0.42 | 0.21 ± 0.03 | 3.89 | 0.27 ± 0.43 | 0.14 ± 0.11 |
| C18:4n−3 | 0.93 ± 1.08 | 1.21 ± 1.85 | 0.00 ± 0.00 | 0.00 ± 0.00 | 5.21 | 2.09 ± 3.51 | 0.97 ± 0.98 |
| C20:0 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.26 | 1.75 ± 0.58 | 0.14 ± 0.15 |
| C20:1n−9 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 | 1.4 ± 1.1 | 0.00 ± 0.01 |
| C20:1n−11 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 2.41 | 1.75 ± 1.92 | 0.00 ± 0.00 |
| C20:2n−6 | 0.01 ± 0.04 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.06 ± 0.11 | 2.18 | 4.13 ± 3.02 | 0.00 ± 0.00 |
| C20:3n−3 | 0.03 ± 0.08 | 0.03 ± 0.08 | 0.06 ± 0.11 | 0.00 ± 0.00 | 0.77 | 6.68 ± 2.94 | 0.17 ± 0.32 |
| C20:3n−6 | 0.02 ± 0.09 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.75 | 0.00 ± 0.00 | 0.01 ± 0.03 |
| C20:4n−6 | 0.8 ± 0.69 | 0.9 ± 1.11 | 0.34 ± 0.09 | 0.27 ± 0.1 | 8.79 | 9.82 ± 4.31 | 0.06 ± 0.09 |
| C20:5n−3 | 3.12 ± 1.23 | 3.24 ± 2.27 | 1.3 ± 0.77 | 1.94 ± 2.18 | 49.24 | 41.5 ± 19.2 | 0.21 ± 0.22 |
| C21:0 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 | 0.07 ± 0.1 | 0.00 ± 0.00 |
| C22:0 | 0.02 ± 0.06 | 0.02 ± 0.06 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 | 1.03 ± 0.7 | 0.05 ± 0.07 |
| C22:1n−9 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 | 0.39 ± 0.52 | 0.5 ± 0.82 |
| C22:2n−6 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 | 2.38 ± 2.05 | 0.00 ± 0.00 |
| C22:6n−3 | 1.11 ± 0.96 | 0.39 ± 0.54 | 0.42 ± 0.4 | 0.46 ± 0.27 | 0.38 | 53.3 ± 27.0 | 0.13 ± 0.21 |
| C23:0 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 | 0.19 ± 0.2 | 0.00 ± 0.00 |
| C24:0 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 | 0.16 ± 0.15 | 0.00 ± 0.00 |
| C24:1n−9 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 1.04 | 2.12 ± 1.56 | 0.4 ± 0.7 |
| i−C15:0 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.19 ± 0.19 | 1.39 | 1.88 ± 1.51 | 0.14 ± 0.16 |
| a−C15:0 | 0.03 ± 0.08 | 0.02 ± 0.06 | 0.07 ± 0.11 | 0.06 ± 0.11 | 0.51 | 1.62 ± 0.52 | 0.29 ± 0.15 |
| i−C16:0 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.06 ± 0.11 | 0.63 | 1.88 ± 0.8 | 0.16 ± 0.16 |
| i−C17:0 | 0.00 ± 0.00 | 0.05 ± 0.13 | 0.00 ± 0.00 | 0.19 ± 0.19 | 0.89 | 3.57 ± 1.49 | 0.13 ± 0.09 |

*Notes:* FA, fatty acids; PUFA, n−3 and n−6 polyunsaturated fatty acids; MUFA, monounsaturated fatty acids; SAFA, saturated fatty acids. The unsaturated fatty acids C18:4 n−3, C20:1 n−9, C20:5 n−3, C22:6 n−3, C24:1 n−9 are biomarkers of algae, whereas the saturated fatty acid C20:0 is a biomarker of terrestrial plants. Mean (± SD) fork length (mm) and total weights (g) are also shown for fish.

