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

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

8

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23 HUFA

## 24 Abstract

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°C and precipitation: +30%)  
30 and chemical (dissolved organic carbon: +10mg L<sup>-1</sup>, total phosphorus: +45µg L<sup>-1</sup> and total nitrogen: +1000µg  
31 L<sup>-1</sup>) 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<sup>-1</sup> 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 (kg EPA+DHA ha<sup>-1</sup>) 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 +2–5 °C  
49 and +10–30%, respectively, by the end of the 21<sup>st</sup> 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 and Smol 2006; Huntington et  
54 al. 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

81 et al., 2017). Furthermore, the subarctic landscape is scattered with lakes that provide abundant and well defined  
82 ecosystems for food web diversity studies (Lau et al. 2020). Increasing temperature and productivity has been  
83 shown to shift subarctic lake communities towards more numerous, diverse, smaller-bodied, warmer-water  
84 adapted taxa which are more reliant on pelagic energy sources (Hayden et al. 2017, Hayden et al. 2019). However,  
85 we do not know how increasing temperature and productivity affects energy transfer efficiency and thus biomass  
86 distribution across different trophic levels. Aquatic food webs in many Arctic areas are based on production and  
87 transfer of lipids from primary producers to top consumers, where seasonal storage of lipids is important for  
88 survival and reproduction of long lived organisms at higher trophic levels (e.g. Jørgensen et al. 1997, Armstrong  
89 and Bond 2013). An important subgroup of lipids are polyunsaturated fatty acids (PUFAs), providing essential  
90 components for cell development and functioning, however the distribution of lipids and fatty acids varies  
91 greatly among taxa and trophic levels. While there are several PUFAs, eicosapentaenoic acid (20:5n-3, EPA)  
92 and docosahexaenoic acid (22:6n-3, DHA) are considered the most important since they are essential for growth,  
93 neural development and reproduction of consumers (Arts et al, 2001, Bou et al. 2017, Yeşilayer and Kaymak  
94 2020). Only certain algae groups, such as dinoflagellates, diatoms and cryptophytes, are able to produce EPA  
95 and DHA efficiently and are abundant in cold and nutrient poor lakes (Taipale et al. 2013, 2016). However, warm  
96 and eutrophic lake primary producer communities, often dominated with cyanobacteria, are inefficient in EPA  
97 and DHA production (Müller-Navarra et al. 2000, 2004, Taipale et al. 2013, 2016). Some species can convert  
98 shorter chain fatty acids to EPA and DHA (Geya et al. 2016, Ishikawa et al. 2019), but in many vertebrates this  
99 process is considered energetically expensive and thus direct sources from high quality prey are often selected  
100 (Twining et al. 2016, Keva et al. 2019). This suggest that at a food web level, differences in primary producer  
101 communities induced by temperature and productivity may govern the quality of higher trophic levels (Hixson  
102 and Arts 2016, Colombo et al. 2020).

