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**Increasing temperature and productivity change biomass, trophic pyramids and community level
omega-3 fatty acid content in subarctic lake food webs**

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Running head: Climate & land-use effects on subarctic lakes

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25 Climate change in the Arctic is outpacing the global average while land-use is intensifying due to exploitation of
26 previously inaccessible or unprofitable natural resources. A comprehensive understanding of how the joint effects
27 of changing climate and productivity modify lake food web structure, biomass, trophic pyramid shape and
28 abundance of physiologically essential biomolecules (omega-3 fatty acids) in the biotic community is lacking.
29 We conducted a space-for-time study in 20 subarctic lakes spanning a climatic ($+3.2^{\circ}\text{C}$ and precipitation: $+30\%$)
30 and chemical (dissolved organic carbon: $+10\text{mg L}^{-1}$, total phosphorus: $+45\mu\text{g L}^{-1}$ and total nitrogen: $+1000\mu\text{g}$
31 L^{-1}) gradient to test how temperature and productivity jointly affect the structure, biomass and community fatty
32 acid content (eicosapentaenoic acid [EPA] and docosahexaenoic acid [DHA]) of whole food webs. Increasing
33 temperature and productivity shifted lake communities towards dominance of warmer, murky-water adapted taxa,
34 with a general increase in the biomass of primary producers, and secondary and tertiary consumers, while primary
35 invertebrate consumers did not show equally clear trends. This process altered various trophic pyramid structures
36 toward an hour glass shape in the warmest and most productive lakes. Increasing temperature and productivity
37 had negative fatty acid content trends (mg EPA+DHA g^{-1} dry weight) in primary producers and primary
38 consumers, but not in secondary and tertiary fish consumers. The massive biomass increment of fish led to
39 increasing areal fatty acid content ($\text{kg EPA+DHA ha}^{-1}$) towards increasingly warmer, more productive lakes, but
40 there were no significant trends in other trophic levels. Increasing temperature and productivity are shifting
41 subarctic lake communities towards systems characterised by increasing dominance of cyanobacteria and
42 cyprinid fish, although decreasing quality in terms of EPA+DHA content was observed only in phytoplankton,
43 zooplankton and profundal benthos.

44

45 1. Introduction

46 Temperature has increased much faster in Arctic regions than the global average, and rate of warming is expected
47 to further accelerate in the future (Cohen et al. 2014). In subarctic Fennoscandia, mean annual air temperature
48 has increased circa 2°C since 1850 and temperature and precipitation are further predicted to change by $+2\text{--}5^{\circ}\text{C}$
49 and $+10\text{--}30\%$, respectively, by the end of the 21st century (IPCC 2015: RCP2.6–RCP8.5). Furthermore,
50 precipitation in the region is more likely to fall as rain rather than snow (e.g. Dai and Song 2020). Such climatic
51 shifts will expand catchment vegetation towards higher altitudes and latitudes, promoting overall greening and

52 facilitating changing land-use practices. In particular, forestry and agriculture are likely to replace traditional
53 livelihoods such as reindeer herding, subsistence hunting and fishing (Schindler & Smol 2006; Huntington et al.
54 2007). Expanding transport networks, settlements, oil drilling and mining activities are rapidly changing the
55 hydrology and productivity of freshwaters (Cott et al. 2015; Denisov et al. 2020; Zubova et al. 2020). Joint effects
56 of changes in climate and land-use in catchment area causes increased leaching of terrestrial dissolved organic
57 carbon, nitrogen and phosphorous, with serious impacts on freshwater species richness, community structure and
58 food web processes (Jeppesen et al. 2012, Nieminen et al. 2015, Hayden et al. 2019, Laske et al. 2019).

59 Globally, species richness tends to show a decreasing trend from the tropics towards the poles, with this linked
60 to a gradient of decreasing temperature and productivity (for overview see e.g. Gaston 2000, Hillebrand 2004).
61 The latitudinal gradient in species richness may be linked to multi-trophic level diversity and food chain length
62 due to common underlying drivers of ecosystem size and productivity (Gaston 2000, Takimoto and Post 2013,
63 Baiser et al. 2019). Productivity and ecosystem size are inherently linked, for example large lakes tend to be less
64 productive but provide broader feeding or breeding areas for diverse communities, with subsequent effects on
65 food chain length (Post et al. 2000; Takimoto et al. 2012, Ward and McCann 2017). Food chain length determines
66 the number of trophic levels and thus largely governs the strength of top-down and bottom-up processes. In
67 systems with three or more trophic levels, primary production is suggested to be resource limited (bottom-up
68 regulation), primary consumers top down regulated and secondary consumers resource limited (Hairston et al.
69 1960, Oksanen et al. 1981, Hansson et al. 2013). Together with bottom-up regulation, top-down predator
70 mediated community-level trophic cascades have been suggested as a factor shaping food web structure driving
71 opposing trends in the biomass of sequential trophic level (i.e. each second trophic level biomass is high; Paine
72 1980, Carpenter et al. 1985, 2001). These processes govern the shape of trophic (Eltonian) pyramids, which may
73 show different forms from a classic pyramidal shape where energetic loss in each trophic level leads to
74 accumulation of max. circa 10% of produced biomass to next trophic level, and in certain cases may even show
75 inverted pyramids (Elton 1927, Brown et al. 2004, McCauley et al. 2018). Simple food webs in low diversity and
76 productivity ecosystems may be prone to size-structured populations, trophic cascades and inverted trophic
77 pyramids, but generally there is very little clear evidence of how food web biomass and trophic pyramid shape
78 are influenced by temperature and productivity gradients.

79 Subarctic regions provide an excellent natural setting to study this phenomenon as they straddle boreal and Arctic
80 biomes, providing clear diversity, climatic and productivity gradients with relatively simple food webs (Hayden

et al., 2017). Furthermore, the subarctic landscape is scattered with lakes that provide abundant and well defined ecosystems for food web diversity studies (Lau et al. 2020). Increasing temperature and productivity has been shown to shift subarctic lake communities towards more numerous, diverse, smaller-bodied, warmer-water adapted taxa which are more reliant on pelagic energy sources (Hayden et al. 2017, Hayden et al. 2019). However, we do not know how increasing temperature and productivity affects energy transfer efficiency and thus biomass distribution across different trophic levels. Aquatic food webs in many Arctic areas are based on production and transfer of lipids from primary producers to top consumers, where seasonal storage of lipids is important for survival and reproduction of long lived organisms at higher trophic levels (e.g. Jørgensen et al. 1997, Armstrong and Bond 2013). An important subgroup of lipids are polyunsaturated fatty acids (PUFAs), providing essential components for cell development and functioning, however the distribution of lipids and fatty acids varies greatly among taxa and trophic levels. While there are several PUFAs, eicosapentaenoic acid (20:5n-3, EPA) and docosahexaenoic acid (22:6n-3, DHA) are considered the most important since they are essential for growth, neural development and reproduction of consumers (Arts et al, 2001, Bou et al. 2017, Yeşilayer and Kaymak 2020). Only certain algae groups, such as dinoflagellates, diatoms and cryptophytes, are able to produce EPA and DHA efficiently and are abundant in cold and nutrient poor lakes (Taipale et al. 2013, 2016). However, warm and eutrophic lake primary producer communities, often dominated with cyanobacteria, are inefficient in EPA and DHA production (Müller-Navarra et al. 2000, 2004, Taipale et al. 2013, 2016). Some species can convert shorter chain fatty acids to EPA and DHA (Geya et al. 2016, Ishikawa et al. 2019), but in many vertebrates this process is considered energetically expensive and thus direct sources from high quality prey are often selected (Twining et al. 2016, Keva et al. 2019). This suggest that at a food web level, differences in primary producer communities induced by temperature and productivity may govern the quality of higher trophic levels (Hixson and Arts 2016, Colombo et al. 2020).