Table 2. Mean (±*SD*) fatty acid content (μg·mg·dry weight$^{-1}$) in the different food web components (macroinvertebrate, benthic mat and terrestrial plant) of Greiner Lake.

| Fatty acid (μg·mg·dry weight$^{-1}$) | Amphipod | *Lepidurus* | Chironomid | Oligochaete | Water mite | Benthic mat | Plant |
|---|---|---|---|---|---|---|---|
| n | 8 | 2 | 6 | 3 | 3 | 8 | 3 |
| Total FA | 348.1 ± 283.8 | 259.8 | 167.7 ± 61.0 | 139.7 ± 43.2 | 258.2 ± 20.3 | 34.2 ± 12.1 | 44.2 ± 11.8 |
| PUFA | 48.69 ± 37.47 | 17.23 | 19.6 ± 14.2 | 12.8 ± 5.47 | 47.5 ± 2.9 | 6.06 ± 7.24 | 28.3 ± 9.0 |
| n−3 FA | 23.4 ± 19.82 | 13.05 | 4.6 ± 4.17 | 6.8 ± 2.18 | 12.7 ± 2.4 | 0.00 ± 0.00 | 24.9 ± 8.3 |
| n−6 FA | 25.3 ± 19.44 | 4.17 | 15.0 ± 10.4 | 6 ± 3.3 | 34.8 ± 3.2 | 6.06 ± 7.24 | 3.41 ± 1.01 |
| EPA+DHA | 5.52 ± 11.66 | 0.38 | 0.31 ± 0.76 | 0.28 ± 0.28 | 0.2 ± 0.34 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| MUFA | 230.2 ± 200.8 | 192.5 | 92.4 ± 48.8 | 97.0 ± 25.6 | 161.3 ± 13.7 | 12.3 ± 7.3 | 2.15 ± 0.65 |
| SAFA | 67.4 ± 46.46 | 48.83 | 53.37 ± 9.84 | 26.8 ± 12.2 | 47.8 ± 4.6 | 15.8 ± 8.19 | 13.7 ± 2.3 |
| C14:0 | 8.15 ± 5.67 | 1.82 | 3.77 ± 2.44 | 1.14 ± 0.22 | 2.94 ± 0.64 | 5.77 ± 6.29 | 0.43 ± 0.07 |
| C14:1n−5 | 0.48 ± 0.63 | 0.24 | 0.96 ± 1.95 | 0.18 ± 0.16 | 1.51 ± 0.86 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C15:0 | 1.09 ± 0.87 | 0.48 | 0.98 ± 0.5 | 0.25 ± 0.05 | 0.19 ± 0.16 | 1.32 ± 2.11 | 0.00 ± 0.00 |
| C15:1n−5 | 0.05 ± 0.1 | 0.00 | 0.08 ± 0.13 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.04 ± 0.1 | 0.00 ± 0.00 |
| C16:0 | 48.46 ± 33.42 | 31.82 | 35.77 ± 8.69 | 9.01 ± 5.45 | 19.0 ± 3.7 | 6.44 ± 5.21 | 12.2 ± 2.1 |
| C16:1n−7 | 126.3 ± 119.8 | 82.11 | 35.3 ± 19.4 | 11.5 ± 1.3 | 27.4 ± 11.1 | 6.30 ± 6.93 | 0.89 ± 0.36 |
| C17:0 | 1.02 ± 1.16 | 1.27 | 1.31 ± 1.18 | 1.87 ± 0.57 | 1.36 ± 0.11 | 0.67 ± 1.08 | 0.00 ± 0.00 |
| C17:1n−7 | 0.72 ± 0.84 | 0.48 | 0.64 ± 0.62 | 0.00 ± 0.00 | 0.19 ± 0.16 | 2.99 ± 7.95 | 0.00 ± 0.00 |
| C18:0 | 7.67 ± 4.98 | 12.27 | 10.84 ± 6.32 | 13.6 ± 5.9 | 22.86 ± 1.1 | 1.56 ± 3.81 | 0.78 ± 0.17 |
| C18:1n−7 | 28.21 ± 27.34 | 52.55 | 27.9 ± 23.4 | 56.0 ± 22.2 | 101.0 ± 2.5 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C18:1n−9 | 73.8 ± 54.66 | 56.13 | 27.2 ± 14.5 | 12.3 ± 1.8 | 30.5 ± 5.4 | 2.67 ± 2.11 | 0.29 ± 0.11 |
| C18:2n−6 | 23.22 ± 18.01 | 4.17 | 14.1 ± 10.3 | 3.88 ± 0.84 | 33.9 ± 3.2 | 5.54 ± 7.65 | 3.19 ± 1 |