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

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

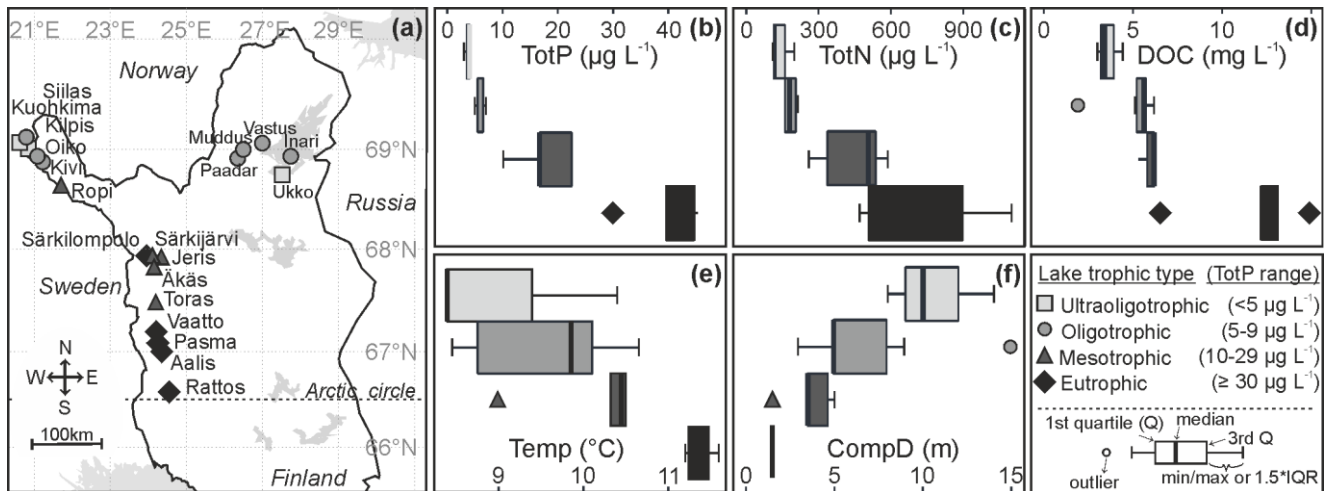
116

## 117 2. Materials and Methods

### 118 2.1 Environmental variables

119 We sampled 20 lakes, located in Finnish Lapland across the Tornio-Muoniojoki and Paatsjoki watercourses,  
120 spanning northern European climatic (average air temperature in June–September from 1980–2010: 8.4–11.6°C  
121 and precipitation 197–257 mm a<sup>-1</sup>) and water chemistry (dissolved organic carbon; DOC: 1.9–14.9 mg L<sup>-1</sup>, total  
122 phosphorus; TotP: 3–48 µg L<sup>-1</sup> and total nitrogen; TotN: 110–1100 µg L<sup>-1</sup>) gradients (Table S1, Fig. 1). Here,  
123 all lakes are considered subarctic and located north of Arctic Circle (AMAP 1998). Climatic differences originate  
124 from latitudinal and altitudinal gradients, with temperature and precipitation lowest in northernmost lakes and  
125 progressively increasing towards the south. Climatic data were derived from nine Finnish Meteorological  
126 Institute weather stations situated within the study region and refer to long-term (1981–2010) average open-water  
127 season June–September air temperature and annual precipitation as rain (Hayden et al. 2019). Differences in lake  
128 productivity originate predominantly from variation in vegetation and land-use practices within the catchment  
129 (Jussila et al. 2014). The northernmost lakes are situated near pristine areas with anthropogenic impacts limited  
130 to nature tourism and reindeer herding, and from the timberline southwards industrial forestry activities including  
131 large-scale clear-cut areas, site preparation and intensive ditching (Jussila et al. 2014; Hayden et al. 2017; Ahonen  
132 et al., 2018, Table S1). Catchment area characteristics and land-use variables were derived with the Finnish  
133 Environment Institute VALUE-tool combining catchment and CORINE-database and open map data (Hayden et  
134 al. 2017; Ahonen et al. 2018). Lake location (coordinates, altitude), morphometrical data (area, depth, mean  
135 depth, volume) and water physical-chemistry (nutrients, light) were derived from the Finnish Environment  
136 Institute (HERTTA-database) and National Survey of Finland, or from our own sampling (Table S1). We  
137 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 ( $< 5 \mu\text{g L}^{-1}$ ,  $n=3$ ), 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).



144  
 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–f) indicating different  
 147 lake types (light grey = ultraoligotrophic, grey = oligotrophic, dark grey = mesotrophic, black = eutrophic). Abbreviations  
 148 in x-axes labels are named as following: TotP=total phosphorous (B), TotN = total nitrogen (c), DOC = dissolved organic  
 149 carbon (d), Temp = average air temperature in June–September 1981–2010 (e), CompD = compensation depth i.e. water  
 150 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) and stored in Lugol solution with added formaldehyde. Phytoplankton cell counts  
 156 were calculated under a microscope using the Utermöhl technique (Utermöhl 1958). Biomass estimations were  
 157 done using taxa morphology specific geometric formulas (Hillebrand et al. 1999) and adjusted with  
 158 experimentally derived carbon-mass ratios (Menden-Deuer and Lessard 2000). Phytoplankton community

159 composition was calculated as class specific percentage from carbon biovolume ( $\text{g C L}^{-1}$ ), and dry mass [dw] per  
160 unit area was calculated as well ( $\text{kg dw ha}^{-1}$ , hereinafter biomass) using lake specific euphotic zone.

