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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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Abstract

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

1. Introduction

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

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

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

Subarctic regions provide an excellent natural setting to study this phenomenon as they straddle boreal and Arctic 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 greately 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,

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^{-1}) and water chemistry (dissolved organic carbon; DOC: 1.9–14.9 mg L^{-1}, total
122 phosphorus; TotP: 3–48 µg L^{-1} and total nitrogen; TotN: 110–1100 µg L^{-1}) 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

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

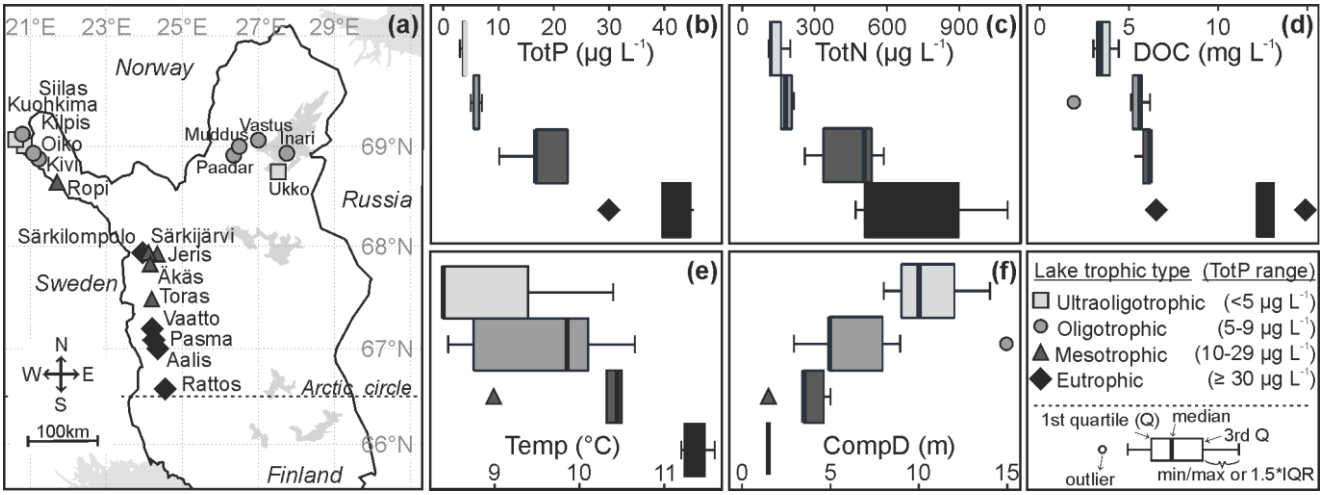


Fig. 1. Map of the study region (a) in northern Fennoscandia and boxplot figures of the basic lake chemistry (b–d) and physics (e–f) of the sampled lakes. The study lakes are marked with grey shade shapes (a) or boxes (b–f) indicating different lake types (light grey = ultraoligotrophic, grey = oligotrophic,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

2.2 Community composition and biomass

Quantitative phytoplankton taxa samples for eight of the study lakes were extracted from the HERTTA database (Finnish Environment Institute) and from a previous study for an additional six lakes (Taipale et al. 2016). Samples were collected from the epilimnion (0–2 m) with a Limnos or corresponding water sampler in late summer (August–September) and stored in Lugol solution with added formaldehyde. Phytoplankton cell counts were calculated under a microscope using the Utermöhl technique (Utermöhl 1958). Biomass estimations were done using taxa morphology specific geometric formulas (Hillebrand et al. 1999) and adjusted with experimentally derived carbon-mass ratios (Menden-Deuer and Lessard 2000). Phytoplankton community

159 composition was calculated as class specific percentage from carbon biovolume (g C L^{-1}), and dry mass [dw] per
160 unit area was calculated as well (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 µm) 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 (mg dw L^{-1}) and biomass was
170 calculated (kg dw ha^{-1}) using lake specific average depth.