| C18:3n−3 | 10.51 ± 8.76 | 8.96 | 3.26 ± 2.75 | 2.07 ± 0.35 | 11.7 ± 2.2 | 0.00 ± 0.00 | 24.9 ± 8.3 |
| C18:3n−6 | 1.53 ± 1.49 | 0.00 | 0.79 ± 0.97 | 0.00 ± 0.00 | 0.67 ± 0.11 | 0.52 ± 0.72 | 0.22 ± 0.03 |
| C18:4n−3 | 2.32 ± 1.57 | 1.93 | 0.3 ± 0.61 | 0.16 ± 0.14 | 0.11 ± 0.18 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C20:0 | 0.14 ± 0.16 | 0.14 | 0.38 ± 0.36 | 0.25 ± 0.05 | 1.16 ± 0.18 | 0.04 ± 0.10 | 0.22 ± 0.03 |
| C20:1n−9 | 0.00 ± 0.00 | 0.00 | 0.00 ± 0.00 | 7.13 ± 1.28 | 0.00 ± 0.00 | 0.22 ± 0.62 | 0.00 ± 0.00 |
| C20:1n−11 | 0.15 ± 0.29 | 0.24 | 0.03 ± 0.08 | 7.68 ± 1.27 | 0.59 ± 0.06 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C20:2n−6 | 0.34 ± 0.47 | 0.00 | 0.00 ± 0.00 | 1.31 ± 2.26 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C20:3n−3 | 5.05 ± 2.29 | 1.79 | 0.74 ± 1.01 | 4.3 ± 1.64 | 0.68 ± 0.11 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C20:3n−6 | 0.06 ± 0.11 | 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C20:4n−6 | 0.16 ± 0.3 | 0.00 | 0.13 ± 0.21 | 0.82 ± 0.28 | 0.2 ± 0.34 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C20:5n−3 | 5.47 ± 11.63 | 0.27 | 0.31 ± 0.76 | 0.28 ± 0.28 | 0.2 ± 0.34 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C21:0 | 0.00 ± 0.00 | 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C22:0 | 0.87 ± 0.65 | 1.04 | 0.31 ± 0.54 | 0.73 ± 0.15 | 0.3 ± 0.03 | 0.00 ± 0.00 | 0.09 ± 0.15 |
| C22:1n−9 | 0.31 ± 0.23 | 0.75 | 0.22 ± 0.54 | 1.57 ± 0.34 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C22:2n−6 | 0.00 ± 0.00 | 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C22:6n−3 | 0.05 ± 0.14 | 0.11 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C23:0 | 0.00 ± 0.00 | 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C24:0 | 0.00 ± 0.00 | 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| C24:1n−9 | 0.16 ± 0.1 | 0.00 | 0.04 ± 0.09 | 0.57 ± 0.01 | 0.09 ± 0.15 | 0.11 ± 0.31 | 0.97 ± 0.29 |
| i-C15:0 | 0.36 ± 0.45 | 0.37 | 0.63 ± 0.92 | 1.73 ± 0.44 | 0.65 ± 0.37 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| a-C15:0 | 0.68 ± 0.37 | 0.13 | 1.02 ± 0.85 | 0.34 ± 0.19 | 0.09 ± 0.15 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| i-C16:0 | 0.25 ± 0.26 | 0.24 | 0.22 ± 0.28 | 0.4 ± 0.14 | 0.29 ± 0.03 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| i-C17:0 | 0.55 ± 0.5 | 0.48 | 0.47 ± 0.14 | 0.6 ± 0.52 | 0.59 ± 0.06 | 0.00 ± 0.00 | 0.00 ± 0.00 |