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

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

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



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

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

### 212 2.3 Lipid extraction and fatty acid analysis

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

215 analysed. Fatty acids were analysed as methyl esters (e.g. Taipale et al. 2016), identified and quantified using a  
216 gas chromatograph attached to mass spectrometer. Samples were spiked with nonadecylic acid (PLFA c19:0).  
217 Lipids were extracted with 3 ml of chloroform-methanol solution (2:1 vol) and with sonicator (15 min). Ultra-  
218 pure water (0.75ml of MilliQ) was add to kimax tubes to separate water soluble compounds from lipids. Lipid  
219 extract was evaporated and 3 ml of 1% H<sub>2</sub>SO<sub>4</sub> add to kimax tube which was incubated in +50 °C for 20 h to  
220 produce fatty acid methyl esters (FAMEs). The produced FAMEs were diluted with hexane and analysed using  
221 a gas chromatograph attached to a mass spectrometer (GC-2010 Plus and QP-2010 Ultra, Shimadzu, Japan) with  
222 Zebron ZB-FAME column (30 m + 5m guardian × 0.25 mm × 0.2 μm). At the begin of the each GCMS run, the  
223 column temperature was held in 50°C for 1 min, followed by raising with 10 °C min<sup>-1</sup> to 130 °C, 7 °C min<sup>-1</sup> to  
224 180 °C, 2 °C min<sup>-1</sup> to 200 °C and was held there for 3 min which after the colon temperature was raised with 10  
225 °C min<sup>-1</sup> to 260 °C. The injection temperature was 270 °C and the interface temperature 250 °C, total column  
226 flow being 27.5 mL min<sup>-1</sup> and linear velocity 36.3 cm s<sup>-1</sup>.