Our main aim in this study was to test how increasing temperature and productivity change structure, biomass and nutritional quality of food web components from primary producers to top consumers using a gradient of Fennoscandian subarctic lakes (n=20) spanning a climate and land-use gradient. Omega-3 fatty acids, EPA and DHA, were selected as proxies for quality of food web components, since they are physiologically important biomolecules for consumers. First, we hypothesized (H1) that communities shift towards warmer and more murky-water adapted species, with a concurrent increase in food web biomass, and expected that increases in algae and fish biomass along the gradient would have effects on trophic pyramid shape (Jeppesen et al. 2010,

Hayden et al. 2017, McCauley et al. 2018). Secondly, we hypothesised (H2) that cyanobacteria form an increasing proportion of the phytoplankton communities in warmer and more productive lakes (Przytulska et al. 2017), thus lowering nutritional quality of primary producers. As such, we expected that this difference would be passed through all higher trophic levels (Müller-Navarra et al. 2000, Taipale et al. 2016). Finally, we hypothesized (H3) that increasing temperature and productivity would increase total community biomass including an increase in physiologically important EPA and DHA of the total lake community (Jeppesen et al. 2000, Hayden et al. 2019).

2. Materials and Methods

2.1 Environmental variables

We sampled 20 lakes, located in Finnish Lapland across the Tornio-Muoniojoki and Paatsjoki watercourses, spanning northern European climatic (average air temperature in June–September from 1980-2010: 8.4–11.6°C and precipitation 197–257 mm a⁻¹) and water chemistry (dissolved organic carbon; DOC: 1.9–14.9 mg L⁻¹, total phosphorus; TotP: 3–48 µg L⁻¹ and total nitrogen; TotN: 110–1100 µg L⁻¹) gradients (Table S1, Fig. 1). Here, all lakes are considered subarctic and located north of Arctic Circle (AMAP 1998). Climatic differences originate from latitudinal and altitudinal gradients, with temperature and precipitation lowest in northernmost lakes and progressively increasing towards the south. Climatic data were derived from nine Finnish Meteorological Institute weather stations situated within the study region and refer to long-term (1981–2010) average open-water season June–September air temperature and annual precipitation as rain (Hayden et al. 2019). Differences in lake productivity originate predominantly from variation in vegetation and land-use practices within the catchment (Jussila et al. 2014). The northernmost lakes are situated near pristine areas with anthropogenic impacts limited to nature tourism and reindeer herding, and from the timberline southwards industrial forestry activities including large-scale clear-cut areas, site preparation and intensive ditching (Jussila et al. 2014; Hayden et al. 2017; Ahonen et al., 2018, Table S1). Catchment area characteristics and land-use variables were derived with the Finnish Environment Institute VALUE-tool combining catchment and CORINE-database and open map data (Hayden et al. 2017; Ahonen et al. 2018). Lake location (coordinates, altitude), morphometrical data (area, depth, mean depth, volume) and water physical-chemistry (nutrients, light) were derived from the Finnish Environment Institute (HERTTA-database) and National Survey of Finland, or from our own sampling (Table S1). We measured visible light in the water column (LI-COR, A-250, visible light 400–700 nm) at deepest point of lake

138 or sampling area (largest lakes) to define 1% surface light level i.e. compensation depth needed to define
 139 proportions of the three major lake habitats littoral, profundal and pelagic (Table S1). Lake trophic states were
 140 categorized with TotP concentrations to ultraoligotrophic ($0\text{--}4\ \mu\text{g L}^{-1}$, $n=3$), oligotrophic ($5\text{--}9\ \mu\text{g L}^{-1}$, $n=7$),
 141 mesotrophic ($10\text{--}29\ \mu\text{g L}^{-1}$, $n=5$) and eutrophic ($\geq 30\ \mu\text{g L}^{-1}$, $n=5$) (Fig. 1; Nürnberg 1996). Phytoplankton,
 142 pelagic zooplankton, littoral and profundal benthic macroinvertebrates (here after benthos) and fish were sampled
 143 in the years 2009-2017. The sampling period was always in late summer (August–September).

145 Fig. 1. Map of the study region (A) in northern Fennoscandia and boxplot figures of the basic lake chemistry (B–D) and
 146 physics (E–F) of the sampled lakes. The study lakes are marked with grey shade shapes (A) or boxes (B–D) indicating
 147 different lake types (light grey = ultraoligotrophic, grey = oligotrophic, dark grey = mesotrophic, black = eutrophic).
 148 Abbreviations in x-axes labels are named as following: TotP=total phosphorous (B), TotN = total nitrogen (C), DOC =
 149 dissolved organic carbon (D), Temp = average air temperature in June–September 1981–2010 (E), CompD = compensation
 150 depth i.e. water depth where 1% surface light is left (F).

151 2.2 Community composition and biomass

152 Quantitative phytoplankton taxa samples for eight of the study lakes were extracted from the HERTTA database
 153 (Finnish Environment Institute) and from a previous study for an additional six lakes (Taipale et al. 2016).
 154 Samples were collected from the epilimnion (0–2 m) with a Limnos or corresponding water sampler in late
 155 summer (August–September), purified using a filter (mesh size: $250\ \mu\text{m}$) and stored in Lugol solution with added
 156 formaldehyde. Phytoplankton cell counts were calculated under a microscope using the Utermöhl technique
 157 (Utermöhl 1958). Biomass estimations were done using taxa morphology specific geometric formulas
 158 (Hillebrand et al. 1999) and adjusted with experimentally derived carbon-mass ratios (Menden-Deuer and
 159 Lessard 2000). Phytoplankton community composition was calculated as class specific percentage from carbon

160 biovolume (g C L^{-1}), and dry mass [dw] per unit area was calculated as well (kg dw ha^{-1} , hereinafter biomass)
161 using lake specific euphotic zone.