*Notes:* FA, fatty acids; PUFA, n−3 and n−6 polyunsaturated fatty acids; MUFA, monounsaturated fatty acids, SAFA, saturated fatty acids. The unsaturated fatty acids C18:4 n−3, C20:1 n−9, C20:5 n−3, C22:6 n−3, C24:1 n−9 are biomarkers of algae, whereas the saturated fatty acid C20:0 is a biomarker of terrestrial plants.

pelagic or by littoral benthic food resources and that the two food webs differed in their PUFA compositions resulting in different nutritional quality.

### *Trophic interactions in the Greiner Lake food web*

Co-existing pelagic and littoral food webs supported the production of key resident fish species in Greiner Lake. Stable isotope values showed

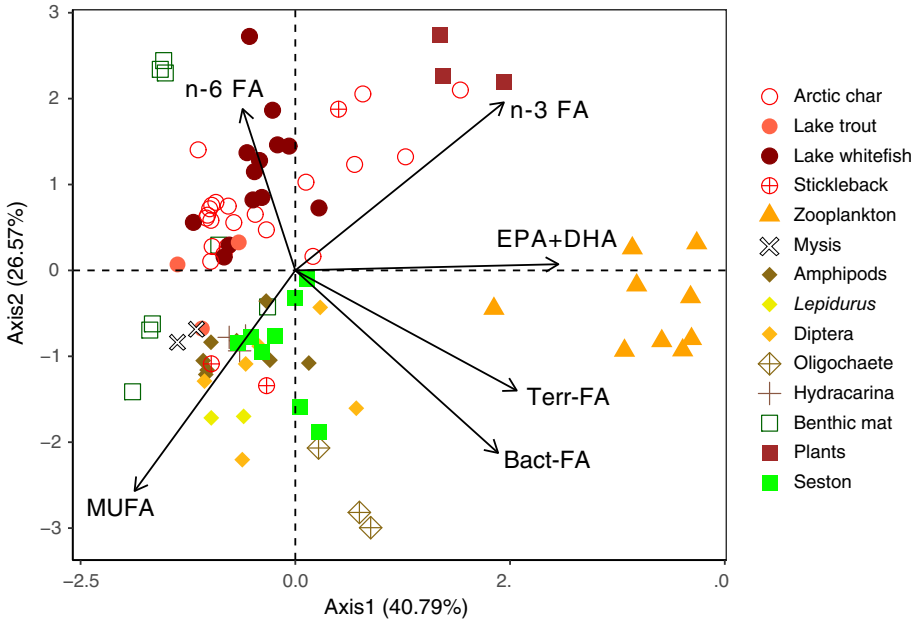


Fig. 4. Principal component analysis showing the distribution of food web samples (symbols) according to the composition (%) of different fatty acid groups (arrows) in Greiner Lake. Axes 1 (40.8%) and 2 (26.6%) explain 67.4% of the total variation in FA composition. Axis 1 represents a distribution according to the %EPA + DHA. Axis 2 represents the distribution of samples along a fatty acid saturation gradient with dominance of polyunsaturated fatty acids (n-3 and n-6 PUFA) on the top end of the axis and long-chain saturated fatty acids (Terr), branched saturated fatty acids (Bact), and MUFA on the lower end of the axis. Terr and Bact are biomarker fatty acids of terrestrial organic matter and bacteria, respectively.

Table 3. Dry weight (mean ± SD) and production of benthic mats (1 m deep), bacterioplankton, seston, and zooplankton (0–5 m deep) in Greiner Lake.

| Date | Benthic mat | Bacterioplankton | Seston | Zooplankton |
|---|---|---|---|---|
| Dry weight (mg DW/m$^2$) | | | | |
| 11 Aug 2015 | … | … | 12,767 ± 4,387 | … |
| 8 Aug 2017 | 147,662 ± 16,048 | … | 12,347 ± 379 | 159 ± 58 |
| 7 Aug 2018 | … | … | 10,004 ± 2,868 | 489 ± 243 |
| 7 Aug 2019 | … | … | … | 168 ± 59 |
| Mean | 147,662 ± 16,048 | | 11,706 ± 1,489 | 281 ± 181 |
| Productivity (mg C•m$^{-2}$•d$^{-1}$) | | | | |
| 8 Aug 2017 | 120.4 | 204.1 | 318.9 | 7.5 |
| 7 Aug 2018 | … | 204.0 | … | 18.3 |
| 7 Aug 2019 | … | 156.0 | … | 2.4 |
| Mean | 120.4 | 188.0 ± 27.8 | 318.9 | 9.4 ± 8.1 |

Empty cells represent years when measurements were not taken in Greiner Lake.

that phytoplankton carbon was assimilated by zooplankton and channeled to lake whitefish and least cisco via the pelagic food web, while macroinvertebrates and mysids transferred resources to lake trout and Arctic char via the littoral food web. Reliance on littoral resources is not uncommon for lake trout in multi-species lakes (Hulsman et al. 2016). Among lake trout and Arctic char, however, reliance on littoral production in Arctic lakes can vary depending upon the extent of anadromy observed within the fish populations (Swanson et al. 2011), life stage