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

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

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

#### 245 2.4. Lake specific community EPA + DHA content and areal content calculations

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

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

#### 268 2.5 Statistical methods

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

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

284

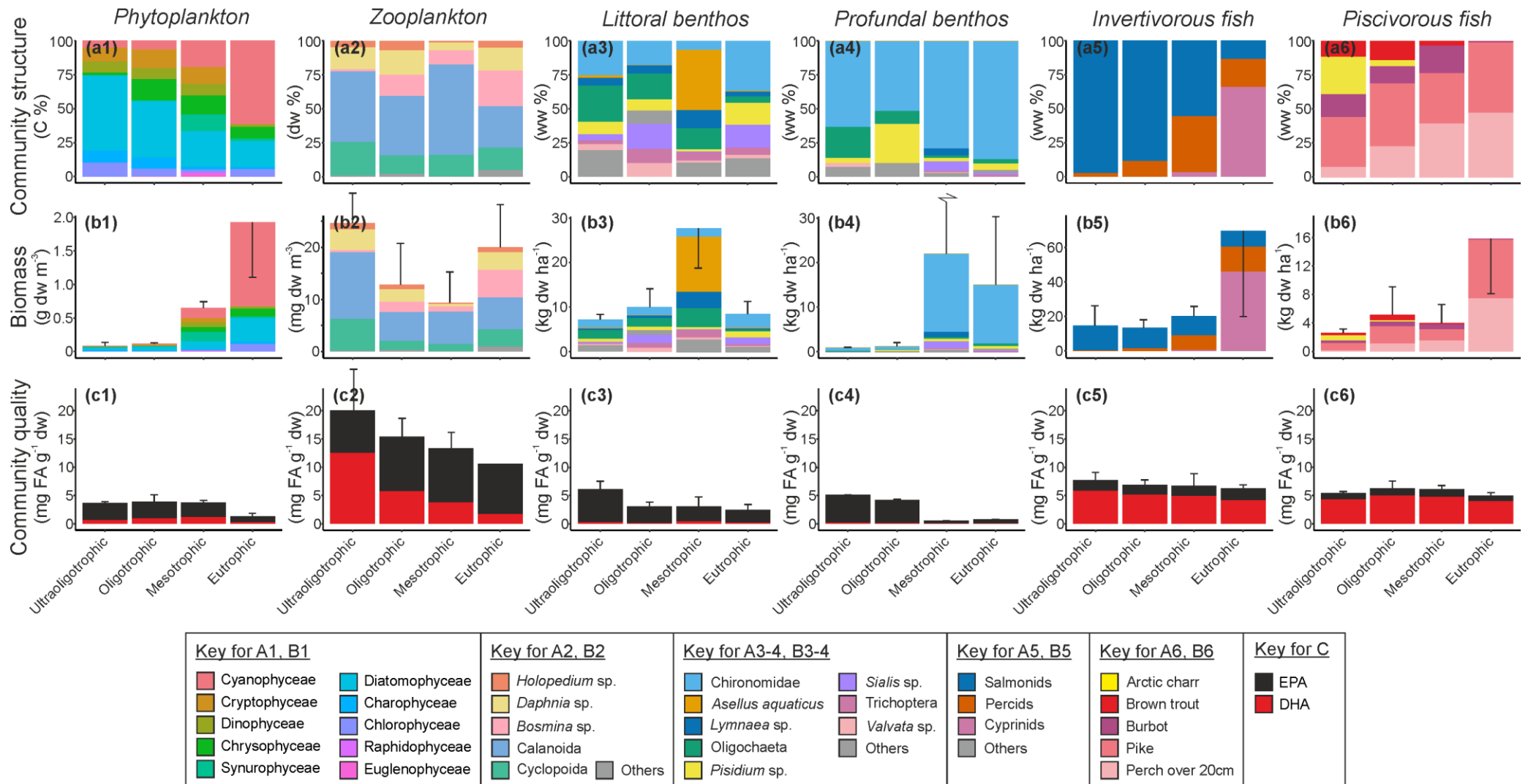
### 285 3. Results

#### 286 3.1 Changes in community structure, food web biomass and trophic pyramid shape (H1)

287 Lake communities showed shifts from cold to warmer adapted taxa with increasing temperature and productivity  
288 (Fig. 2). Phytoplankton changed from diatom dominated communities in ultraoligotrophic lakes towards  
289 cyanobacteria dominance in eutrophic lakes (Fig. 2 a1). Copepods contributed 50–80% of the total zooplankton  
290 community biomass along this gradient and calanoids had the highest biomass percentage in every lake type.  
291 However, copepod contribution was lowest in eutrophic lakes where cladocerans, especially *Bosmina* had a high  
292 biomass percentage (Fig. 2 a2). Littoral benthos communities were diverse throughout the lake gradient (Fig. 2  
293 a3): *Asellus* sp. and *Lymnaea* sp. reached the highest proportional contribution in mesotrophic lakes, whereas  
294 oligochaetes had the highest biomass contribution in ultraoligotrophic lakes and lowest in eutrophic lakes.  
295 Profundal benthos was mainly dominated by chironomids and their biomass contribution increased from  
296 ultraoligotrophic lakes (ca. 50%) towards eutrophic lakes (ca. 90%) (Fig. 2 a4). Invertivorous fish communities  
297 were dominated by salmonids (whitefish, vendace) in ultraoligotrophic lakes; by percids (perch and ruffe,  
298 *Gymnocephalus cernuus*) and salmonids in oligotrophic-mesotrophic lakes; and by cyprinids (roach *Rutilus*

299 *rutilus*, bleak *Alburnus alburnus*) in eutrophic lakes (Fig. 2 a5). Piscivorous pike and perch increased their  
300 biomass contribution progressively from ultraoligotrophic lakes (ca. 35% and 5%) towards eutrophic lakes (ca.  
301 50% for both species), whilst piscivorous Arctic charr and brown trout disappeared completely along the same  
302 gradient (Fig. 2 a6).