162 Quantitative pelagic zooplankton samples were collected with a net (diameter 25 cm, mesh size 50 μm) using
163 three replicate vertical hauls from the deepest point of each lake (or, in very large lakes, the deepest point of the
164 sampling area) and immediately stored in a 5% formaldehyde solution (Hayden et al. 2017). We collected pelagic
165 zooplankton for fatty acid analyses from the same point using repeated vertical hauls and these samples were
166 condensed, frozen and freeze-dried in the laboratory. In quantitative samples, all crustaceans were identified to
167 class level, and the body size of 30 first encountered individuals of each class were measured for density and
168 biomass calculations. Biomass was calculated from identified individuals and length measured taxa using size-
169 biomass (length to dry weight) conversion factors from McCauley (1984). The overall zooplankton community
170 composition was calculated as taxon specific percentage from dry mass biovolume (mg dw L^{-1}) and biomass was
171 calculated (kg dw ha^{-1}) using lake specific average depth.

172 Benthic macroinvertebrates were collected only from soft bottom with an Ekman grab (area 272 cm^2) from a
173 transect (depths 1, 2, 3, 5, 10, 15, 20, 30, 40 m) spanning from the littoral zone to the deepest point of lake or
174 sampling area. Three separate replicates were taken from each depth and animals were stored in plastic buckets
175 with lake water followed by sorting in laboratory. Animals were identified to lowest feasible level, sorted,
176 counted and total wet biomass of each taxa were weighed (accuracy 0.1 mg) and areal biomass (g ww m^{-2}) was
177 calculated for each sample using Ekman area to m^2 conversion factor 36.8. For the lake specific biomass
178 calculations, we transformed wet weights to dry weights by using a conversion factor of 0.2 for all taxa (Smit et
179 al. 1993). For each lake, we used water column light level to define compensation depth to define which sampling
180 depths belong to littoral ($\geq 1\%$ light) or profundal ($< 1\%$ light). Then whole lake bathymetry was used to calculate
181 mean benthic macroinvertebrate biomass (kg dw ha^{-1}) in soft sediments in littoral and profundal regions.

182 Fish were sampled from three major lake habitats (littoral, profundal and pelagic) using a gill net series
183 composing of eight 30 m long and 1.8 m high nets (mesh sizes 12–60 mm knot to knot) and one Nordic net with
184 dimensions of 30×1.5 m (12 mesh sizes 5–55 mm). A minimum of three gill netting nights per major habitat was
185 conducted and sampling amount was increased proportional to lake area (Malinen et al. 2014; Hayden et al.
186 2017). Fishing depth of gill nets were verified with echosounder and each fishing period length was recorded
187 with accuracy of a minute. In most cases, gill nets were set overnight in the evening and collected during

188 following morning (6–10 hours soaking time), but in the most eutrophic lakes we had to use shorter sampling
189 time (<2 hours) to avoid oversaturation due to a massive increase in fish density in these lakes (Hayden et al.
190 2017). Fish were immediately killed during net lifting by cerebral concussion and chilled in ice. In the field
191 laboratory, each fish was identified to species level, but whitefish (*Coregonus lavaretus*) were assigned to the
192 morph (subspecies) level and whitefish × vendace (*Coregonus albula*) hybrids were separated based on
193 morphology and colour, as well as head shape and gill raker count (Kahilainen et al. 2011, Kahilainen et al.
194 2017). This subspecies level delineation was considered essential as many of the northern lakes in the study area
195 are dominated by variable proportions of ecologically contrasting whitefish morphs (2–4 morphs in a lake) that
196 play differential roles in food web structure, energy flows and fatty acid dynamics (Thomas et al. 2017, Thomas
197 et al. 2019).

198 Total length (accuracy 1 mm) and wet mass (0.1 g) were measured and the relative abundance of each species
199 was calculated as catch per unit effort (CPUE) i.e. number of individual per species gill net⁻¹ hour⁻¹. In addition
200 to gill net data, we have previously collected both relative abundance (CPUE) and quantitative estimates of
201 whitefish and vendace density in pelagic habitat (individuals ha⁻¹) by using vertical echosounding and gill netting
202 from subset of the lakes analysed in the current study (Malinen et al. 2014). We calculated a linear regression
203 equation between CPUE and echosounding derived quantitative density in order to transform relative densities
204 of whitefish and vendace to absolute densities. As one or both of these species are present in all sampled lakes,
205 we used their calculated absolute density and their proportion of total catches to get fish density values for
206 different species in each lake. These density values for each species and their mean individual mass in gill net
207 catch were multiplied to get biomass (kg ha⁻¹). For consistency with other trophic levels, we transformed fish
208 wet weight to dry weight with conversion factor of 0.2 (e.g. Ahlgren et al. 1996). In trophic level analyses, fish
209 were classified as secondary consumers i.e. invertivorous (most species and morphs) and tertiary consumers i.e.
210 piscivorous species (only pike, *Esox lucius*; burbot, *Lota lota*, Arctic charr, *Salvelinus alpinus*; brown trout, *Salmo*
211 *trutta*; and >20 cm perch *Perca fluviatilis*) based on previous dietary and stable isotope studies of a subset of the
212 studied lakes (Kahilainen and Lehtonen 2003, Thomas et al. 2017, Hayden et al. 2019).

213 2.3 Lipid extraction and fatty acid analysis

214 Homogenized freeze-dried (–50 °C for 48 h) invertebrate and fish dorsal muscle samples were weighed ca. 0.5–
215 1 mg and 3–4 mg respectively to kimax glass test tubes. If material was not limited, duplicate samples were

216 analysed. Fatty acids were analysed as methyl esters (e.g. Taipale et al. 2016), identified and quantified using a
217 gas chromatograph attached to mass spectrometer. Samples were spiked with nonadecylic acid (PLFA c19:0).
218 Lipids were extracted with 3 ml of chloroform-methanol solution (2:1 vol) and with sonicator (15 min). Ultra-
219 pure water (0.75ml of MilliQ) was add to kimax tubes to separate water soluble compounds from lipids. Lipid
220 extract was evaporated and 3 ml of 1% H₂SO₄ add to kimax tube which was incubated in +50 °C for 20 h to
221 produce fatty acid methyl esters (FAMES). The produced FAMES were diluted with hexane and analysed using
222 a gas chromatograph attached to a mass spectrometer (GC-2010 Plus and QP-2010 Ultra, Shimadzu, Japan) with
223 Zebron ZB-FAME column (30 m + 5m guardian × 0.25 mm × 0.2 µm). At the begin of the each GCMS run, the
224 column temperature was held in 50°C for 1 min, followed by raising with 10 °C min⁻¹ to 130 °C, 7 °C min⁻¹ to
225 180 °C, 2 °C min⁻¹ to 200 °C and was held there for 3 min which after the colon temperature was raised with 10
226 °C min⁻¹ to 260 °C. The injection temperature was 270 °C and the interface temperature 250 °C, total column
227 flow being 27.5 mL min⁻¹ and linear velocity 36.3 cm s⁻¹.

