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1 **From clear lakes to murky waters - tracing the functional response of high-latitude lake**
2 **communities to concurrent ‘greening’ and ‘browning’**

3

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27

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32

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43

44 **Abstract**

45 Climate change and the intensification of land use practices are causing widespread
46 eutrophication of subarctic lakes. The implications of this rapid change for lake ecosystem
47 function remain poorly understood. To assess how freshwater communities respond to such
48 profound changes in their habitat and resource availability, we conducted a space-for-time
49 analysis of food-web structure in 30 lakes situated across a temperature-productivity gradient
50 equivalent to the predicted future climate of subarctic Europe (temperature +3°C, precipitation
51 +30% and nutrient +45 $\mu\text{g L}^{-1}$ total phosphorus). Along this gradient, we observed an increase in
52 the assimilation of pelagic-derived carbon from 25 to 75% throughout primary, secondary and
53 tertiary consumers. This shift was overwhelmingly driven by the consumption of pelagic detritus
54 by benthic primary consumers and was not accompanied by increased pelagic foraging by higher
55 trophic level consumers. Our data also revealed a convergence of the carbon isotope ratios of
56 pelagic and benthic food web endmembers in the warmest, most productive lakes indicating that
57 the incorporation of terrestrial derived carbon into aquatic food webs increases as land use
58 intensifies. These results, reflecting changes along a gradient characteristic of the predicted
59 future environment throughout the subarctic, indicate that climate and land use driven
60 eutrophication and browning are radically altering the function and fuelling of aquatic food webs
61 in this biome.

62

63 **Introduction**

64 Climate change and intensification of land use practices are modifying ecosystem productivity
65 across the globe (Vitousek 1994; Flynn *et al.* 2009). These changes are most pronounced in
66 Arctic and subarctic areas, where increases in temperature and precipitation exceed global
67 averages, resulting in an extension of the annual growth period (Bokhorst *et al.* 2008), an overall

68 greening of the landscape (Xu *et al.* 2013) and the range expansion of warm-adapted species
69 (Rolls *et al.* 2017). Increased exploitation of natural resources (e.g. infrastructure development,
70 forestry and mining) in these regions has increased supply of carbon, nitrogen and phosphorus
71 from catchments into watercourses (Payette *et al.* 2001). The co-occurrence of both stressors and
72 their effect on biodiversity has long been recognized as a key driver of ecosystem level response
73 to climate change in lakes (Post *et al.* 2009). Increases in temperature and nutrient availability in
74 lakes intensifies pelagic productivity, leading to increased biomass of phyto- and zooplankton
75 (de Senerpont Domis *et al.* 2013), and ultimately changing the fish community structure from
76 large generalist taxa to smaller pelagic feeding fishes (Jeppesen *et al.* 2005, 2012; Hayden *et al.*
77 2017). However, the majority of data collected regarding these changes relates to shallow
78 temperate lakes (Meerhoff *et al.* 2012), and considerably less is known about the mechanisms
79 through which climate change will modify thermally stratifying subarctic or Arctic lakes (Adrian
80 *et al.* 2009).

81 Subarctic lakes are generally cold, clear, nutrient-poor ecosystems. Primary production in
82 these systems is dominated by benthic algae, with a seasonal plankton bloom in late summer
83 (Vadeboncoeur *et al.* 2003; de Senerpont Domis *et al.* 2013). The fish communities are
84 comprised primarily of cold-water adapted salmonid species which forage on both benthic and
85 pelagic prey, but predominantly assimilate carbon synthesised by benthic algae (Zanden &
86 Rasmussen 1996; Hampton *et al.* 2011). Increasing temperature and productivity in the region
87 has led to the eutrophication (Vadeboncoeur *et al.* 2003) and browning (Leech *et al.* 2018) of
88 these lakes, increasing the duration and intensity of pelagic production and creating a habitat for
89 warmer adapted consumers which occupy distinct benthic and pelagic niches (Hayden *et al.*
90 2017). Evidence from marine systems indicates that increased pelagic productivity may also

91 result in an increase in pelagic-benthic coupling, whereby benthic communities are increasingly
92 fuelled by pelagic detritus (Docmac *et al.* 2017). Initial descriptions of coupling within lake food
93 webs focussed on the degree to which ecological communities integrate resources produced in
94 different habitats through “a set of processes that functionally link the ecological dynamics of
95 benthic, riparian and pelagic habitats of lakes” (Schindler & Scheuerell 2002). Although this
96 definition explicitly focusses on coupling of energy and resources which may be driven by
97 sessile benthic organisms (e.g. Higgins & Vander Zanden 2010), most investigations of this
98 phenomenon in lakes have focussed on foraging behaviour of fishes rather than nutrient
99 pathways (Tunney *et al.* 2014; Guzzo *et al.* 2017), and comparatively few studies have detailed
100 how changes in climate and productivity will affect pelagic-benthic coupling and lake ecosystem
101 function across multiple trophic levels. Meerhoff *et al.* (2012) synthesised data from multiple
102 space-for-time studies of shallow lakes, revealing that the response of biota to climate change are
103 often counterintuitive and nonlinear due to predator-prey dynamics within these ecosystems.
104 Consequently, targeted research containing a range of different lake types is necessary to
105 understand how lake communities in specific biomes will respond to environmental change.
106 Such research is particularly relevant to subarctic lakes as freshwater fishes comprise a
107 significant proportion of human diet in this region. Hence, changes to the quantity and quality of
108 fishes are likely to impact subsistence fisheries and may be subsequently detrimental to human
109 health.

110 To determine how climate and productivity influence pelagic-benthic coupling in lake
111 food webs, we quantified food-web structure in 30 lakes situated on a space-for-time gradient
112 reflecting the predicted future climate and land use scenarios for Northern Fennoscandia (Kovats
113 *et al.* 2014, Fig. S1). We hypothesized that increased productivity associated with higher

114 temperature and nutrient availability would incrementally shift food webs from a ‘clear’ to a
115 ‘murky’ state (Leech et al. 2018), whereby consumers would increasingly be supported by
116 pelagic production (Fig. 1). We predicted that a) increased pelagic-benthic coupling at the
117 primary consumer level (i.e. benthic macroinvertebrates) would propagate pelagic-derived
118 resources upwards through lake food webs to invertivorous and ultimately piscivorous fishes;
119 and b) consumers with different foraging strategies would display distinct functional responses to
120 this change, i.e. pelagic specialists would forage on pelagic prey throughout the gradient,
121 generalist consumers would switch from benthic to pelagic foraging, and benthic specialists
122 would feed on benthic prey, but assimilate an increased proportion of pelagic resources due to
123 strengthened pelagic-benthic coupling by primary consumers (Fig. 1).