303 Phytoplankton mean mass increased more than twenty-fold between ultraoligotrophic ( $0.08 \pm 0.05$ ; mean  $\pm$  SD g  
304  $\text{dw m}^{-3}$ ) and eutrophic lakes  $1.9 \pm 0.8$  g  $\text{dw m}^{-3}$  (Fig. 2 b1), which was also evident for biomass along our lake  
305 gradient CPi (PC1) from north to south based on linear regression analysis (Fig. 3 a1). The lowest zooplankton  
306 biomass was observed in mesotrophic lakes ( $9.27 \pm 5.96$  mg  $\text{dw m}^{-3}$ ) (Fig. 2 b2), however no clear trend in  
307 biomass was observed along the lake gradient (CPi) based on linear regression (Fig. 3 a2). The overall highest  
308 littoral benthos biomass was observed in mesotrophic lakes (Fig. 2 b3), but no clear trend in biomass along the  
309 continuous CPi axis (Fig. 3 a3). The profundal benthos biomass was low in ultraoligotrophic lakes ( $0.4 \pm 0.3$  kg  
310  $\text{dw ha}^{-1}$ ) and increased towards eutrophic lakes ( $8.2 \pm 11.3$  kg  $\text{dw ha}^{-1}$ ). This trend was mainly caused by  
311 increasing chironomid biomass (Fig. 2 b4) and driven mainly by extremely high profundal benthos densities in  
312 two lakes with low oxygen (Fig. 3 a4). Generally invertivorous fish biomass was circa five times higher in  
313 eutrophic lakes ( $69.7 \pm 49.0$  kg  $\text{dw ha}^{-1}$ ) compared to other lake types (pooled average:  $15.8 \pm 12.9$  kg  $\text{dw ha}^{-1}$ )  
314 (Fig. 2 b5; Fig. 3 a5). The biomass of piscivorous fish was around four times higher in eutrophic lakes ( $15.9 \pm$   
315  $7.8$  kg  $\text{dw ha}^{-1}$ ) than other lake types (pooled average:  $4.2 \pm 3.2$  kg  $\text{dw ha}^{-1}$ ). (Fig. 2 b6), and a clear linear trend  
316 along the CPi axis was observed (Fig. 3 a6). These massive increases in primary producer and secondary  
317 consumer biomass compared primary and tertiary consumers were evident in changes to the trophic pyramid  
318 shape (Fig. 4, Fig. S2). Ultraoligotrophic and oligotrophic lakes showed variable shapes from typical pyramids  
319 to inverted pyramids to across different lakes, whilst most mesotrophic lakes were generally typical pyramids  
320 and eutrophic lakes had hour glass shaped biomass distributions (Fig. 4, Fig. S2).