228 Fatty acids were identified based on ion spectrums and quantified based on four-point standard mixture
229 calibration curves (15 ng µL⁻¹, 50 ng µL⁻¹, 100 ng µL⁻¹, 250 ng µL⁻¹; GLC 566c, Nu-Chek Prep, USA) with
230 GCMS solution software version 4.42 (Shimadzu, Japan). The calibration curves were ran before each run. The
231 coefficient of determination between peak area and standard FA concentrations were always higher than 0.999.
232 To validate the calibration curves, we run at least one external EPA and DHA standard (Sigma Aldrich
233 CRM47571 & CRM47570) per batch, average recovery % ± RSD of the analysed external standards were 119.2
234 ± 21.4 % (n=11) and 104.9 ± 20.5 % (n=11) for EPA and DHA. The average sum of percent error between sample
235 duplicate (n=47) FA profiles and EPA+DHA contribution were 2.0 ± 1.3 % and 0.6 ± 0.7 %, respectively. The
236 mean ± SD recovery of our internal standard nonadecylic acid in our samples was 90.7 ± 24.2% (n=503) and the
237 individual recovery % was used to adjust the sample FA concentrations. EPA and DHA were the only fatty acids
238 used in the subsequent data analysis.

239 We combined a small subset of fatty acid data from previous studies having a different focus (Taipale et al. 2016,
240 Vesterinen et al. 2020). Total dataset consisted of 868 samples (Table S2: phytoplankton=32, zooplankton=26,
241 littoral benthos=209, profundal benthos=34, invertivorous fish=377, piscivorous fish=190). Community specific
242 lake average FA sample coverage of taxa specific biomass contributions stands as following: phytoplankton 93.2
243 ± 5.4 %, littoral benthos 59.6 ± 24.3 %, profundal benthos 71.9 ± 19.9 %, invertivorous fish 92.9 ± 9.0 %,

244 piscivorous fish 89.7 ± 23.0 % Table S3. For zooplankton only bulk samples were used in community quality
245 calculations, thus assuming coverage being 100% (Table S3).

246 2.4. Lake specific community EPA + DHA content and areal content calculations

247 Computational phytoplankton EPA + DHA content ($\text{mg g}^{-1} \text{C}$) was calculated for study lakes using the class
248 specific carbon mass and their corresponding FA production estimates from laboratory experiments (Taipale et
249 al. 2016). The laboratory-culture experiment derived FA production of phytoplankton taxa might be different
250 from those found in nature, due to varying environmental conditions in natural environments. However, we think
251 this estimation is relevant as microscopy data of phytoplankton community composition and biomass data was
252 available for the study systems. For the consumer communities, EPA + DHA content ($\text{mg g}^{-1} \text{dw}$) was weighed
253 with taxa specific biomass contribution (%) determined for each lake and taxa, except for zooplankton which was
254 sampled as a whole community. Lake, habitat and taxa specific mean FA content values was used in the
255 community EPA + DHA calculations where possible. If taxa specific fatty acid content was unavailable from a
256 lake, we used measured taxa average FA content from different habitat (for benthos) or same type of lakes (e.g.
257 oligotrophic), with this we supplemented our FA sample coverage near to 100% for each community (Table S3).

258 Biomass calculations (in section 2.2.) facilitated the calculation of trophic pyramids, where total food web
259 biomass was divided among trophic levels. Here, we followed above classifications where the first trophic level
260 are primary producers (i.e. phytoplankton), the second is primary consumers (zooplankton and benthic
261 macroinvertebrates), the third is secondary consumers (invertivorous fish), whilst the fourth is tertiary consumers
262 (piscivorous fish). To calculate community EPA + DHA mass per unit area ($\text{kg EPA + DHA ha}^{-1}$, herein after:
263 areal content) for primary producers and different consumers, we multiplied community biomass (kg dw ha^{-1})
264 and EPA + DHA content. For fish community areal EPA+DHA content we used only muscle tissue of fish instead
265 of whole fish. Furthermore, we used community EPA + DHA areal content (kg FA ha^{-1}) to calculate trophic
266 pyramids for these assimilated biomolecules through food webs. Our biomass calculations should be considered
267 as minimum estimates, since we did not have any quantitative biomass and FA data from littoral primary
268 producers (periphyton, macrophytes) nor small organisms such as bacteria, rotifers and microbenthos.

269 2.5 Statistical methods

270 We calculated a climate-productivity index (CPI) that equals the principal component analysis (PCA) axis one
271 based on lake chemistry (TotP, TotN, DOC), and catchment properties (air temperature, precipitation) to reduce

the number of environmental variables when testing H1 and H2 (Table S1, Hayden et al. 2019). Here, the PC1 axis (i.e. CPi) explained 81% of the variation in lake environmental data, and was the only PC used in subsequent analyses (Fig. S1) due to inherent collinearity with land-use practices (Hayden et al. 2019). Within the final derived index, lakes with higher temperature and productivity receive higher CPi values. We built general linear models with forward and backward selection predicting each community biomass with CPi, prey item quality (EPA+DHA content) and predator biomass, where Akaike information criterion (AIC) was used for selection of the best models. To summarize general linear model results, CPi was the main factor affecting community biomass (Table S4-5). Therefore, we used a simple linear regression model to examine the relation between CPi (PC1 scores) and community total biomass (H1) and EPA + DHA areal content (H2). We also used linear regression analysis to test the dependence of community EPA + DHA areal content on lake total biomass (H3). An alpha level of 0.05 was used in each statistical analysis and tests were conducted using R through RStudio version 3.4.1 with the default base package (R Core Team 2017). Figures were drawn using base graphics and ggplot2 package (Wickham 2016).

285

286 3. Results

287 3.1 Changes in community structure, food web biomass and trophic pyramid shape (H1)

288 Lake communities showed shifts from cold to warmer adapted taxa with increasing temperature and productivity
289 (Fig. 2). Phytoplankton changed from diatom dominated communities in ultraoligotrophic lakes towards
290 cyanobacteria dominance in eutrophic lakes (Fig. 2 A1). Copepods contributed 50–80% of the total zooplankton
291 community biomass along this gradient and calanoids had the highest biomass percentage in every lake type.
292 However, copepod contribution was lowest in eutrophic lakes where cladocerans, especially *Bosmina* had a high
293 biomass percentage (Fig. 2 A2). Littoral benthos communities were diverse throughout the lake gradient (Fig. 2
294 A3): *Asellus* sp. and *Lymnaea* sp. reached the highest proportional contribution in mesotrophic lakes, whereas
295 oligochaetes had the highest biomass contribution in ultraoligotrophic lakes and lowest in eutrophic lakes.
296 Profundal benthos was mainly dominated by chironomids and their biomass contribution increased from
297 ultraoligotrophic lakes (ca. 50%) towards eutrophic lakes (ca. 90%) (Fig. 2 A4). Invertivorous fish communities
298 were dominated by salmonids (whitefish, vendace) in ultraoligotrophic lakes; by percids (perch and ruffe,
299 *Gymnocephalus cernuus*) and salmonids in oligotrophic-mesotrophic lakes; and by cyprinids (roach *Rutilus*

300 *rutilus*, bleak *Alburnus alburnus*) in eutrophic lakes (Fig. 2 A5). Piscivorous pike and perch increased their
301 biomass contribution progressively from ultraoligotrophic lakes (ca. 35% and 5%) towards eutrophic lakes (ca.
302 50% for both species), whilst piscivorous Arctic charr and brown trout disappeared completely along the same
303 gradient (Fig. 2 A6).