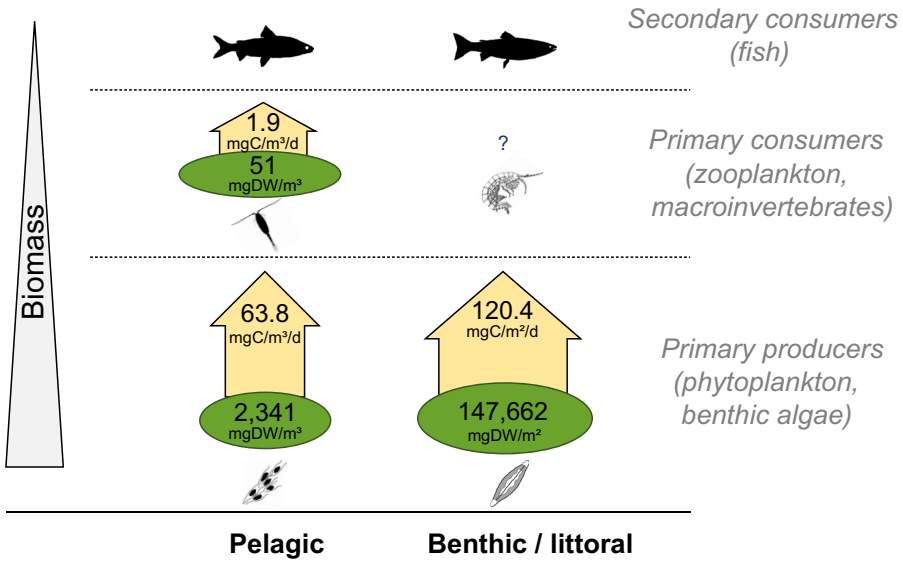


Fig. 5. Biomass (as dry weight) and productivity in producers and consumers of the Greiner Lake food webs. Biomass (ellipses) and production (arrows) are expressed per $m^3$ for the pelagic and sub-surface for benthic/littoral food web.

(immature vs. mature), forage fish populations in the lake (Power et al. 2002, Murdoch et al. 2013), and between morphotypes when multiple forms exist within the same lake (Guiguer et al. 2002, Chavarie et al. 2016). Nevertheless, when a well-developed littoral zone with reasonable resource production is present, it is not unusual to see the dominant fish species using one specific habitat as a primary foraging zone (Eloranta et al. 2010, 2013). Zonal specialization may be further strengthened by size-related competition within species. For example, in Alaskan lakes, large lake trout restrict access to dietary resources by small lake trout, causing the latter to feed more pelagically than the former (Keyse et al. 2007). In the Ungava region of northern Québec, the reverse is seen, with larger lake trout feeding more pelagically than smaller lake trout as a result of the reliance of large lake trout on pelagic prey fishes (Power et al. 2002).

Stomach content analyses corroborated the longer term stable isotope inferred trophic relationships that integrate fish diet over several months (Weidel et al. 2011) adding precision to the food web characterization of Fig. 2. Large-bodied epibenthic amphipod and mysid macroinvertebrates as well as sticklebacks were identified as major components of lake trout diet in Greiner Lake as in other Canadian Arctic and sub-Arctic lakes (Murdoch et al. 2013, Hulsman et al. 2016), Alaskan lakes (Keyse et al. 2007), and high mountain lakes (Ellis et al. 2011). Exploitation of benthic invertebrate prey, as found here, is also common in northern lake trout (e.g., Murdoch et al. 2013, Hulsman et al. 2016), although it tends to decline as size increases. Lake Greiner Arctic char favored amphipods and sticklebacks from the littoral food web but also to consumed zooplankton. Although zooplankton reliance was not readily apparent from the isotopic analyses, Arctic char are known to be opportunistic feeders in the pelagic zone (Power et al. 2008) and to seasonally adjust feeding to reduce inter-specific competition (Hammar 2014). Thus, previous studies have shown zooplankton to be an important part of Arctic char summer diets, with benthic invertebrates and mysids relied upon in winter (Dahl-Hansen et al. 1994, Hammar 1998, Gantner et al. 2010).

Similar to Arctic char, lake whitefish exhibit dietary plasticity and in Greiner Lake are at the northern fringe of their geographical distribution as are lake trout (Scott and Crossman 1973). In lakes to south (e.g., in the Northwest Territories),

dietary plasticity is manifested by ontogenetic shifts marked by an increasing littoral diet and declining trophic position with increasing body size (Cott et al. 2011). The dominance of pelagic zooplankton in lake whitefish stomachs does not preclude them reaching the sizes captured in this study (334–471 mm) as has been observed in Flathead Lake, Montana (Tohtz 1993), or Little Teslin Lake, Yukon (Bodaly 1979). Lake whitefish reliance on zooplankton production in Greiner Lake may in part derive from competitive exclusion from the littoral zone by lake trout, with the resulting formation of independent fish communities in the pelagic and littoral zones of the lake (Johnson 1976). The separation between the species is reflected here in both the stable isotope and fatty acid data and confirmed by the absence of lake whitefish in lake trout stomachs (e.g., Johnson 1975, Fig. 2). As Johnson (1976) has suggested, the separation further implies that all lower trophic level production is ultimately used to support the high biomass of fish observed in Greiner Lake and reflected in its Inuit name "*Ekaluktutiak*" ("a good fishing place").