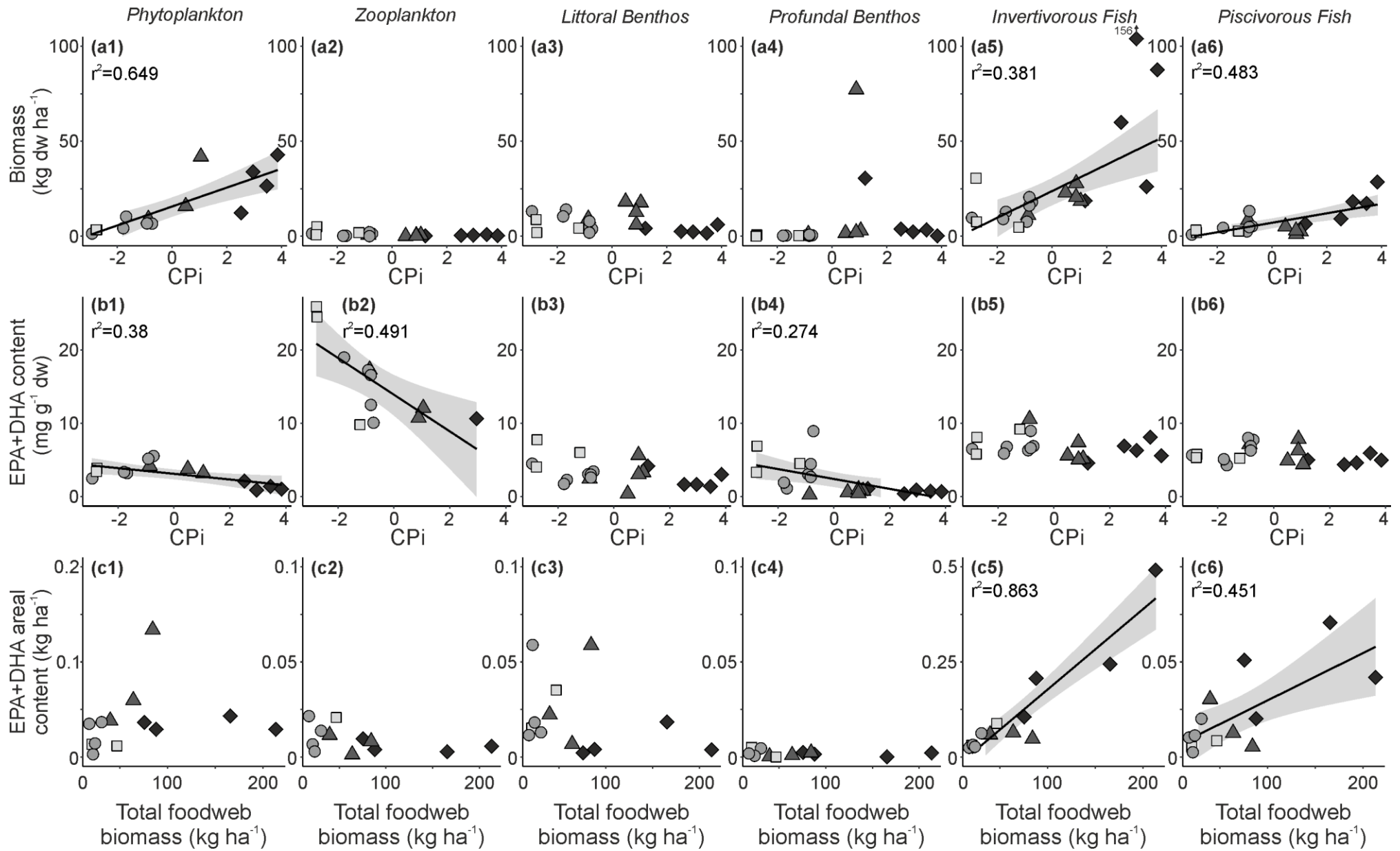
321  
 322 Fig. 2. Community structure (a), biomass (b) and computed community quality (FA content, c) across different lake types (x-axis). Food web community compartments: phytoplankton (1),  
 323 zooplankton (2), littoral benthos (3), profundal benthos (4), invertivorous fish (5) and piscivorous fish (6) are presented in different columns. The coloured bars indicate average taxa values of  
 324 different lake types as following: normalized relative community composition (a: biomass %), lake type average biomass (b1: g dw m<sup>-3</sup>, b2: mg dw m<sup>-3</sup>, b3–b6: kg dw ha<sup>-1</sup>) and lake type average  
 325 community EPA and DHA content (c: mg FA g<sup>-1</sup> dw). Lake specific community bulk FA content is derived from the FA analysed bulk sample (c2: zooplankton) and calculated for other food  
 326 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.

### 327 3.2 Changes in fatty acid content of food web components (H2)

328 Phytoplankton quality (EPA + DHA) was highest in oligotrophic and mesotrophic lakes, and clearly the lowest  
329 in eutrophic lakes (Table S6, Fig. 2 c1). Zooplankton quality was the highest in ultraoligotrophic lakes ( $20.1 \pm$   
330  $8.9 \text{ mg g}^{-1} \text{ dw}$ ; mean  $\pm$  SD) and progressively decreased towards eutrophic lakes ( $10.6 \text{ mg g}^{-1} \text{ dw}$ ) (Fig. 2 c2),  
331 but due to high variance and low sample size the EPA + DHA distributions did not differ statistically among the  
332 lake types (Table S6). Benthos quality was limited to the presence of EPA. Littoral and profundal benthos quality  
333 were the highest in ultraoligotrophic lakes and the lowest in eutrophic lakes (Table S6, Fig. 2 c3–4). There was  
334 no statistically significant differences in quality of invertivorous and piscivorous communities between lake types  
335 as EPA+DHA content remained stable (Table S6, Fig. 2 c5–6). EPA and DHA content of primary producers and  
336 consumers decreased along the CPi axis, but there was no statistically significant trend in secondary or tertiary  
337 consumers (Fig. 3 b1–6, Fig. S3).