304 Phytoplankton mean mass increased more than twenty-fold between ultraoligotrophic (0.08 ± 0.05 ; mean $\pm$ SD g
305 dw m⁻³) and eutrophic lakes 1.9 ± 0.8 g dw m⁻³ (Fig. 2 B1), which was also evident for biomass along our lake
306 gradient CPi (PC1) from north to south based on linear regression analysis (Fig. 3 A1). The lowest zooplankton
307 biomass was observed in mesotrophic lakes (9.27 ± 5.96 mg dw m⁻³) (Fig. 2 B2), however no clear trend in
308 biomass was observed along the lake gradient (CPi) based on linear regression (Fig. 3 A2). The overall highest
309 littoral benthos biomass was observed in mesotrophic lakes (Fig. 2 B3), but no clear trend in biomass along the
310 continuous CPi axis (Fig. 3 A3). The profundal benthos biomass was low in ultraoligotrophic lakes (0.4 ± 0.3 kg
311 dw ha⁻¹) and increased towards eutrophic lakes (8.2 ± 11.3 kg dw ha⁻¹). This trend was mainly caused by
312 increasing chironomid biomass (Fig. 2 B4) and driven mainly by extremely high profundal benthos densities in
313 two lakes with low oxygen (Fig. 3 A4). Generally invertivorous fish biomass was circa five times higher in
314 eutrophic lakes (69.7 ± 49.0 kg dw ha⁻¹) compared to other lake types (pooled average: 15.8 ± 12.9 kg dw ha⁻¹)
315 (Fig. 2 B5; Fig. 3 A5). The biomass of piscivorous fish was around four times higher in eutrophic lakes ($15.9 \pm$
316 7.8 kg dw ha⁻¹) than other lake types (pooled average: 4.2 ± 3.2 kg dw ha⁻¹). (Fig. 2 B6), and a clear linear trend
317 along the CPi axis was observed (Fig. 3 A6). These massive increases in primary producer and secondary
318 consumer biomass compared primary and tertiary consumers were evident in changes to the trophic pyramid
319 shape (Fig. 4, Fig. S2). Ultraoligotrophic and oligotrophic lakes showed variable shapes from typical pyramids
320 to inverted pyramids to across different lakes, whilst most mesotrophic lakes were generally typical pyramids
321 and eutrophic lakes had hour glass shaped biomass distributions (Fig. 4, Fig. S2).

Fig. 2. Community structure (A), biomass (B) and computed community quality (FA content, C) across different lake types (x-axis). Food web community compartments: phytoplankton (1), zooplankton (2), littoral benthos (3), profundal benthos (4), invertivorous fish (5) and piscivorous fish (6) are presented in different columns. The coloured bars indicate average taxa values of different lake types as following: normalized relative community composition (A: biomass %), lake type average biomass (B1–B2: mg dw m⁻³, B3–B6: kg dw ha⁻¹) and lake type average community EPA and DHA content (C: mg FA g⁻¹ dw). Lake specific community bulk FA content is derived from the FA analysed bulk sample (C2: zooplankton) and calculated for other food web community compartments (C1, C3–C6) from taxa specific biomass contribution and fatty acid content. Whiskers on top of the lake type average (B and C rows) represents + SD.

328 3.2 Changes in fatty acid content of food web components (H2)

329 Phytoplankton quality (EPA + DHA) was highest in oligotrophic and mesotrophic lakes, and clearly the lowest
330 in eutrophic lakes (Table S6, Fig. 2 C1). Zooplankton quality was the highest in ultraoligotrophic lakes ($20.1 \pm$
331 $8.9 \text{ mg g}^{-1} \text{ dw}$; mean $\pm$ SD) and progressively decreased towards eutrophic lakes ($10.6 \text{ mg g}^{-1} \text{ dw}$) (Fig. 2 C2),
332 but due to high variance and low sample size the EPA + DHA distributions did not differ statistically among the
333 lake types (Table S6). Benthos quality was limited to the presence of EPA. Littoral and profundal benthos quality
334 were the highest in ultraoligotrophic lakes and the lowest in eutrophic lakes (Table S6, Fig. 2 C3–4). There was
335 no statistically significant differences in quality of invertivorous and piscivorous communities between lake types
336 as EPA+DHA content remained stable (Table S6, Fig. 2 C5–6). EPA and DHA content of primary producers and
337 consumers decreased along the CPi axis, but there was no statistically significant trend in secondary or tertiary
338 consumers (Fig. 3 B1–6, Fig. S3).

339 3.3 Changes in community EPA + DHA areal content (H3)

340 The highest values of community EPA + DHA areal content came from invertivorous fish (pooled average $\pm$ SD:
341 $0.188 \pm 0.214 \text{ kg ha}^{-1}$), followed by piscivorous fish ($0.050 \pm 0.054 \text{ kg ha}^{-1}$), phytoplankton ($0.036 \pm 0.030 \text{ kg}$
342 ha^{-1}), littoral benthos ($0.023 \pm 0.019 \text{ kg ha}^{-1}$), pelagic zooplankton ($0.015 \pm 0.026 \text{ kg ha}^{-1}$) and profundal benthos
343 ($0.007 \pm 0.017 \text{ kg ha}^{-1}$), respectively. Trends in EPA + DHA areal content of phytoplankton, zooplankton, and
344 benthos communities with total food web biomass were not significant (Fig. 3C1-4), though showing generally
345 opposing patterns between trophic levels: EPA + DHA areal content of phytoplankton community was smallest
346 in oligotrophic lakes but remained relatively stable in meso- and eutrophic lakes, whilst invertebrate taxa showed
347 the opposite pattern. The areal contents of EPA + DHA of invertivorous ($\text{adj.}r^2=0.86$) and piscivorous
348 ($\text{adj.}r^2=0.45$) fish communities were positively related to total biomass of food web (Fig. 3C 5–6, Table S7).
349 Community EPA + DHA areal content showed a similar pattern as total biomass along the studied lake gradient,
350 emphasizing the fundamental link between total community biomass and EPA + DHA areal content (Fig. 3A, C,
351 Table S7).