124

125 **Methods**

126 Field sampling

127 *Environmental variables*

128 Sampling was conducted in a series of 30 lakes in Finnish Lapland in August or September
129 between 2004 and 2014 (Fig. S1, environmental classifications for each lake are provided in
130 Table S1). Principal Component Analysis was used to reduce variation in temperature,
131 precipitation, total nitrogen (TN), total phosphorus (TP) and dissolved organic carbon (DOC) to
132 a single composite variable (the Climate – Productivity index; hereafter CPi) which explained
133 80% of this variation (Fig. S2, S3). Land use within the catchment of each lake was estimated
134 from the CORINE database, but was not included in final models as land use variables were
135 highly collinear with CPi (Supporting information, Supplemental Methods, Fig S4, S5).

136

137 *Benthic macroinvertebrates*

138 Benthic macroinvertebrate community structure was assessed along a depth transect from the
139 shoreline to the deepest point in each lake and subsamples from each depth were frozen for
140 stable isotope analysis. In subsequent analysis, we considered bivalves (*Pisidium* sp.) and
141 gastropods (*Valvata* sp. and *Lymnaea* sp.) to be obligate pelagic and benthic feeding specialists,
142 respectively (Post 2002). Pooled Chironomidae, Oligochaeta and Trichoptera samples were each
143 classed as generalists, as these groups may contain multiple foraging guilds (Merritt *et al.* 2008).

144

145 *Fish*

146 Fish were sampled from littoral, pelagic and profundal zones using gill nets (Hayden *et al.*
147 2014b). All fish were identified to species level and individually weighed (wet mass, ± 0.1 g).
148 The relative abundance of each species in each lake was estimated as Biomass Per Unit Effort
149 (BPUE g net series⁻¹ hour⁻¹) and subsamples of each species (n = 30 where possible) were frozen
150 for subsequent stable isotope and stomach content analyses. Of invertivorous fishes, we collected
151 obligate planktivores (e.g. vendace *Coregonus albula*, bleak *Alburnus alburnus*), obligate
152 benthivores (e.g. small burbot *Lota lota*, ruffe *Gymnocephalus cernua*), and generalists which
153 forage in both benthic and pelagic habitats (e.g. whitefish *Coregonus lavaretus*, perch *Perca*
154 *fluviatilis*, roach *Rutilus rutilus*) from each lake (Hayden *et al.* 2017). The most abundant
155 piscivorous fishes found in pelagic (brown trout *Salmo trutta*), generalist (large perch and Arctic
156 charr *Salvelinus alpinus*) and benthic niches (large burbot and pike *Esox lucius*) were also
157 included in our analysis (Amundsen *et al.* 2003; Kahilainen & Lehtonen 2003).

158

159 Laboratory analysis

160 *Stable isotope analysis*

161 We assessed the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of benthic invertebrates
162 and fishes and estimated pelagic resource reliance (SIApel) of each benthic invertebrate sample
163 and individual fish using stable isotope mixing models (Post 2002). Benthic grazers (principally
164 *Valvata* sp.) and pelagic zooplankton (pooled cladocerans and copepods), which integrate the
165 carbon isotope ratios of benthic and pelagic primary producers, respectively (Post 2002), were
166 selected as baseline endmembers in all mixing models (Fig S6). We subsequently calculated the
167 proportion (by biomass) of benthic invertebrates, invertivorous fishes and piscivorous fishes
168 supported by pelagic productivity in each lake (Supplemental Methods).

169

170 *Diet analysis*

171 Fish stomach contents were identified to the lowest feasible taxonomic level (usually family) and
172 the relative contribution of each prey to the total stomach fullness points was determined using a
173 points method (Swynnerton & Worthington 1940). Invertebrate and fish prey items were
174 identified as pelagic, benthic or generalist in origin (Hayden *et al.* 2017). The relative proportion
175 of pelagic prey (GCApel, measured on a 0-1 scale as the relative abundance of benthic and
176 pelagic prey in fish stomach contents) to the diet of each fish was calculated as the proportion of
177 pelagic prey plus 0.5 times the proportion of generalist prey, reflecting an assumption that
178 generalist prey are themselves foraging across both benthic and pelagic habitats. We then
179 calculated the proportion (by biomass) of invertivorous and piscivorous fish communities in each
180 lake that forage on pelagic prey (Supplemental Methods).

181

182 Data analysis

183 We used Generalised Linear Models (GLM) and Generalised Linear Mixed Effects Models
184 (GLMM) to test whether littoral area (Litt), lake area (Area), fish species richness (Species), and
185 Climate-Productivity index (CPI) influenced community and individual level estimates of pelagic
186 resource reliance and pelagic foraging. Sample depth (Depth) was included in the GLMM
187 models of SIAPel for benthic macroinvertebrates but not for fish, due to the assumption that fish
188 move between depths. Full methods and summary data supporting all analyses and plots are
189 provided in the Supplemental Methods (Supporting Information).

190

191 **Results**

192 Carbon isotope ratios of food web endmembers and consumers displayed considerable variation
193 across the dataset. The littoral endmember $\delta^{13}\text{C}$ values shifted from approximately -25‰ to -
194 28‰, whereas the pelagic endmember increased from -33‰ to -30‰ (Fig. 2). Commensurate
195 with this, most consumers became depleted in ^{13}C with increasing CPI. Mixing models
196 performed on this dataset revealed a major shift in the productivity pathways fuelling subarctic
197 lake food webs along a climate and productivity gradient. The proportion of pelagic-derived
198 carbon assimilated by benthic macroinvertebrates displayed a strong positive relationship with
199 lake temperature and productivity (i.e. CPI). The assimilation of pelagic-derived carbon by
200 benthic macroinvertebrates increased from approximately zero to over 90% across the CPI
201 gradient (GLM: $\beta = 0.5 \pm 0.2$ SE; $p < 0.001$; Fig. 3, Table S2). The proportion of invertivorous
202 fish biomass supported by pelagic-derived carbon increased from 25% to 75% with increasing
203 CPI ($\beta = 0.1 \pm 0.02$ SE; $p < 0.01$; Fig. 3, Table S3). However, this could not be explained by
204 increased pelagic productivity, as CPI was not included among the best fitting models describing
205 invertivore diet (Table S4, Fig. S6). Similar, albeit weaker, relationships were observed in

206 piscivorous fishes (Fig. 3), whose integration of phytoplankton-derived carbon displayed a
207 positive relationship with CPi ($\beta = 0.1 \pm 0.02$; $p = 0.01$; Fig. 3, Table S3), despite there being no
208 change in their consumption of pelagic prey.