171 Benthic macroinvertebrates were collected only from soft bottom with an Ekman grab (area 272 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 (g ww m^{-2}) was
176 calculated for each sample using Ekman area to 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 (≥1% light) or profundal (<1% light). Then whole lake bathymetry was used to calculate
180 mean benthic macroinvertebrate biomass (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 30×1.5 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^{-1} hour^{-1}. 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^{-1}) 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^{-1}). 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 <u>2.3 Lipid extraction and fatty acid analysis</u>

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

analysed. Fatty acids were analysed as methyl esters (e.g. Taipale et al. 2016), identified and quantified using a gas chromatograph attached to mass spectrometer. Samples were spiked with nonadecylic acid (PLFA c19:0). Lipids were extracted with 3 ml of chloroform-methanol solution (2:1 vol) and with sonicator (15 min). Ultra-pure water (0.75ml of MilliQ) was add to kimax tubes to separate water soluble compounds from lipids. Lipid extract was evaporated and 3 ml of 1% H_2SO_4 add to kimax tube which was incubated in +50 °C for 20 h to produce fatty acid methyl esters (FAMEs). The produced FAMEs were diluted with hexane and analysed using a gas chromatograph attached to a mass spectrometer (GC-2010 Plus and QP-2010 Ultra, Shimadzu, Japan) with Zebron ZB-FAME column (30 m + 5m guardian × 0.25 mm × 0.2 µm). At the begin of the each GCMS run, the 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 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 °C min^{-1} to 260 °C. The injection temperature was 270 °C and the interface temperature 250 °C, total column flow being 27.5 mL min^{-1} and linear velocity 36.3 cm s^{-1}.

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

We combined a small subset of fatty acid data from previous studies having a different focus (Taipale et al. 2016, Vesterinen et al. 2020). Total dataset consisted of 868 samples (Table S2: phytoplankton=32, zooplankton=26, littoral benthos=209, profundal benthos=34, invertivorous fish=377, piscivorous fish=190). Community specific lake average FA sample coverage of taxa specific biomass contributions stands as following: phytoplankton 93.2 ± 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 ± 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 (mg g^{-1} 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 (mg g^{-1} 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 (kg EPA + DHA ha^{-1}, herein after:
262 areal content) for primary producers and different consumers, we multiplied community biomass (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 (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*

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

Phytoplankton mean mass increased more than twenty-fold between ultraoligotrophic (0.08 ±0.05; mean ± SD g 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 gradient CPi (PC1) from north to south based on linear regression analysis (Fig. 3 a1). The lowest zooplankton biomass was observed in mesotrophic lakes (9.27 ± 5.96 mg dw m^{-3}) (Fig. 2 b2), however no clear trend in biomass was observed along the lake gradient (CPi) based on linear regression (Fig. 3 a2). The overall highest littoral benthos biomass was observed in mesotrophic lakes (Fig. 2 b3), but no clear trend in biomass along the continuous CPi axis (Fig. 3 a3). The profundal benthos biomass was low in ultraoligotrophic lakes (0.4 ± 0.3 kg dw ha^{-1}) and increased towards eutrophic lakes (8.2 ± 11.3 kg dw ha^{-1}). This trend was mainly caused by increasing chironomid biomass (Fig. 2 b4) and driven mainly by extremely high profundal benthos densities in two lakes with low oxygen (Fig. 3 a4). Generally invertivorous fish biomass was circa five times higher in 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}) (Fig. 2 b5; Fig. 3 a5). The biomass of piscivorous fish was around four times higher in eutrophic lakes (15.9 ± 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 along the CPi axis was observed (Fig. 3 a6). These massive increases in primary producer and secondary consumer biomass compared primary and tertiary consumers were evident in changes to the trophic pyramid shape (Fig. 4, Fig. S2). Ultraoligotrophic and oligotrophic lakes showed variable shapes from typical pyramids to inverted pyramids to across different lakes, whilst most mesotrophic lakes were generally typical pyramids and eutrophic lakes had hour glass shaped biomass distributions (Fig. 4, Fig. S2).