Fig. 3. Linear regression models showing A–B: Community biomass (kg dw ha^{-1}) and quality ($\text{mg EPA+DHA g}^{-1} \text{ dw}$) against climate-productivity index (CPI) and C: EPA + DHA areal content ($\text{kg EPA+DHA ha}^{-1}$) against total food web biomass (kg dw ha^{-1}). Food web community compartments: phytoplankton (1), zooplankton (2), littoral benthos (3), profundal benthos (4), invertivorous fish (5) and piscivorous fish (6) are presented in different columns. The grey shaded shapes indicate different lake trophy corresponding to Fig. 1: light grey square = ultraoligotrophic, grey dot = oligotrophic, dark grey triangle = mesotrophic, black diamond = eutrophic. Linear regressions fits (bolded line), 95% confidence limit (grey shaded areas) and adjusted coefficient of determination (r^2) are presented in the figures if the model was statistically significant ($p < 0.05$). Linear regression equations, F statistics, adjusted r^2 and p values are presented for each model in Table S6.

4. Discussion

4.1 Major trends

Based on our findings, we suggest that increasing temperature and productivity fundamentally alter the structure and function of subarctic lake communities. Here, warmer, more nutrient rich waters promote communities with an increasing share of blue-green algae, smaller-bodied zooplankton, smaller benthic macroinvertebrate taxa and warmer water adapted cyprinid fishes. Moreover, we observed clear positive trends in biomass in each second trophic level (i.e. phytoplankton and invertivorous fish), which increased along the lake gradient. Deviating trends in contrasting trophic levels had subsequent effects on shaping trophic pyramids, where only eutrophic lakes seems to settle into a common hour glass shape. The omega-3 content ($\text{mg EPA + DHA g}^{-1} \text{ dw}$) of primary producers and consumers decreased along the climate-productivity gradient, but these trends were not observed in longer living secondary and tertiary consumers (i.e. fishes). Increasing total biomass of food webs along the climate-productivity gradient increased community EPA + DHA areal content, with this especially visible in invertivorous and piscivorous fish communities.

4.1 Changes in community structure, biomass and trophic pyramids (H1)

Across our study lake gradient — from northern ultraoligotrophic lakes to eutrophic lakes — food webs shifted towards dominance of warmer and murky water adapted species. These changes were the clearest in primary producers, where communities moved from diatom dominance to cyanobacteria, and secondary consumers, where salmonids were replaced by cyprinids. While many of our biomass calculations follow the relative density results, obtained in a previous study conducted along a partially overlapping gradient (Hayden et al. 2017), there were clear differences in biomass trends among trophic levels. Here, primary producers and secondary consumer

382 biomass increased most dramatically from cold ultraoligotrophic lakes towards warm eutrophic systems, but there
383 were no clear trends in primary consumers and biomass increment of tertiary consumers was shallower. Past food
384 web level studies have found similar patterns, whereby phytoplankton and invertivorous fish biomass tend to
385 respond most strongly to increasing nutrient concentrations (Hanson and Leggett 1982, Jeppesen et al. 2000,
386 Carpenter et al. 2001). Moreover, joint effects of increasing temperature and productivity boost food web level
387 change where oligotrophic subarctic lakes are mainly fuelled by benthic algae, but gradually shift towards
388 phytoplankton derived energy sources towards warmer and more productive lakes (Vadeboncoeur et al. 2003,
389 Hayden et al. 2019). As key drivers of the biomass increment in our data set for primary producers are
390 cyanobacteria and for secondary consumers cyprinid fish those are both adapted to warm waters (Kosten et al.
391 2012, Rolls et al. 2017). Both are competitively superior in warmer and productive environment as many
392 cyanobacterial taxa can fix nitrogen directly from air and form dense colonies to avoid predation, whilst cyprinids
393 across the region have omnivorous diets and very high fecundity (Kosten et al. 2012; Winfield and Nelson 1991,
394 Lappalainen et al. 2008). Such uneven changes in community structure and biomass in different trophic levels
395 were critical in shaping food webs and trophic pyramids.

396 Biomass patterns across trophic levels showed contrasting trends in response to increasing temperature and
397 productivity. This corroborates the “Green World Hypothesis”, where primary producers (phytoplankton) are
398 bottom-up controlled by nutrients, and primary consumers (zooplankton and benthos) are top-down controlled
399 by invertivorous fish (Hairston et al. 1960). However, this model is a simplification of complex aquatic food
400 webs such as the study lakes, as all additionally contain tertiary consumers (e.g. Arctic charr, pike; although their
401 relative biomass and proportional contribution to trophic pyramids was variable). Whilst top consumers biomass
402 increment was shallower compared to invertivorous fish biomass with increasing temperature and productivity,
403 the most diverse piscivore communities colonizing all lake habitats inhabited coldest and most nutrient poor lakes
404 only. Previous work from these cold and clear lakes suggest a strong top-down role of piscivorous fish on
405 invertivorous fish density and biomass (Jensen et al. 2015, Thomas et al. 2017, Kahilainen et al. 2019). These
406 cold and nutrient poor lakes have generally low biodiversity that promotes both highly size structured fish
407 populations, i.e. strong year class dominance for 10–15 years, and potential for strong trophic cascades (Byström
408 2006, Hayden et al. 2014a, Kahilainen et al. 2019). This likely explains the diverse shape of trophic pyramids we
409 observed, especially in ultra-oligotrophic and oligotrophic lakes. Increasing temperature and nutrients are
410 fundamental controls that decrease piscivore top-down control and boost bottom-up processes, whereas trophic

pyramids seem to stabilize into a hourglass shape in eutrophic lakes. Such trophic pyramid shape is obviously very persistent as common biomanipulation efforts of mass removal of invertivorous consumers (e.g. roach) tend to quickly return to original state (Carpenter et al. 1985, Hansson et al. 1998). Therefore, it is likely that especially in eutrophic lakes the piscivore predation on invertivorous fish is not limiting their population size, as observed elsewhere (e.g. Bartrons et al. 2020). Nutrient concentration is well-known driver of alternative stable states of lakes (Scheffer and Carpenter 2003) and underlying mechanisms maintaining resilience of eutrophic state may include a hourglass shape of trophic pyramid driven by proportionally high biomass of primary producers and secondary consumers (Jeppesen et al. 2010). Yet, the nutrient level and reason for the possible tipping point of the lake food web communities should be further evaluated in future.

Fig. 4. Relative biomass (A) and FA stock (B) pyramids by food web compartments for the lake types. The pyramid steps represent lake type averages of relative biomass or EPA+DHA areal content and are ordered with trophic level from bottom-up order: 1) phytoplankton, 2) invertebrates, 3) invertivorous fish and 4) piscivorous fish. The second trophic level (invertebrates) are divided among profundal benthos, littoral benthos and zooplankton with patterns: transparent, spots, stripes respectively. Different lake types, ultraoligotrophic, oligotrophic, mesotrophic and eutrophic respectively, are separated into different columns delineated with dashed lines and additionally with light grey, grey, dark grey, black respectively. The lake specific data is presented at Fig. S2. Abbreviations in legend are BMI = benthic macroinvertebrates and ZPL = zooplankton.