209

210 The assimilation of phytoplankton-derived carbon (SI_{Apel}) by benthic macroinvertebrates was
211 primarily explained by foraging guild, as pelagic specialists assimilated more pelagic-derived
212 carbon than benthic specialists, whilst generalists were intermediate in their use of the two
213 resource types (Fig. 4, Table 1). Assimilation of pelagic-derived carbon by benthic specialist
214 macroinvertebrates was positively related to CPi ($\beta = 1.5 \pm 0.2$ SE, $p < 0.001$, Fig. 3, Fig. S6)
215 and sampling depth ($\beta = 3.1 \pm 0.3$ SE, $p < 0.01$) and negatively related to lake area ($\beta = -0.3 \pm$
216 0.1 SE, $p < 0.05$, Fig. S4, Table 1). Despite occupying benthic habitats, generalist and benthic
217 specialist invertebrates mainly integrated phytoplankton-derived carbon in lakes with high CPi
218 scores (Fig. 4, Table S2).

219

220 The level of assimilation of phytoplankton-derived carbon (SI_{Apel}) by invertivorous fishes was
221 positively related to CPi ($\beta = 1.1 \pm 0.2$ SE, $p < 0.001$) and lake area ($\beta = 0.5 \pm 0.2$ SE, $p < 0.05$),
222 and differed between foraging guilds (Table 1). SI_{Apel} of pelagic specialist invertivorous fishes
223 was consistently high (approximately 65%) throughout the study region, whereas SI_{Apel} of
224 benthic specialist invertivores increased from 25% to 100% with increasing CPi. A similar,
225 though less-pronounced increase (approx. 35% to 70%), was observed in generalist invertivores
226 (Fig. 4, Table 1). Strikingly, pelagic prey consumption of all invertivore feeding guilds
227 (GC_{Apel}) was unrelated to CPi, indicating that fishes did not change their foraging behaviour
228 along the gradient. However, variation in pelagic foraging associated with CPi was evident in

229 certain species (Fig S7). Perch, a cool-water generalist, and whitefish, a cold-water generalist,
230 integrated more pelagic-derived carbon in high CPi lakes. However, pelagic foraging by perch
231 increased with increasing CPi, whereas pelagic foraging by whitefish decreased (Table S4).

232

233 Broadly similar patterns were observed in piscivorous fishes, though the strength of the
234 relationship was slightly lower than in invertivores (Fig. 4, Fig. S6). Across guilds, piscivore
235 SIAPel was positively related to CPi ($\beta = 0.7 \pm 0.2$ SE, $p < 0.01$) and lake area ($\beta = 0.7 \pm 0.3$ SE,
236 $p < 0.01$), while the slope of regression for benthivores was slightly lower than for generalists or
237 pelagic specialists (Fig. 4). Interestingly, piscivore pelagic foraging (GCApel) was not related to
238 CPi, but was primarily associated with lake area ($\beta = 0.5 \pm 0.1$ SE, $p < 0.01$) and fish species
239 richness ($\beta = -0.3 \pm 0.1$ SE, $p < 0.01$, Fig. 4, Table 1).

240

241 **Discussion**

242 Elevated temperature and productivity were associated with a profound shift from benthic to
243 pelagic fuelled food webs in the 30 subarctic lakes analysed. The disconnect between pelagic
244 resource assimilation and pelagic foraging across all consumer communities indicates that this
245 shift was driven by pelagic-benthic coupling, i.e. a functional link between the ecological
246 dynamics of benthic, riparian and pelagic habitats of lakes (sensu Schindler & Scheuerell 2002)
247 at low trophic levels, rather than increased pelagic foraging by higher trophic level consumers.
248 Our results highlight the establishment of an indirect 'green' trophic pathway following
249 eutrophication of subarctic lakes. Phytoplankton synthesise organic carbon in the pelagic zone,
250 and then settle on the lake bed, where they are consumed by benthic macroinvertebrates and
251 ultimately fuel a benthic food chain. These results derived from a subarctic climate-productivity

252 gradient are likely relevant to lakes globally as temperature, light and nutrient availability
253 determine the dominant primary production pathway in lakes (Adrian *et al.* 2009).

254 Our results show that pelagic-benthic coupling by benthic invertebrates is capable of
255 shifting an entire lake food web towards a reliance on pelagic-derived carbon. A similar
256 mechanism of pelagic-benthic coupling by primary consumers is responsible for pelagic-fuelled
257 littoral food chains in productive marine habitats (Docmac *et al.* 2017). Although Vadeboncoeur
258 *et al.* (2003) demonstrate that the contribution of pelagic primary production to zoobenthos
259 scales with lake productivity, evidence of this pathway in freshwater systems is mostly limited to
260 a small number of taxa-specific examples of diatom blooms fuelling deep-water chironomid
261 communities and fluvial snails feeding on phytoplankton (Goedkoop & Johnson 1996; Kathol *et al.*
262 *et al.* 2011). Comparable coupling has been recorded in lake food webs following the establishment
263 of invasive bivalves, e.g. Dreissenid mussels. These mussels filter phytoplankton and pelagic
264 detritus from the water column and transfer it to the lake bed in the form of pseudofaeces, where
265 it becomes a resource for benthic consumers (Higgins & Vander Zanden 2010). The majority of
266 studies analysing this dynamic report an increase in benthic production due to increased water
267 clarity following invasion (Madenjian *et al.* 2013; Fera *et al.* 2017), which is a reversal of the
268 shift detailed in our results. It would be highly interesting to assess the degree to which benthic
269 consumers in those systems are fuelled by pelagic-derived energy. In contrast to littoral
270 invertebrates, both marine (France 1995) and freshwater profundal communities are known to be
271 fuelled by pelagic detritus (Goedkoop & Johnson 1996). Our results reveal that this trait is also
272 characteristic of benthic consumers within the photic zone of subarctic lakes. This mechanism
273 may also explain a widely observed phenomenon whereby benthic and pelagic invertebrates have
274 distinct $\delta^{13}\text{C}$ isotope values in oligotrophic lakes, but comparatively similar values in more

275 productive systems (Vadeboncoeur *et al.* 2003). The $\delta^{13}\text{C}$ values of littoral grazers are regularly
276 used as a proxy for benthic algal primary production in stable isotope mixing models (Post
277 2002). However, in productive lakes, these values are often identical to those of pelagic
278 consumers, negating the ability to distinguish between pelagic and benthic resource use using
279 $\delta^{13}\text{C}$ alone (Phillips *et al.* 2014). Indeed, in this study, we were forced to omit data from one
280 eutrophic lake as we could not accurately determine the $\delta^{13}\text{C}$ values of the littoral baseline
281 (Supplemental Methods). The widespread integration of pelagic derived carbon by the littoral
282 invertebrate community is commensurate with the convergence of $\delta^{13}\text{C}$ values between pelagic
283 and benthic endmembers in eutrophic lakes (Vadeboncoeur *et al.* 2003).