### *Fatty acid content among species*

The most concentrated apex fish species in total FA and PUFA were Arctic char and lake whitefish because of their dietary dependence on lipid-rich zooplankton, a result which demonstrates the key role of pelagic crustaceans in the transfer of total FA and PUFA. The EPA + DHA content of Arctic char in the high-Arctic Greiner Lake (4.2 μg FA/mg DW) closely compare to predatory fishes (including Arctic char) found in ultraoligotrophic sub-arctic lakes from Northern Finland (5.4 μg FA/mg DW; Keva et al. 2021). Lake Greiner Lake whitefish EPA + DHA contents (3.6 μg FA/mg DW) similarly parallel those of European whitefish (*Coregonus laveratus*) from sub-Arctic northern Finland during reproduction (3.1 μg FA/mg DW) but were lower than annual average (7.8 μg FA/mg DW; Keva et al. 2019). Lake trout diet included mysids, as noted by Ellis et al. (2011) who showed a similar important trophic role for mysids as the key determinant of lake trout population success in Flathead Lake (Montana, USA). Lake trout was the least concentrated in EPA + DHA and ARA among all top consumer fish species, implying that the species is of least nutritional interest for the Inuit community who often use the fish for dog food. Overall, the results did not support our hypothesis that fish species feeding in the littoral zone would be more concentrated in PUFA (including EPA, DHA, and ARA). Instead, by selecting the best quality diet in each habitat, fish were provided with the highest possible PUFA content, that is, fish feeding on pelagic zooplankton and/or littoral mysids were most concentrated in PUFA.

Mysids collected in Greiner Lake were the most concentrated in total FA, mostly composed of monounsaturated FA, but also had the second highest concentration of essential FA (Fig. 3, Table 2). The result parallels marine systems where mysids are known for their high FA content (Navarro and Villanueva 2000, Richoux et al. 2005). Zooplankton was the most concentrated taxa in PUFA, characterized by n-3 FA, mostly EPA + DHA (94 μg FA/mg DW), and exceeded the macroinvertebrates sampled within the lake. The dominance of zooplankton over macroinvertebrates in terms of PUFA content has been observed in both Swedish boreal forest and Finnish sub-Arctic lakes (Lau et al. 2012, Vesterinen et al. 2021). Macroinvertebrates and sticklebacks were trophically equivalent. Several macroinvertebrate taxa and sticklebacks showed high variability in $\delta^{13}C$ suggestive of the utilization of a variety of dietary resources (Layman et al. 2007) and, as a consequence, FA sources. Nine-spine sticklebacks can occupy both top and intermediate trophic levels in Arctic lakes, making their role as a link between invertebrates and upper level predatory fishes important (Laske et al. 2017) because of their ability to mediate the transfer of energy from littoral habitats to predatory pelagic fishes (Gallagher and Dick 2011). In contrast to the specialist diet of macroinvertebrates based on dead organic material, living micro-organisms, or living macro-organisms (Usseglio-Polatera et al. 2000), the stickleback diet is more variable (Cameron et al. 1973). In Arctic environments, stickleback diets typically include dipterans (largely chironomid larvae), zooplankton, cladocerans, and ostracods (Laske et al. 2017). Our study included the Arctic tadpole shrimp (*Lepidurus arcticus*) that also has a variable diet, feeding on dead and living material from sediments, but also preying on pelagic cladocerans (Christoffersen 2001). The tadpole

shrimp typically lives in fishless ponds and lakes but can co-occur with predatory fish at low densities (Jeppesen et al. 2001). In Greiner Lake, while they might have an important ecological role as scavengers, the role is probably mostly confined to the shallow littoral zones where we sampled them and where fish predation pressure would be reduced due to depth. Despite their high content in monounsaturated FA and relatively high n-3 FA content (Table 1, Fig. 3), which to our knowledge is reported here for the first time, *L. arcticus* is probably not an important supplier of fatty acids for top consumer fish in Greiner Lake owing to their low littoral zone density and observed absence from fish stomachs.

Benthic mats were the most important aquatic producers of PUFA, containing 2 times more PUFA than seston. However, phytoplankton in seston were the only producers of n-3 FA (including EPA and DHA). The lack of n-3 FA in benthic mats has been observed for other Arctic lakes (Mariash et al. 2014) and may be explained by the high abundance of cyanobacteria in the benthic mats (Lionard et al. 2012). Although our results only represent benthic microbial communities from the littoral, we assume, based on the absence of n-3 FA in the deep soft sediments of Greiner Lake (H. Kivilä, *unpublished data*) that the overall benthic n-3 FA production was essentially zero. When pelagic primary production is compared with littoral algal mat production and standardized to the mean depth of the pelagic (5 m) and littoral (1 m) zones, phytoplankton communities dominate the carbon production between these habitats (318.9 vs 120.4 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$) in Greiner Lake. Similar results have been reported for other Arctic lakes where higher nutritional value for pelagic consumers has been shown (Quesada et al. 2008).