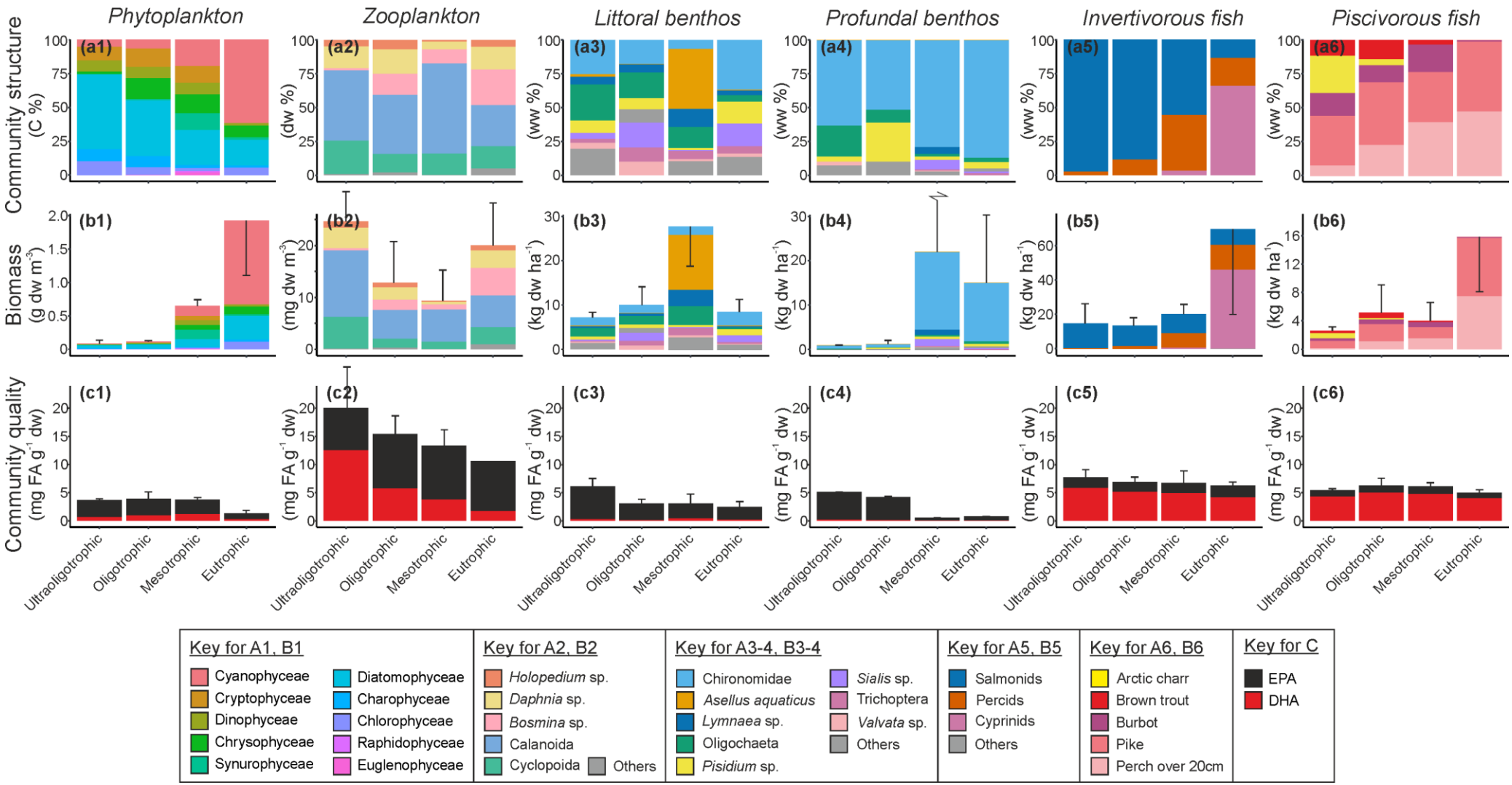


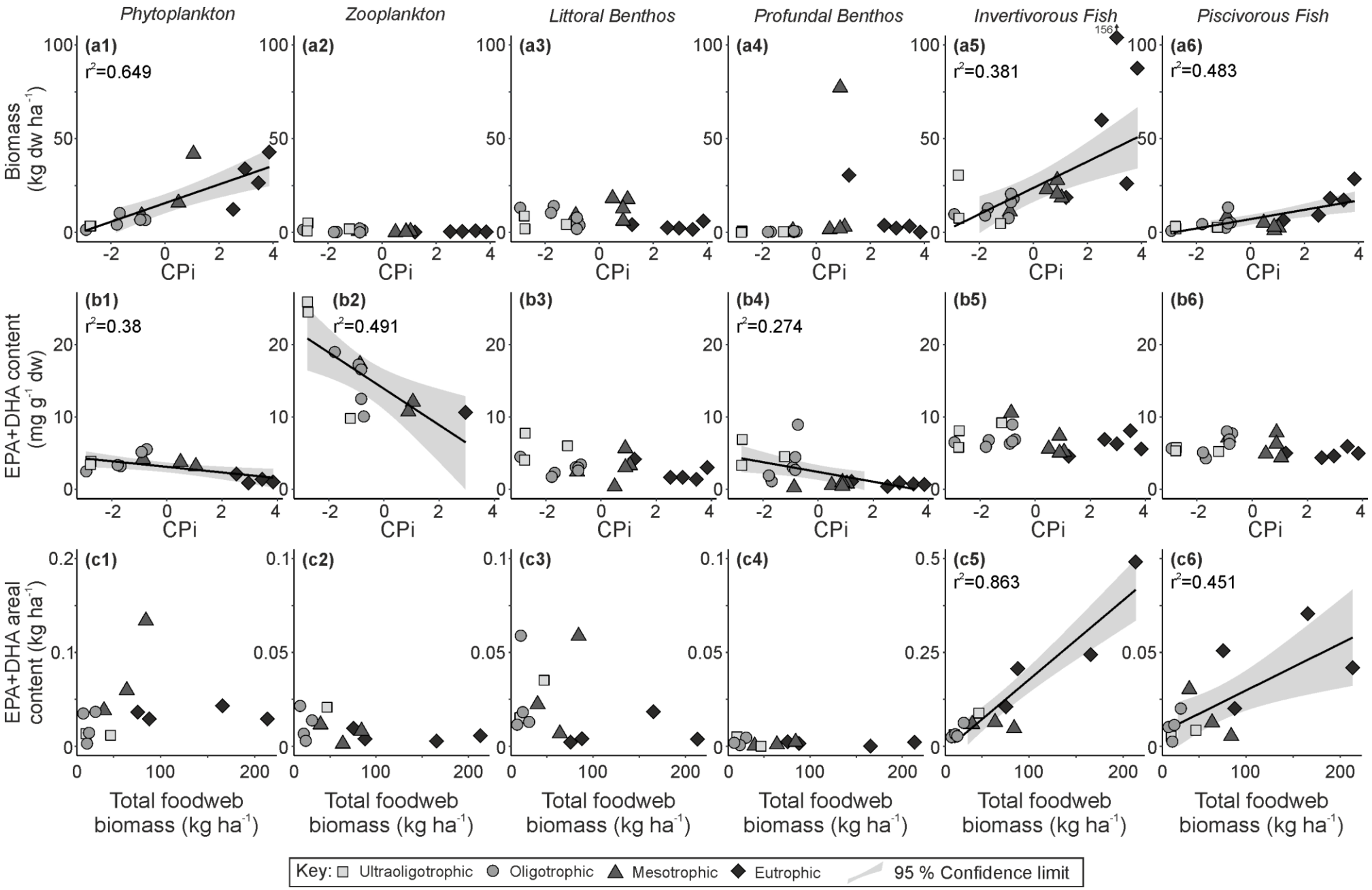
Fig. 2. Community structure (a), biomass (b) and computed community quality (FA content, c) across different lake types (x-axis). Food web community compartments: phytoplankton (1), zooplankton (2), littoral benthos (3), profundal benthos (4), invertivorous fish (5) and piscivorous fish (6) are presented 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: g dw m^{-3}, 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.

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

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

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

The highest values of community EPA + DHA areal content came from invertivorous fish (pooled average ± SD: 0.188 ± 0.214 kg ha^{-1}), followed by piscivorous fish (0.050 ± 0.054 kg ha^{-1}), phytoplankton (0.036 ± 0.030 kg ha^{-1}), littoral benthos (0.023 ± 0.019 kg ha^{-1}), pelagic zooplankton (0.015 ± 0.026 kg ha^{-1}) and profundal benthos (0.007 ± 0.017 kg ha^{-1}), respectively. Trends in EPA + DHA areal content of phytoplankton, zooplankton, and benthos communities with total food web biomass were not significant (Fig. 3 c1-4), though showing generally opposing patterns between trophic levels: EPA + DHA areal content of phytoplankton community was smallest in oligotrophic lakes but remained relatively stable in meso- and eutrophic lakes, whilst invertebrate taxa showed the opposite pattern. The areal contents of EPA + DHA of invertivorous (adj.r^2=0.86) and piscivorous (adj.r^2=0.45) fish communities were positively related to total biomass of food web (Fig. 3 c5–6, Table S7). Community EPA + DHA areal content showed a similar pattern as total biomass along the studied lake gradient, emphasizing the fundamental link between total community biomass and EPA + DHA areal content (Fig. 3a, c, Table S7).