284 The conversion of carbon isotope ratio values in our data also indicates that terrestrial
285 derived carbon is increasingly important in eutrophic lakes as land use intensifies with increasing
286 CPi. Low CPi lakes are associated with ecotourism and reindeer herding, which shifts first to
287 mild and then intensive forestry at the high CPi extreme of the gradient (Hayden *et al.* 2017).
288 This shift in land use leads to increased terrestrial carbon entering the water system resulting in
289 lower light penetration and brownification of the waterbody (Graneli 2012). Primary consumers,
290 e.g. pelagic zooplankton, may utilise poor quality terrestrial carbon, especially when
291 phytoplankton is not available (Taipale *et al.* 2016). Carbon isotope ratios of the pelagic and
292 benthic primary consumer endmembers in our study system showed some evidence of this
293 phenomenon. Littoral endmembers became depleted in ^{13}C , shifting $\delta^{13}\text{C}$ from -22 to -25‰,
294 whereas pelagic zooplankton became ^{13}C -enriched, shifting $\delta^{13}\text{C}$ from -32 to -29‰. Terrestrial
295 primary consumers in this region typically have $\delta^{13}\text{C}$ values of -28 to -27‰ (Milardi *et al.* 2016),
296 and convergence of both endmembers towards this value is commensurate with brownification of
297 the food web. The degree to which aquatic primary producers and consumers utilise terrestrial-

298 derived carbon has been a topic of considerable debate in the limnological literature (Brett *et al.*
299 2017). While our data cannot resolve that debate, it does indicate that increasing terrestrial
300 carbon along intensification of land use will change the base of lake food webs, adding a further
301 dimension to the pelagic-benthic convergence detailed by Vadeboncoeur *et al* (2003).

302 The space-for-time approach we used to assess the relationship between environmental
303 drivers and ecosystem function allowed us to observe changes in the actual environment rather
304 than extrapolating from micro- or mesocosm studies. However, it also conferred several
305 disadvantages; collinearity between our key predictor variables, namely temperature and
306 productivity, negates our ability to determine the effects of climate and land use change
307 independently, along with any characterisation of synergistic or additive effects associated with
308 these variables (Thomaz *et al.* 2012; Blois *et al.* 2013). As land use intensification occurs in
309 conjunction with climate change across the globe, it is challenging to identify locations where
310 these factors may be disentangled in the field. Further investigation on this topic may require
311 additional mesocosm-based studies. In addition, though we consider lakes as independent
312 replicates in our models, variation in lake morphometry in conjunction with light availability
313 may alter the relative abundance of pelagic, littoral and profundal habitat amongst lakes with
314 clear implications for the relative contribution of pelagic and benthic primary production to the
315 food web (Hayden *et al.* 2014b). In our study, lake area had a positive association with the
316 degree to which fishes foraged on pelagic prey and assimilated pelagic-derived carbon. Though
317 these effects were weaker than the shift associated with CPI, they do raise interesting questions
318 regarding the interaction between lake productivity change and morphometry. In larger lakes the
319 ‘greening’ of the food web extends an already existing pathway, whereas in small lakes it could
320 potentially create novel pelagic niches, facilitating the encroachment of warm-water adapted taxa

321 adapted to foraging under such conditions (Hayden *et al.* 2017). Additional studies in a
322 controlled environment, or specifically comparing large and small lakes, would be necessary to
323 test this conclusively.

324 The range of trophic states evident along this gradient of lakes mirrors the alternative
325 stable states of shallow temperate lakes, in which a regime shift from ‘clear’ water, macrophyte-
326 dominated state to a turbid, phytoplankton-dominated state is initiated by changes to lake
327 productivity and maintained by a shift in the functional community structure of the consumers
328 (Scheffer & Carpenter 2003). Previously documented ‘regime shifts’ are often associated with a
329 critical tipping point and may be reversed when one or both of these forcing mechanisms are
330 relaxed (Scheffer & Carpenter 2003). However, our data show that climate-productivity induced
331 shifts in subarctic lakes are incremental and it is therefore likely that a much stronger
332 environmental forcing is needed to return these lakes to their original ‘clear’ state (Scheffer *et al.*
333 1993). Our data are commensurate with a considerable body of work from temperate, shallow
334 lakes suggesting that such regime shifts in response to climate change occur slowly and are only
335 reversed following considerable forcing spanning multiple trophic levels (Moss *et al.* 2011; Hilt
336 *et al.* 2013). Earlier studies of subarctic lakes in the region have shown that the CPi gradient is
337 characterised by an increase in fish biomass, a decrease in mean fish size and a change in
338 community structure from dominance by few large-bodied generalists, to functionally diverse
339 communities of intermediate-sized specialists, and finally to communities dominated by small-
340 sized pelagic foraging fishes (Hayden *et al.* 2017). Despite these changes in functional diversity,
341 the degree to which fishes foraged on pelagic prey remained remarkably consistent along the CPi
342 gradient, diminishing the chances of return to ‘clear’ state through a modification of the
343 ecological community alone.

344 Subarctic lakes provide opportunities for transport, drinking water and year-round
345 subsistence fisheries to indigenous local communities (Sjölander 2011). Eutrophication caused
346 by increasing water temperature and intensification of land use is threatening these ecosystem
347 services, reducing water quality (Przytulska *et al.* 2017), shifting fish fauna towards less
348 nutritious and smaller-sized species (Hayden *et al.* 2017), and reducing the growth and condition
349 of resident cold water adapted salmonids (Guzzo *et al.* 2017). Our results indicate an additional
350 sensitivity, as a shift towards pelagic reliance represents a major ecological change in food webs
351 that, in their original state, are reliant on benthic algae (Sierszen *et al.* 2003). Benthic algal
352 communities in subarctic lakes are strongly dominated by diatoms, an algal group capable of
353 producing abundant quantities of essential fatty acids, whereas highly productive lakes typically
354 support blue-green algae, diminishing the capacity to provide equivalently high-quality resources
355 to pelagic consumers (Goedkoop & Johnson 1996; Müller-Navarra *et al.* 2004). This shift from
356 benthic to pelagic productivity pathways may correspond to a negative shift in nutritional
357 capacity of food webs and has major bottom-up effects by reducing the quality of local fish
358 catches (Hayden *et al.* 2017). In addition, the reduction of benthic energy pathways will diminish
359 food web complexity and associated stability in subarctic lakes (Rooney & McCann 2012;
360 McMeans *et al.* 2015), making them more vulnerable to annual and long-term fluctuations of
361 pelagic production, a feature which is characteristic of eutrophic lakes (Donohue *et al.* 2016).