The lack of n-3 FA in shallow water benthic mats suggests that in Greiner Lake, zooplankton and macroinvertebrates assimilate their PUFA from seston or from terrestrial organic carbon. EPA, important for cladoceran growth (Mariash et al. 2017), and DHA, utilized mainly by copepods (Hiltunen et al. 2016), were likely largely assimilated from seston (Table 2). While seston is known to be the primary source of food resources for planktonic and benthic heterotrophs in large lakes worldwide, the benthic microbial mats of small, oligotrophic Arctic lakes and ponds have been shown to supplement zooplankton and macroinvertebrates (Mariash et al. 2011, 2014). In Greiner Lake, however, zooplankton may be exclusively supported by seston because of the relative importance of the pelagic over the benthic habitat.

Terrestrial plants contained relatively high contents of PUFA and were mainly characterized by the fatty acids ALA (C18:3n-3) and LA (C18:2n-6) (Table 2) known to be common in living higher plants (Arts et al. 2009, Gladyshev et al. 2009). Usually, these plants become accessible to aquatic consumers only in their final decomposition stage when they enter the lake in particulate or dissolved form (Polis et al. 1997). Particulate decomposed material which is low in PUFA and n-3 FA (Taipale et al. 2014) and dissolved terrestrial carbon which is the residual carbon that was not degraded by bacteria within watershed soils (Wetzel 1995) have, therefore, been considered as poor resources for aquatic production (Taipale et al. 2015*a*). However, any living plant material entering a lake can sustain littoral shredders, for example, amphipods or chironomids (Graça 2001). While the $\delta^{13}C$ values of terrestrial material were close to the values recorded for some Lake Greiner macroinvertebrates, benthic consumers may consume a substantially mixed diet from complex benthic mats composed of different primary producer taxa and detritus (Kelly and Scheibling 2012). Contrarily to the dominant role of phytoplankton as the main FA resource for zooplankton in Greiner Lake, benthic support of littoral invertebrates is more complex and may be supplemented by terrestrial inputs.

### *Productivity and biomass of the Greiner Lake food web*

Among the Greiner Lake aquatic primary producers, benthic communities produced 120 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ which is in the lower range of estimations for high-Arctic lakes (Quesada et al. 2008). Phytoplankton production equaled 318.9 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ when calculated using the mean depth of the lake, yielding a value which corresponds to the upper end of the range of estimates for Arctic lakes in Alaska and Sweden (Seekell et al. 2015) and may explain the apparently high stocks of fish found in Greiner Lake. Based on our estimates,

Greiner Lake is a primarily phytoplankton run ecosystem, contrasting it with Arctic ponds and small lakes that are often considered to be dominated by benthic primary production (Ask et al. 2009, Rautio et al. 2011, Mariash et al. 2014). Although the level of primary production will change with light and nutrient availability (Karlsson et al. 2009), we argue that a high reliance on phytoplankton is a normal for Greiner Lake. Indeed the reliance may be even more pronounced in late spring-early summer (May–June) when the lake is still ice covered but some PAR can penetrate through the ice to trigger phytoplankton production (Imbeau et al. 2021). The chl *a* concentrations under the ice range as high as 4 μg/L, which is nearly twice the concentration observed in August. Even during the ice-melt period in June–July when the lake is surrounded by a moat, littoral production is not expected to exceed pelagic production based on seasonal patterns reported for another high-Arctic lake (Bégin et al. 2021), most likely because PAR penetration through ice in the pelagic zone is sufficiently high to saturate under ice phytoplankton.