### 338 3.3 Changes in community EPA + DHA areal content (H3)

339 The highest values of community EPA + DHA areal content came from invertivorous fish (pooled average  $\pm$  SD:  
340  $0.188 \pm 0.214 \text{ kg ha}^{-1}$ ), followed by piscivorous fish ( $0.050 \pm 0.054 \text{ kg ha}^{-1}$ ), phytoplankton ( $0.036 \pm 0.030 \text{ kg}$   
341  $\text{ha}^{-1}$ ), 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  
342 ( $0.007 \pm 0.017 \text{ kg ha}^{-1}$ ), respectively. Trends in EPA + DHA areal content of phytoplankton, zooplankton, and  
343 benthos communities with total food web biomass were not significant (Fig. 3 c1-4), though showing generally  
344 opposing patterns between trophic levels: EPA + DHA areal content of phytoplankton community was smallest  
345 in oligotrophic lakes but remained relatively stable in meso- and eutrophic lakes, whilst invertebrate taxa showed  
346 the opposite pattern. The areal contents of EPA + DHA of invertivorous (adj. $r^2=0.86$ ) and piscivorous  
347 (adj. $r^2=0.45$ ) fish communities were positively related to total biomass of food web (Fig. 3 c5–6, Table S7).  
348 Community EPA + DHA areal content showed a similar pattern as total biomass along the studied lake gradient,  
349 emphasizing the fundamental link between total community biomass and EPA + DHA areal content (Fig. 3a, c,  
350 Table S7).





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

## 361 4. Discussion

### 362 4.1 Major trends

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

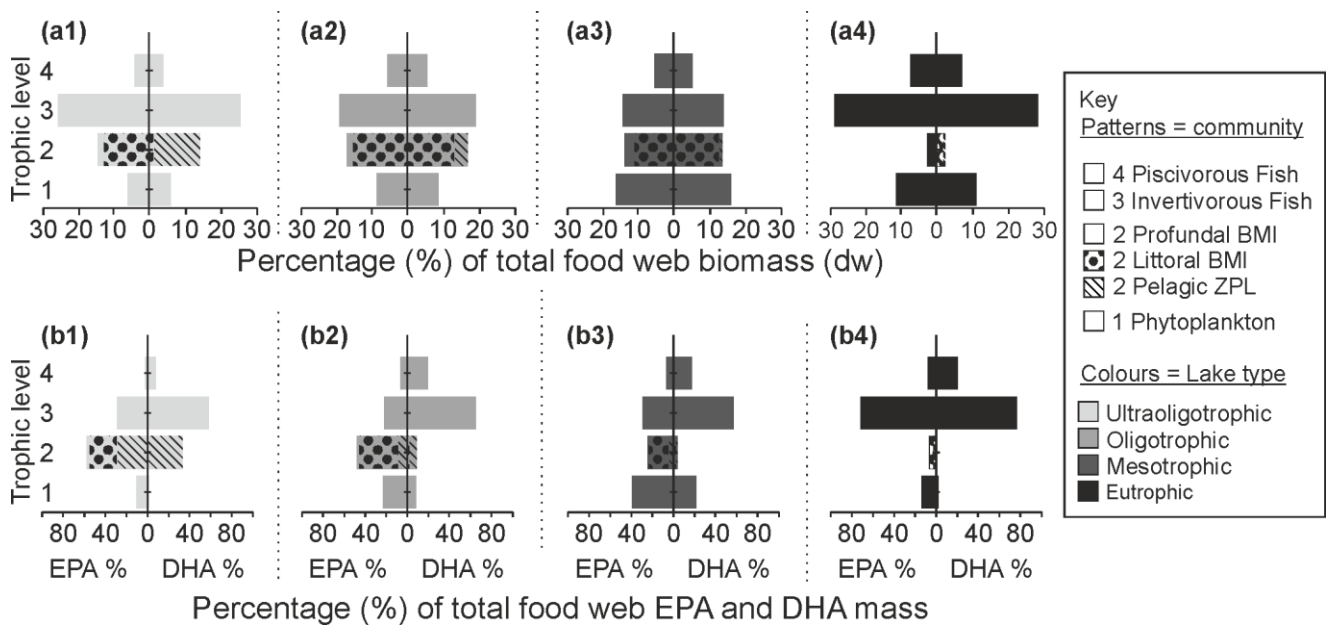
### 374 4.1 Changes in community structure, biomass and trophic pyramids (H1)