362 In conclusion, we detail a major regime shift from benthic- to pelagic-fuelled food webs,
363 driven not only by an increased prevalence of pelagic consumers (Hayden *et al.* 2017), but also
364 by the amplification of a pelagic-fuelled, benthic food chain following eutrophication. Such a
365 profound change in the basis of food webs along a 3°C temperature and land use gradient reveals
366 that the eutrophication of subarctic lakes is radically altering lake ecosystem function.

367 Furthermore, the fundamental importance of temperature, light and nutrient availability to
368 primary production pathways in lakes (Jeppesen *et al.* 2003) suggests that the mechanisms
369 outlined in this study have relevance to freshwater ecosystems across the globe.

370

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380

381 **References**

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- 383 Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., *et al.* (2009).
384 Lakes as sentinels of climate change. *Limnol. Oceanogr.*, 54, 2283–2297.
- 385 Amundsen, P.-A., Bøhn, T., Popova, O.A., Staldvik, F.J., Reshetnikov, Y.S., Kashulin, N.A., *et*
386 *al.* (2003). Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish
387 guild. *Hydrobiologia*, 497, 109–119.
- 388 Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T. & Ferrier, S. (2013). Space can
389 substitute for time in predicting climate-change effects on biodiversity. *Proc. Natl. Acad.*
390 *Sci.*, 110, 9374–9379.
- 391 Bokhorst, S., Bjerke, J.W., Bowles, F.W., Melillo, J., Callaghan, T.V. & Phoenix, G.K. (2008).
392 Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf
393 shrub heathland. *Glob. Change Biol.*, 14, 2603–2612.
- 394 Brett, M.T., Bunn, S.E., Chandra, S., Galloway, A.W.E., Guo, F., Kainz, M.J., *et al.* (2017). How
395 important are terrestrial organic carbon inputs for secondary production in freshwater
396 ecosystems? *Freshw. Biol.*, 62, 833–853.

- 397 Docmac, F., Araya, M., Hinojosa, I.A., Dorador, C. & Harrod, C. (2017). Habitat coupling writ
398 large: pelagic-derived materials fuel benthivorous macroalgal reef fishes in an upwelling
399 zone. *Ecology*, 98, 2267–2272.
- 400 Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., *et al.*
401 (2016). Navigating the complexity of ecological stability. *Ecol. Lett.*, 19, 1172–1185.
- 402 Fera, S.A., Rennie, M.D. & Dunlop, E.S. (2017). Broad shifts in the resource use of a
403 commercially harvested fish following the invasion of dreissenid mussels. *Ecology*, 98,
404 1681–1692.
- 405 Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., *et al.*
406 (2009). Loss of functional diversity under land use intensification across multiple taxa.
407 *Ecol. Lett.*, 12, 22–33.
- 408 France, R.L. (1995). Carbon-13 enrichment in benthic compared to planktonic algae: foodweb
409 implications. *Mar. Ecol. Prog. Ser.*, 124, 307–312.
- 410 Goedkoop, W. & Johnson, R.K. (1996). Pelagic-benthic coupling: Profundal benthic community
411 response to spring diatom deposition in mesotrophic Lake Erken. *Limnol. Oceanogr.*, 41,
412 636–647.
- 413 Graneli, W. (2012). Brownification of Lakes. In: *Encyclopedia of Lakes and Reservoirs* (eds.
414 Bengtsson, L., Herschy, R.W. & Fairbridge, R.W.). Springer Netherlands, Dordrecht, pp.
415 117–119.
- 416 Guzzo, M.M., Blanchfield, P.J. & Rennie, M.D. (2017). Behavioral responses to annual
417 temperature variation alter the dominant energy pathway, growth, and condition of a
418 cold-water predator. *Proc. Natl. Acad. Sci.*, 114, 9912–9917.
- 419 Hampton, S.E., Fradkin, S.C., Leavitt, P.R. & Rosenberger, E.E. (2011). Disproportionate
420 importance of nearshore habitat for the food web of a deep oligotrophic lake. *Mar.*
421 *Freshw. Res.*, 62, 350–358.
- 422 Hayden, B., Harrod, C. & Kahilainen, K.K. (2014). Lake morphometry and resource
423 polymorphism determine niche segregation between cool- and cold-water adapted fish.
424 *Ecology*, 95, 538–552.
- 425 Hayden, B., Myllykangas, J.-P., Rolls, R.J. & Kahilainen, K.K. (2017). Climate and productivity
426 shape fish and invertebrate community structure in subarctic lakes. *Freshw. Biol.*, 62,
427 990–1003.
- 428 Higgins, S.N. & Vander Zanden, M.J. (2010). What a difference a species makes: a meta-
429 analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecol. Monogr.*, 80, 179–
430 196.
- 431 Hilt, S., Köhler, J., Adrian, R., Monaghan, M.T. & Sayer, C.D. (2013). Clear, crashing, turbid
432 and back – long-term changes in macrophyte assemblages in a shallow lake. *Freshw.*
433 *Biol.*, 58, 2027–2036.
- 434 Jeppesen, E., Jensen, J.P., Jensen, C., Faafeng, B., Hessen, D.O., Søndergaard, M., *et al.* (2003).
435 The Impact of Nutrient State and Lake Depth on Top-down Control in the Pelagic Zone
436 of Lakes: A Study of 466 Lakes from the Temperate Zone to the Arctic. *Ecosystems*, 6,
437 313–325.
- 438 Jeppesen, E., Mehner, T., Winfield, I.J., Kangur, K., Sarvala, J., Gerdeaux, D., *et al.* (2012).
439 Impacts of climate warming on the long-term dynamics of key fish species in 24
440 European lakes. *Hydrobiologia*, 694, 1–39.