Phytoplankton
Zooplankton
Littoral Benthos
Profundal Benthos
Invertivorous Fish
Piscivorous Fish
(a1)
r2=0.649
(a2)
(a3)
(a4)
(a5)
r2=0.381
156
(a6)
r2=0.483
Biomass (kg dw ha-1)
CPi
(b1)
r2=0.38
(b2)
r2=0.491
(b3)
(b4)
r2=0.274
(b5)
(b6)
EPA+DHA content (mg g-1 dw)
(c1)
(c2)
(c3)
(c4)
(c5)
r2=0.863
(c6)
r2=0.451
EPA+DHA areal content (kg ha-1)
Total foodweb biomass (kg ha-1)
Key: Ultraoligotrophic Oligotrophic Mesotrophic Eutrophic 95 % Confidence limit

351

Fig. 3. Linear regression models showing (a–b): Community biomass (kg dw ha^{-1}) and quality (mg EPA+DHA g^{-1} dw) against climate-productivity index (CPi) and (c): EPA + DHA areal content (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 (mg EPA + DHA g^{-1} 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.

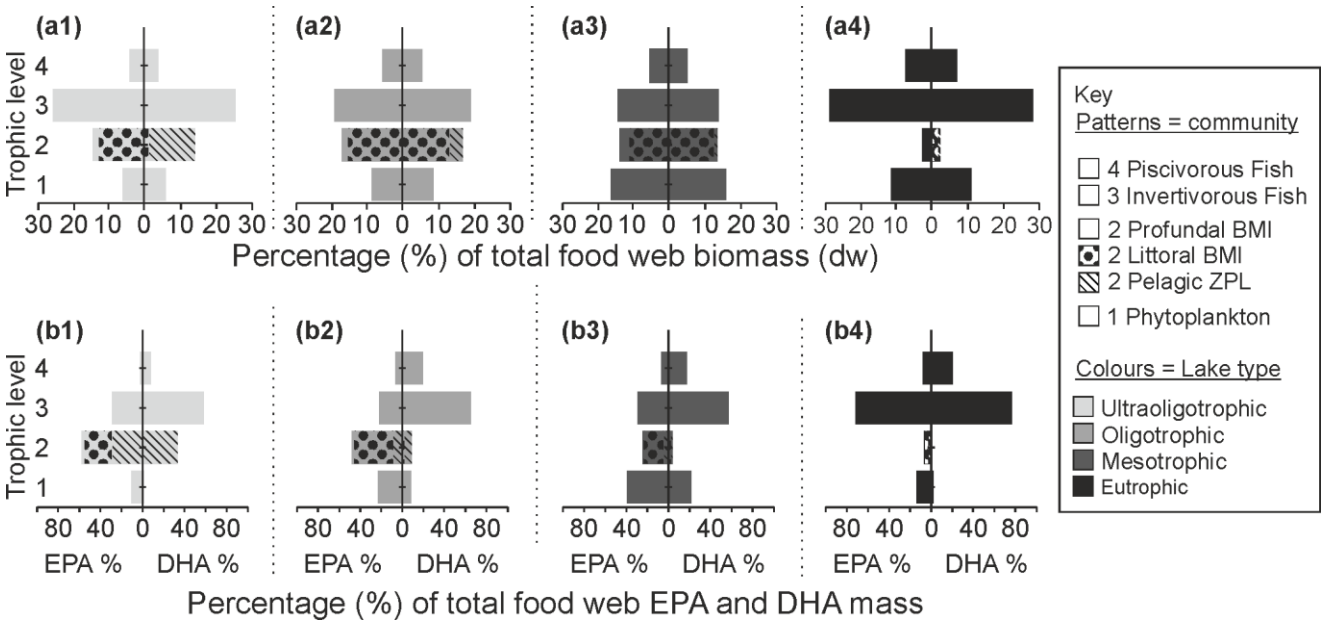
4.1 Changes in community structure, biomass and trophic pyramids (H1)

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

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.



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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 (µg EPA + DHA mg^{-1} 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 µg L^{-1}) and colour (dissolved organic carbon 2–10 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 (µg EPA + DHA mg^{-1} 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 (Vadeboncouer et al.
497 2003, Hayden et al. 2019), but could be important in other types of lakes too (Vesterinen et al. 2016,
498 Vadeboncouer 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

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

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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7. Figure legends

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

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: g dw m^{-3}, 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.

Fig. 3. Linear regression models showing (a–b): Community biomass (kg dw ha^{-1}) and quality (mg EPA+DHA g^{-1} dw) against climate-productivity index (CPi) and (c): EPA + DHA areal content (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.

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.