429 4.2 Changes in EPA+DHA content of food web components (H2)

430 The nutritional quality ($\mu\text{g EPA} + \text{DHA mg}^{-1} \text{ dw}$) of primary producers and consumers with short lifecycles (i.e.
431 invertebrates) showed a decreasing trend towards warmer and more productive lakes, while in secondary and
432 tertiary vertebrate consumers (i.e. fishes) such trends in nutritional quality were not apparent. Along the
433 environmental gradient, the phytoplankton community shifted towards more cyanobacteria-dominated
434 communities, which are non-EPA and non-DHA synthesizing phytoplankton (e.g. Taipale et al. 2016). The
435 decrease in zooplankton EPA + DHA content varied with an increasing abundance of small cladoceran and
436 cyclopoid copepods. There are many differences in life history strategies between different zooplankton taxa,
437 where the calanoid *Eudiaptomus graciloides*, the dominant copepod in cold oligotrophic lakes, tends to
438 accumulate lipids (including FAs) to survive winter, whereas short-lived cladocerans form resting stages and do
439 not need high body fat reserves (Hiltunen et al. 2016, Grosbois et al. 2017). In a recent study, Senar et al. (2019)
440 investigated a similar nutrient (total phosphorus 6–48 $\mu\text{g L}^{-1}$) and colour (dissolved organic carbon 2–10 mg L^{-1})
441 gradient in Canadian lakes, but did not record clear decrease in zooplankton taxa FA content. However, their
442 study region was warmer and did not contain strong temperature gradients, which have clear influence on lipid
443 rich copepod abundance in zooplankton communities and thus PUFA content (Gladyshev et al. 2011, Hiltunen
444 et al. 2016, Senar et al. 2019).

445 Decreasing nutritional quality ($\mu\text{g EPA} + \text{DHA mg}^{-1} \text{ dw}$) in primary producers was predicted to result in similar
446 trends in secondary and tertiary consumers (Ahlgren et al. 1996, Taipale et al. 2016). However, we did not find
447 this to be the case and instead the EPA + DHA content of fish population was generally stable, in contrast to our
448 second hypothesis. This could be related to diversity in lipid metabolism of different fish species during different
449 development stages, since our study included many fish species at different developmental stages. A range of
450 aquaculture and experimental studies indicate that EPA and DHA supplement increase fish individual growth
451 and to some extent the muscle FA content of adult fish (Bou et al. 2017, Yeşilayer and Kaymak 2020). However,
452 similar evidence from the wild is very difficult to obtain due to limited food resources, slow growth rate of fish,
453 long turnover time of muscle tissue, reproduction cycle, and species-specific differences in lipid storages
454 (Jørgensen et al. 1997, Thomas and Crowther 2015, Keva et al. 2019). One alternative for stable fish EPA + DHA
455 content could be that the ability for conversion of DHA from ALA varies greatly among fish species and
456 development stage (Geay et al. 2016, Kabeya et al. 2018, Ishikawa et al. 2019). Since, benthic macroinvertebrates
457 included only a minor amount of DHA as reported also previously, zooplankton is clearly the most likely dietary

source of DHA for fish (e.g. Makhutova et al. 2016; Vesterinen et al. 2020). The EPA + DHA content of fish muscle did not differ among feeding habitats (zooplanktivore, benthivore, piscivore), possibly providing evidence for selective transfer or utilization of FAs in fish (Strandberg et al. 2015). Previous results from subarctic lakes indicated that the turnover rate of whitefish (*Coregonus lavaretus*) muscle is slow, and thus stable isotope ratios and fatty acid content responded very slowly to any diet change (Thomas and Crowther 2015, Hayden et al. 2014a, Keva et al. 2019, Thomas et al. 2019). Our results did not support the idea that prey quality is essential to supporting fish consumer biomass or quality. Together, these results suggest that lipid metabolism is variable and complex among different fish species and their life stages, where generalization of temperature and productivity induced responses to fatty acid content and even further to consumer biomass require more laboratory and field work with wild fish populations.

4.3 Changes in community EPA + DHA areal content (H3)

The climate-productivity gradient of subarctic study lakes included both eutrophication and browning processes from cold and clear water lakes toward warm and murky waters (Hayden et al. 2019). While the EPA + DHA content of primary producers and consumers did show a clear decrease as suggested by earlier studies (Taipale et al. 2016, Creed et al. 2018), the EPA + DHA areal content at a systemic level did not show corresponding decrease due to massive increase of total biomass; similar patterns have previously been observed in mesocosm studies of benthic communities (Scharnweber et al. 2020). Surprisingly, EPA + DHA areal content in secondary and tertiary consumers indeed increased towards more murky lakes, indicating that total biomass clearly overrode the decline of quality. Changes in phytoplankton EPA + DHA areal content were highest in more eutrophic lakes, even if cyanobacteria contribution to this would be bypassed highlighting the importance of biomass to community EPA + DHA areal content and potentially to production as well. The total areal FA content does not exhibit a 1:1 relationship with the production of phytoplankton due to taxa specific production rates (Taipale et al. 2020). However, even with a far lower areal content to production ratio in eutrophic lakes, the system level production of EPA + DHA would still be higher in more eutrophic lakes due to massive phytoplankton biomass increment from oligotrophic towards eutrophic lakes. Therefore, we argue that in the studied climate and productivity gradient the total production of fatty acids are higher in warm murky than cold and clear water lakes.

484 4.4 Caveats

485 While our sampling protocol did not cover all the food web components, our results from sampled organisms are
486 in general comparable to previous studies conducted from subarctic or boreal lakes. The biomass estimates of
487 fish consumers were derived from simultaneously collected echosounding and gill net CPUE data of pelagic
488 whitefish and vendace, which were collected from a subset of the same study lakes during optimal sampling
489 window using standardized protocols suitable for these two species inhabiting all lakes in current study (Malinen
490 et al. 2014). Our total fish biomass estimates of from ultra-oligotrophic to mesotrophic lakes corroborates well
491 with biomass estimates derived from subarctic Canada (Samarasin et al. 2015). In addition, results from our
492 eutrophic lakes correspond to biomass estimates derived from mark-recapture, population analysis and
493 echosounding methods of boreal eutrophic lakes (Olin et al. 2017, Rask et al. 2020). The comparison of biomass
494 results of primary producers and primary consumer values to earlier studies from boreal lakes (Leppä et al. 2003,
495 Nurminen et al. 2018) indicate broadly similar estimates, but clearly lower values than hypereutrophic and
496 warmer lakes (Jeppesen et al. 2000, Gyllström et al. 2005). Future studies should include biomass estimates of
497 benthic algae as they are very important sources of energy in oligotrophic subarctic lakes (Vadeboncouer et al.
498 2003, Hayden et al. 2019), but could be important in other types of lakes too (Vesterinen et al. 2016,
499 Vadeboncouer and Power 2017). Assuming a high benthic-to-pelagic production ratio (70%) in our
500 ultraoligotrophic lakes and low ratio (0%) in shallow eutrophic lakes (Vadeboncoeur et al. 2008) the increment
501 in primary producer biomass among the lake gradient would be less pronounced and this would affect also the
502 biomass pyramids. However, whole food web primary production is known to increase along phosphorous
503 gradients (Vadeboncoeur et al. 2003) and the biomass pyramids are more persistent to the changes in one trophic
504 level biomass share due to multiple trophic levels accounting the total biomass. To make future fatty acid budget
505 and production calculations more accurate we suggest analysing whole fish or creating species specific
506 conversion factors from muscle tissue to whole body.