- 441 Jeppesen, E., Søndergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., *et al.*
442 (2005). Lake responses to reduced nutrient loading - an analysis of contemporary long-
443 term data from 35 case studies. *Freshw. Biol.*, 50, 1747–1771.
- 444 Kahilainen, K.K. & Lehtonen, H. (2003). Piscivory and prey selection of four predator species in
445 a whitefish dominated subarctic lake. *J. Fish Biol.*, 63, 659–672.
- 446 Kathol, M., Fischer, H. & Weitere, M. (2011). Contribution of biofilm-dwelling consumers to
447 pelagic–benthic coupling in a large river. *Freshw. Biol.*, 56, 1160–1172.
- 448 Kovats, R.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D., Martin, E., *et al.* (2014).
449 Europe. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B:
450 Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of
451 the Intergovernmental Panel of Climate Change* (eds. Barros, V.R., Field, C.B., Dokken,
452 D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., *et al.*). Cambridge University Press,
453 Cambridge, United Kingdom and New York, NY, USA, pp. 1267–1326.
- 454 Leech, D.M., Pollard, A.I., Labou, S.G. & Hampton, S.E. (2018). Fewer blue lakes and more
455 murky lakes across the continental U.S.: Implications for planktonic food webs. *Limnol.
456 Oceanogr.*, 63, 2661–2680.
- 457 Madenjian, C.P., Rutherford, E.S., Stow, C.A., Roseman, E.F. & He, J.X. (2013). Trophic Shift,
458 Not Collapse. *Environ. Sci. Technol.*, 47, 11915–11916.
- 459 McMeans, B.C., McCann, K.S., Humphries, M., Rooney, N. & Fisk, A.T. (2015). Food Web
460 Structure in Temporally-Forced Ecosystems. *Trends Ecol. Evol.*, 30, 662–672.
- 461 Meerhoff, M., Teixeira-de Mello, F., Kruk, C., Alonso, C., González-Bergonzoni, I., Pacheco,
462 J.P., *et al.* (2012). 4 - Environmental Warming in Shallow Lakes: A Review of Potential
463 Changes in Community Structure as Evidenced from Space-for-Time Substitution
464 Approaches. In: *Advances in Ecological Research*, Global Change in Multispecies
465 Systems Part 1 (eds. Jacob, U. & Woodward, G.). Academic Press, pp. 259–349.
- 466 Merritt, R.W., Cummins, K.W. & Berg, M.B. (2008). *An Introduction to Aquatic Insects of
467 North America*. 4th edn. Kendall / Hunt Publishing Co., Dubuque, USA.
- 468 Milardi, M., Thomas, S.M. & Kahilainen, K.K. (2016). Reliance of brown trout on terrestrial
469 prey varies with season but not fish density. *Freshw. Biol.*, 61, 1143–1156.
- 470 Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., *et al.* (2011).
471 Allied attack: climate change and eutrophication. *Inland Waters*, 1, 101–105.
- 472 Müller-Navarra, D.C., Brett, M.T., Park, S., Chandra, S., Ballantyne, A.P., Zorita, E., *et al.*
473 (2004). Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes.
474 *Nature*, 427, 69–72.
- 475 Payette, S., Fortin, M.-J. & Gamache, I. (2001). The Subarctic Forest–Tundra: The Structure of a
476 Biome in a Changing Climate The shifting of local subarctic tree lines throughout the
477 forest–tundra biome, which is linked to ecological processes at different spatiotemporal
478 scales, will reflect future global changes in climate. *BioScience*, 51, 709–718.
- 479 Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., *et al.* (2014).
480 Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.*,
481 92, 823–835.
- 482 Post, D.M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and
483 assumptions. *Ecology*, 83, 703–718.
- 484 Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling,
485 B., *et al.* (2009). Ecological Dynamics Across the Arctic Associated with Recent Climate
486 Change. *Science*, 325.

487 Przytulska, A., Bartosiewicz, M. & Vincent, W.F. (2017). Increased risk of cyanobacterial
488 blooms in northern high-latitude lakes through climate warming and phosphorus
489 enrichment. *Freshw. Biol.*, 62, 1986–1996.

490 Rolls, R.J., Hayden, B. & Kahilainen, K.K. (2017). Conceptualising the interactive effects of
491 climate change and biological invasions on subarctic freshwater fish. *Ecol. Evol.*, 7,
492 4109–4128.

493 Rooney, N. & McCann, K.S. (2012). Integrating food web diversity, structure and stability.
494 *Trends Ecol. Evol.*, 27, 40–45.

495 Scheffer & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to
496 observation. *Trends Ecol. Evol.*, 18, 648–656.

497 Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B. & Jeppesen, E. (1993). Alternative
498 equilibria in shallow lakes. *Trends Ecol. Evol.*, 8, 275–279.

499 Schindler, D.E. & Scheuerell, M.D. (2002). Habitat coupling in lake ecosystems. *Oikos*, 98, 177–
500 189.

501 de Senerpont Domis, L.N., Elser, J.J., Gsell, A.S., Huszar, V.L.M., Ibelings, B.W., Jeppesen, E.,
502 *et al.* (2013). Plankton dynamics under different climatic conditions in space and time.
503 *Freshw. Biol.*, 58, 463–482.

504 Sierszen, M.E., McDonald, M.E. & Jensen, D.A. (2003). Benthos as the basis for arctic lake food
505 webs. *Aquat. Ecol.*, 37, 437–445.

506 Sjölander, P. (2011). What is known about the health and living conditions of the indigenous
507 people of northern Scandinavia, the Sami? *Glob. Health Action*, 4, 8457.

508 Swynnerton, G.H. & Worthington, E.B. (1940). Note on the Food of Fish in Haweswater
509 (Westmorland). *J. Anim. Ecol.*, 9, 183–187.

510 Taipale, S.J., Galloway, A.W.E., Aalto, S.L., Kahilainen, K.K., Strandberg, U. & Kankaala, P.
511 (2016). Terrestrial carbohydrates support freshwater zooplankton during phytoplankton
512 deficiency. *Sci. Rep.*, 6, 30897.

513 Thomaz, S.M., Agostinho, A.A., Gomes, L.C., Silveira, M.J., Rejmánek, M., Aslan, C.E., *et al.*
514 (2012). Using space-for-time substitution and time sequence approaches in invasion
515 ecology. *Freshw. Biol.*, 57, 2401–2410.

516 Tunney, T.D., McCann, K.S., Lester, N.P. & Shuter, B.J. (2014). Effects of differential habitat
517 warming on complex communities. *Proc. Natl. Acad. Sci.*, 111, 8077–8082.

518 Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup, H.-H., Christoffersen, K. &
519 Lodge, D.M. (2003). From Greenland to green lakes: cultural eutrophication and the loss
520 of benthic pathways in lakes. *Limnol. Oceanogr.*, 48, 1408–1418.