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

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

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

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



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

## 428 4.2 Changes in EPA+DHA content of food web components (H2)

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

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

457 source of DHA for fish (e.g. Makhutova et al. 2016; Vesterinen et al. 2020). The EPA + DHA content of fish  
458 muscle did not differ among feeding habitats (zooplanktivore, benthivore, piscivore), possibly providing evidence  
459 for selective transfer or utilization of FAs in fish (Strandberg et al. 2015). Previous results from subarctic lakes  
460 indicated that the turnover rate of whitefish (*Coregonus lavaretus*) muscle is slow, and thus stable isotope ratios  
461 and fatty acid content responded very slowly to any diet change (Thomas and Crowther 2015, Hayden et al.  
462 2014a, Keva et al. 2019, Thomas et al. 2019). Our results did not support the idea that prey quality is essential to  
463 supporting fish consumer biomass or quality. Together, these results suggest that lipid metabolism is variable and  
464 complex among different fish species and their life stages, where generalization of temperature and productivity  
465 induced responses to fatty acid content and even further to consumer biomass require more laboratory and field  
466 work with wild fish populations.

#### 467 4.3 Changes in community EPA + DHA areal content (H3)

468 The climate-productivity gradient of subarctic study lakes included both eutrophication and browning processes  
469 from cold and clear water lakes toward warm and murky waters (Hayden et al. 2019). While the EPA + DHA  
470 content of primary producers and consumers did show a clear decrease as suggested by earlier studies (Taipale  
471 et al. 2016, Creed et al. 2018), the EPA + DHA areal content at a systemic level did not show corresponding  
472 decrease due to massive increase of total biomass; similar patterns have previously been observed in mesocosm  
473 studies of benthic communities (Scharnweber et al. 2020). Surprisingly, EPA + DHA areal content in secondary  
474 and tertiary consumers indeed increased towards more murky lakes, indicating that total biomass clearly overrode  
475 the decline of quality. Changes in phytoplankton EPA + DHA areal content were highest in more eutrophic lakes,  
476 even if cyanobacteria contribution to this would be bypassed highlighting the importance of biomass to  
477 community EPA + DHA areal content and potentially to production as well. The total areal FA content does not  
478 exhibit a 1:1 relationship with the production of phytoplankton due taxa specific production rates (Taipale et al.  
479 2020). However, even with a far lower areal content to production ratio in eutrophic lakes, the system level  
480 production of EPA + DHA would still be higher in more eutrophic lakes due to massive phytoplankton biomass  
481 increment from oligotrophic towards eutrophic lakes. Therefore, we argue that in the studied climate and  
482 productivity gradient the total production of fatty acids are higher in warm murky than cold and clear water lakes.

#### 483 4.4 Caveats

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

#### 506 4.5. Conclusions

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

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

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534 564/2013 & FI-487/2013) and the European Union directive (2010/63/EU) on the protection of animals used for  
535 scientific purposes were applied.

## 536 Author contributions

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

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

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#### 545 Data sharing and data accessibility

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

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829 7. Figure legends

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

836 Fig. 2. Community structure (a), biomass (b) and computed community quality (FA content, c) across different lake types  
837 (x-axis). Food web community compartments: phytoplankton (1), zooplankton (2), littoral benthos (3), profundal benthos  
838 (4), invertivorous fish (5) and piscivorous fish (6) are presented in different columns. The coloured bars indicate average  
839 taxa values of different lake types as following: normalized relative community composition (a: biomass %), lake type  
840 average biomass (b1: g dw m<sup>-3</sup>, b2: mg dw m<sup>-3</sup>, b3–b6: kg dw ha<sup>-1</sup>) and lake type average community EPA and DHA content  
841 (c: mg FA g<sup>-1</sup> dw). Lake specific community bulk FA content is derived from the FA analysed bulk sample (c2: zooplankton)  
842 and calculated for other food web community compartments (c1, c3–c6) from taxa specific biomass contribution and fatty  
843 acid content. Whiskers on top of the lake type average (b and c rows) represents + SD.

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

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

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