507 4.5. Conclusions

508 While climate warming trends have been evident in the last decades in Finnish Lapland (Hayden et al. 2014b),
509 increases in lake productivity via catchment greening and especially encroachment of the treeline will likely take
510 much longer to become apparent. Historically, the treeline of Scots pine has been located in the highest latitude
511 lakes of our study with circa 2.5° C higher July air temperatures, indicating the potential for alteration of
512 catchment vegetation and lake productivity towards north (Kultti et al. 2006). While the lake productivity shifts

apparent in our study systems originate from intensive forestry activities, there is increasing evidence of resource use related land-use in subarctic focusing on oil and gas drilling, and mining, as well as their associated infrastructure such as roads, pipelines and tailing ponds; activities that are simultaneously changing catchments and lake ecosystems with climate (e.g. Schindler & Smol 2006; Cott et al. 2015, Denisov et al. 2020). Under current study settings, we show that increasing temperature and productivity have major impacts on lake ecosystems, shifting communities towards warm and murky water adapted taxa, where especially biomass of cyanobacteria and cyprinid fish are increasing. These have a major effect on lake food webs, where increasing biomass of primary producers and secondary consumers shift trophic pyramid shapes towards a persistent hourglass shape. Based on our findings, increasing temperature and productivity did reduce phytoplankton, zooplankton and profundal benthos community EPA + DHA content, but these changes in prey quality did not alter fish community EPA + DHA content. Instead, fish community areal EPA+DHA content did increase along the gradient due to a massive increment in fish biomass. While we are not proposing direct predictions of near future food web structure and quality, our results from a pronounced climate and productivity gradient clearly showed that warmer and murkier water adapted species will likely increase their biomass share, whereas a decrement in EPA+DHA content may only be observed in primary producers and consumers.

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Author contributions

KKK provided the original idea for the paper. KKK, SJT and OK contributed planning the manuscript. Field work was conducted mainly by KKK, SMT and BH. Fatty acid extraction and analysis was performed mostly by

OK, with contributions from SJT, SMT, JV, PK. OK compiled data, conducted statistical analyses and drafted the first version of the manuscript. All authors contributed to subsequent revisions of the manuscript.

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Data sharing and data accessibility

Supplementary data including 7 tables and 3 figures related to this article can be found at Global Change Biology web page [type URL here]. More data that support the findings of this study are available from the corresponding author upon reasonable request.

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826 7. Figure legends

827 Fig. 1. Map of the study region (A) in northern Fennoscandia and boxplot figures of the basic lake chemistry (B–D) and
 828 physics (E–F) of the sampled lakes. The study lakes are marked with grey shade shapes (A) or boxes (B–D) indicating
 829 different lake types (light grey = ultraoligotrophic, grey = oligotrophic, dark grey = mesotrophic, black = eutrophic).
 830 Abbreviations in x-axes labels are named as following: TotP=total phosphorous (B), TotN = total nitrogen (C), DOC =
 831 dissolved organic carbon (D), Temp = average air temperature in June–September 1981–2010 (E), CompD = compensation
 832 depth i.e. water depth where 1% surface light is left (F).

833 Fig. 2. Community structure (A), biomass (B) and computed community quality (FA content, C) across different lake types
 834 (x-axis). Food web community compartments: phytoplankton (1), zooplankton (2), littoral benthos (3), profundal benthos
 835 (4), invertivorous fish (5) and piscivorous fish (6) are presented in different columns. The coloured bars indicate average
 836 taxa values of different lake types as following: normalized relative community composition (A: biomass %), lake type
 837 average biomass (B1–B2: mg dw m⁻³, B3–B6: kg dw ha⁻¹) and lake type average community EPA and DHA content (C: mg
 838 FA g⁻¹ dw). Lake specific community bulk FA content is derived from the FA analysed bulk sample (C2: zooplankton) and
 839 calculated for other food web community compartments (C1, C3–C6) from taxa specific biomass contribution and fatty acid
 840 content. Whiskers on top of the lake type average (B and C rows) represents + SD.

841 Fig. 3. Linear regression models showing A–B: Community biomass (kg dw ha⁻¹) and quality (mg EPA+DHA g⁻¹ dw)
 842 against climate-productivity index (CPi) and C: EPA + DHA areal content (kg EPA+DHA ha⁻¹) against total food web
 843 biomass (kg dw ha⁻¹). Food web community compartments: phytoplankton (1), zooplankton (2), littoral benthos (3),
 844 profundal benthos (4), invertivorous fish (5) and piscivorous fish (6) are presented in different columns. The grey shaded
 845 shapes indicate different lake trophy corresponding to Fig. 1: light grey square = ultraoligotrophic, grey dot = oligotrophic,
 846 dark grey triangle = mesotrophic, black diamond = eutrophic. Linear regressions fits (bolded line), 95% confidence limit
 847 (grey shaded areas) and adjusted coefficient of determination (r^2) are presented in the figures if the model was statistically
 848 significant ($p < 0.05$). Linear regression equations, F statistics, adjusted r^2 and p values are presented for each model in Table
 849 S6.

850 Fig. 4. Relative biomass (A) and FA stock (B) pyramids by food web compartments for the lake types. The pyramid steps
 851 represent lake type averages of relative biomass or EPA+DHA areal content and are ordered with trophic level from bottom-
 852 up order: 1) phytoplankton, 2) invertebrates, 3) invertivorous fish and 4) piscivorous fish. The second trophic level
 853 (invertebrates) are divided among profundal benthos, littoral benthos and zooplankton with patterns: transparent, spots,
 854 stripes respectively. Different lake types, ultraoligotrophic, oligotrophic, mesotrophic and eutrophic respectively, are
 855 separated into different columns delineated with dashed lines and additionally with light grey, grey, dark grey, black
 856 respectively. The lake specific data is presented at Fig. S2. Abbreviations in legend are BMI = benthic macroinvertebrates
 857 and ZPL = zooplankton.

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