521 Vitousek, P.M. (1994). Beyond global warming - ecology and global change. *Ecology*, 75, 1861–
522 1876.

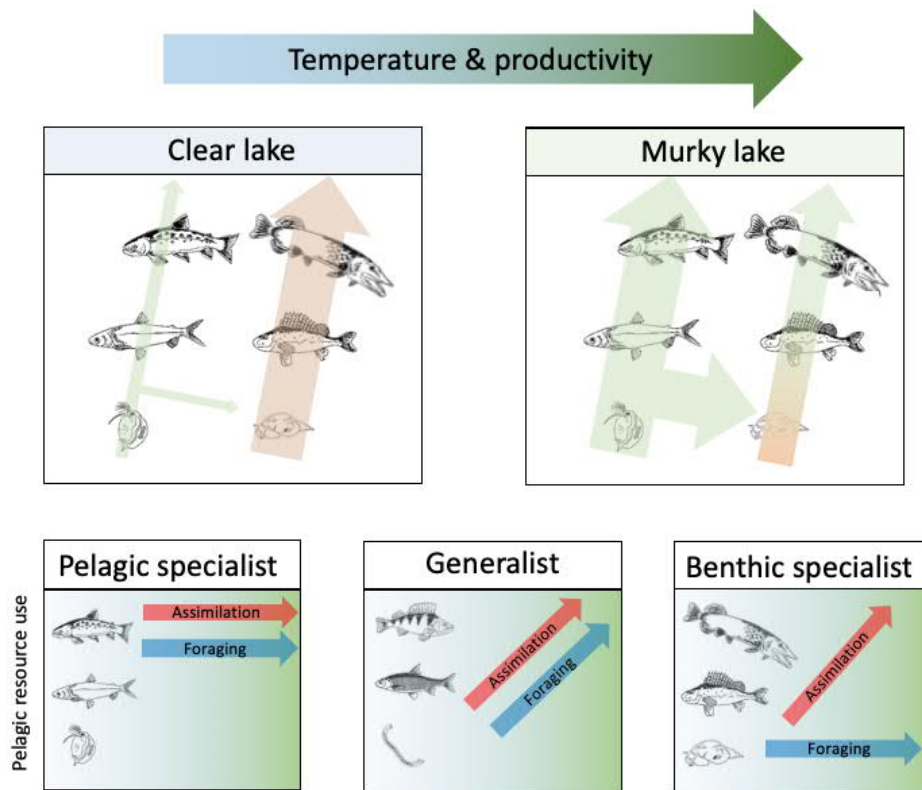
523 Xu, L., Myneni, R.B., Iii, F.S.C., Callaghan, T.V., Pinzon, J.E., Tucker, C.J., *et al.* (2013).
524 Temperature and vegetation seasonality diminishment over northern lands. *Nat. Clim.*
525 *Change*, 3, 581–586.

526 Zanden, M.J.V. & Rasmussen, J.B. (1996). A Trophic Position Model of Pelagic Food Webs:
527 Impact on Contaminant Bioaccumulation in Lake Trout. *Ecol. Monogr.*, 66, 451–477.
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530

531 **Table 1.** Summary of Generalised Linear Mixed Effects Models assessing the influence of climate-productivity index (CPI),
532 Sampling Depth (Depth), relative littoral area (Litt), lake area (Area), fish species richness (Species), and foraging guild
533 (benthic/generalist/pelagic) on variation in pelagic-derived carbon (SIA) and pelagic foraging (GCA) of benthic macroinvertebrates
534 (BMI), invertivorous and piscivorous fishes. The values present Parameter Estimates ($\beta \pm SD$, equivalent to effect size) for each
535 explanatory variable, with significant effects highlighted with asterisks. Taxon, Lake and the interaction between the latitude and
536 longitude of the midpoint of each lake were included as random effects in each model. Sample Depth was solely included in models
537 assessing variation in benthic macroinvertebrates (BMI) due to the assumption that fishes move between depths.

Variable	<u>BMI</u>	<u>Invertivores</u>	GCA	<u>Piscivores</u>	GCA
	SIA	SIA		SIA	
<i>Fixed Effects</i>					
CPI	1.49 (0.17)***	1.11 (0.18)***	-	0.74 (0.23)**	-
Depth	3.14 (0.27)***	NA	NA	NA	NA
Litt	-	-	-0.26 (0.15)	-	-
Area	-0.29 (0.11)*	0.52 (0.19)*	-	0.72 (0.27)**	0.48 (0.09)***
Species	-	-	-	-	-0.27 (0.08)**
Guild - Benthic	-0.55 (0.51)	0.03 (0.28)	-2.79 (0.21)***	-1.28 (0.29)***	-1.69 (0.14)***
Guild - Generalist	0.83 (0.26)**	-0.55 (0.21)*	-0.52 (0.15)***	-0.51 (0.28)	-0.83 (0.11)***
Guild - Pelagic	2.35 (0.42)***	0.55 (0.26)*	1.76 (0.18)***	-0.26 (0.32)	-0.43 (0.14)**
<i>Random Effects</i>					
Taxon	0.01 (0.01)	1.21 (1.09)	3.09 (1.76)	0.01 (0.01)	0.01 (0.01)
Lake	0.24 (0.49)	0.21 (0.46)	0.30 (0.54)	0.01 (0.01)	0.01 (0.01)
Lat*Long	0.04 (0.19)	0.41 (0.63)	0.34 (0.58)	0.01 (0.01)	0.01 (0.01)