The pelagic primary production in Greiner sustained 1.5 mg $C{\cdot}m^{-3}{\cdot}d^{-1}$ of zooplankton production, which when extrapolated to the 5 m water column equals 9.4 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$, or 2.9% of the pelagic primary production. To our knowledge, this is the first time zooplankton production has been estimated for an Arctic lake using the chitobiase enzyme method and, therefore, no comparisons to other Arctic freshwater zooplankton production are possible. The August somatic production of the most abundant species *Pseudocalanus minutus* in Ogac Lake (landlocked fjord on Baffin Island) is <5 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$ which represent half of our crustacean community production in Greiner Lake. This supports the idea that Greiner Lake has a high production of zooplankton that support a high fish biomass compared to other Arctic ecosystems. In boreal lakes, St-Gelais et al. (2017) estimated zooplankton production rates between 0.3 and 15.3 mg C $m^{-3}$ $d^{-1}$ (mean = 3.2 mg C $m^{-3}$ $d^{-1}$) based on chitobiase estimations which places the high-Arctic Greiner Lake at the lower end of the boreal range (1.9 mg C $m^{-3}$ $d^{-1}$). Although the comparison needs to be treated with caution due to the differences in method, seasons, and ecosystems, the similarity suggests that zooplankton production in Greiner Lake is relatively high compared to measurements reported for other Canadian Arctic lake ecosystems.

Bacterial production rates were 37.6 mg $C{\cdot}m^{-3}{\cdot}d^{-1}$ and equaled 59% of the phytoplankton production. The estimates are high for an Arctic lake and most likely represent the highest production rate of the year as bacterial production is highly influenced by water temperature (Adams et al. 2010). In comparison, maximum bacteria production rates measured 22.4 mg $C{\cdot}m^{-3}{\cdot}d^{-1}$ in Toolik Lake, Alaska (O'Brien et al. 1997, Adams et al. 2010). Similar high bacteria production rates are known for other lakes in Greiner watershed and explained by the relatively high DOC and nutrient concentrations in the lakes (Ayala-Borda et al. 2021). However, bacterial production rates in boreal Northern Sweden (90–370 mg $C{\cdot}m^{-3}{\cdot}d^{-1}$) are much higher (Berggren et al. 2009). The large watershed to lake ratio, the dominance of small shallow ponds within the watershed, and the strong hydrological connectivity in the watershed brings terrestrial carbon and nutrients to the Greiner Lake to support pelagic plankton communities and production as has been shown for other Arctic regions (Wauthy and Rautio 2020).

The high-Arctic Greiner Lake showed higher zooplankton biomass (51 mg DW/$m^3$) than sub-Arctic lakes in northern Finland that ranged from 10 mg DW/$m^3$ in mesotrophic lakes to 25 mg DW/$m^3$ in ultraoligotrophic lakes (Keva et al. 2021). The high biomass is aligned with the high zooplankton productivity (above) and abundance (6970 ± 790 ind./$m^3$, August 2017 and 2018, $N = 5$) that was 55% higher than the mean zooplankton abundance reported to 17 lakes in northern Canada and Finnish Lapland (Rautio and Vincent 2006). It is also supported by the high zooplankton biomass in Keyhole Lake located 50 km away from Greiner Lake (Hunter 1968). Seston dry weight, used as a proxy for phytoplankton biomass, in Greiner Lake (2,341 mg DW/$m^3$) was slightly higher than the range (100–2000 mg DW/$m^3$) observed in Finish sub-Arctic lakes (Keva et al. 2021), in accordance with the Inuit Traditional Knowledge about the high productivity of Greiner Lake as well as the scientific evidence of high phytoplankton biovolume in lakes near Cambridge Bay (Ayala-Borda et al. 2021).

## Conclusions

Understanding the factors that determine the functioning of a given ecosystem, for instance the dynamic transfer of biomass among food web components, is essential for understanding ecosystem ecology. Greiner Lake has long been known by the *Ekaluktutiak* Inuit community for its substantial fish production, an important ecosystem service for which this study has identified some of the key ecological determining factors. We demonstrated that Greiner Lake harbors two well-defined food webs and that zooplankton are essential for the transfer of PUFA to pelagic fish consumers, while zoobenthos and sticklebacks are essential for the transfer of PUFA to littoral fish communities. Arctic chars, which are the most concentrated in PUFA, are able to feed on diverse benthic invertebrates and littoral mysids and supplement their diets and nutritional needs with smaller fish and zooplankton. The apex pelagic consumer, lake whitefish, were the second most concentrated in n-3 FA as a result of feeding mostly on zooplankton. Lake trout were the least concentrated in PUFA, feeding on mysids and the littoral food web. While benthic mats provided the highest amount of PUFA, only the phytoplankton community was able to provide n-3 FA to the upper trophic levels of the lake. The benthic food web was thus probably subsidized by external PUFA inputs in terms of its essential FA. Finally, the results of this study provide important baseline data and unique PUFA estimates for the open-water season essential for understanding the possible nature of lake ecosystem responses to rapidly changing environmental conditions.

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## Data Availability

The data are available from Nordicana D: https://doi.org/10.5885/45687CE-2D09FF14B1E34246

## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3881/full