538 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

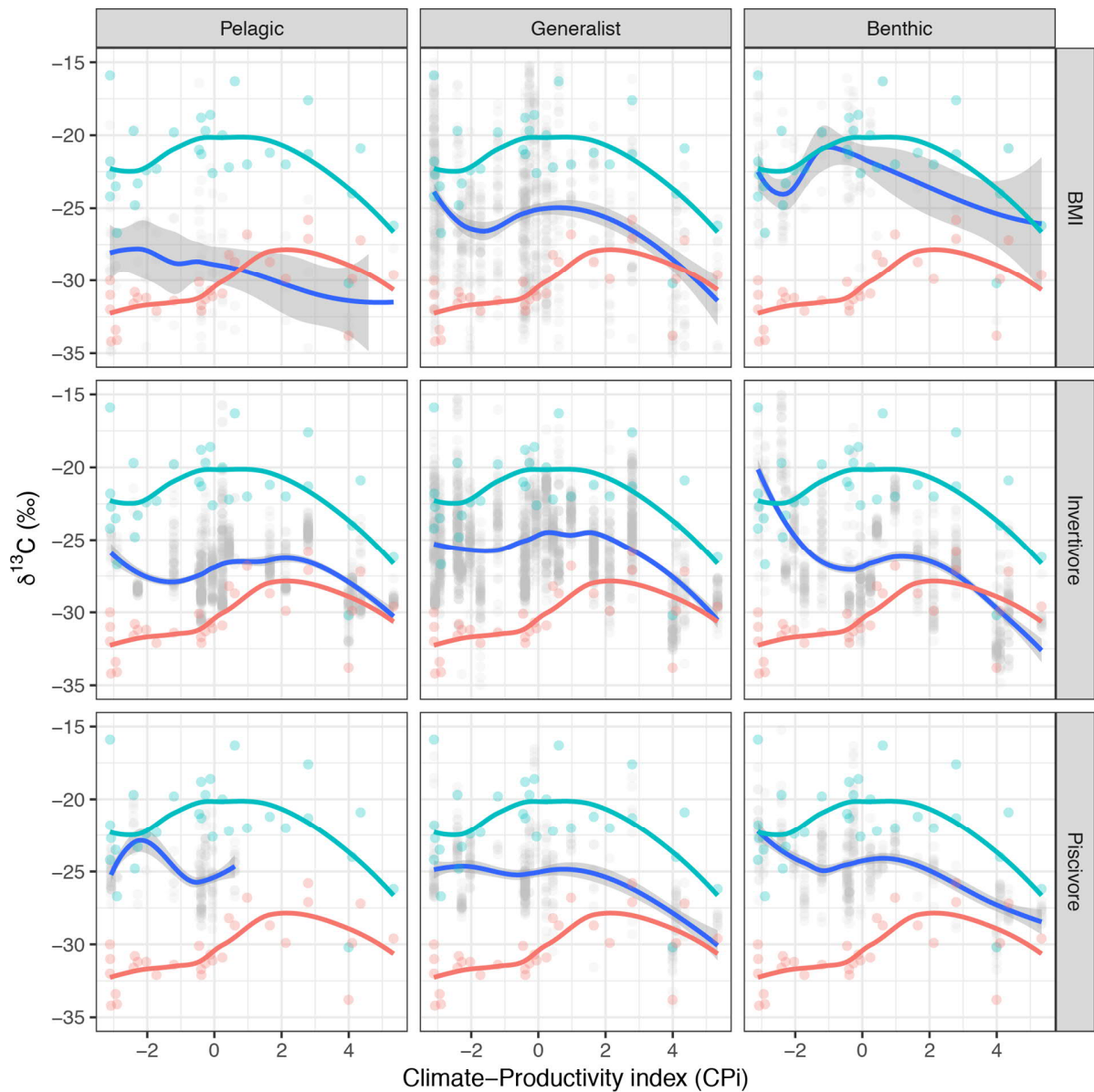


539

540 **Fig. 1.** Conceptual model of the predicted changes in subarctic lake food webs in response to
 541 increasing temperature and productivity. Top row: lake food webs are fuelled by either pelagic
 542 (green arrows) or littoral benthic (brown arrows) production, with arrow size reflecting
 543 importance of each pathway. Pelagic-benthic coupling due to benthic primary consumers
 544 assimilating pelagic detritus is elevated in 'green' state lakes, resulting in a benthic food chain
 545 fuelled by pelagic-derived resources. Bottom row: we predicted that lakes would shift from
 546 'clear' to 'murky' states with greater temperature and productivity, and that this shift will have
 547 complex repercussions: pelagic specialists continue to assimilate and forage in the pelagic food
 548 chain, generalists shift from benthic to pelagic prey, and benthic specialists continue to forage on
 549 benthic prey but increasingly assimilate pelagic carbon resources.

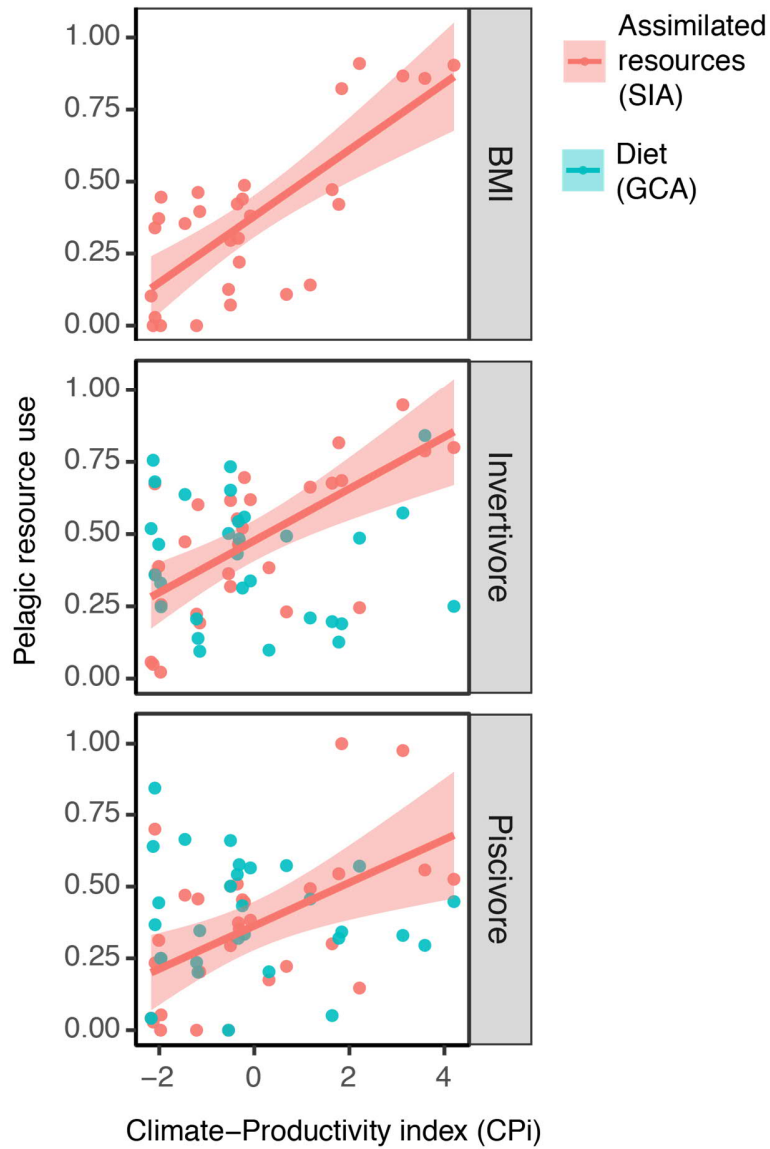
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 553 **Fig 2.** Scatter plots outlining the variation in littoral (light blue) and pelagic (red) food web
 554 endmembers and consumers (grey circles and dark blue smoother) along the climate -
 555 productivity gradient. Loess smoothers (shaded area denotes 95% confidence interval) are fitted
 556 to the data for illustrative purposes.

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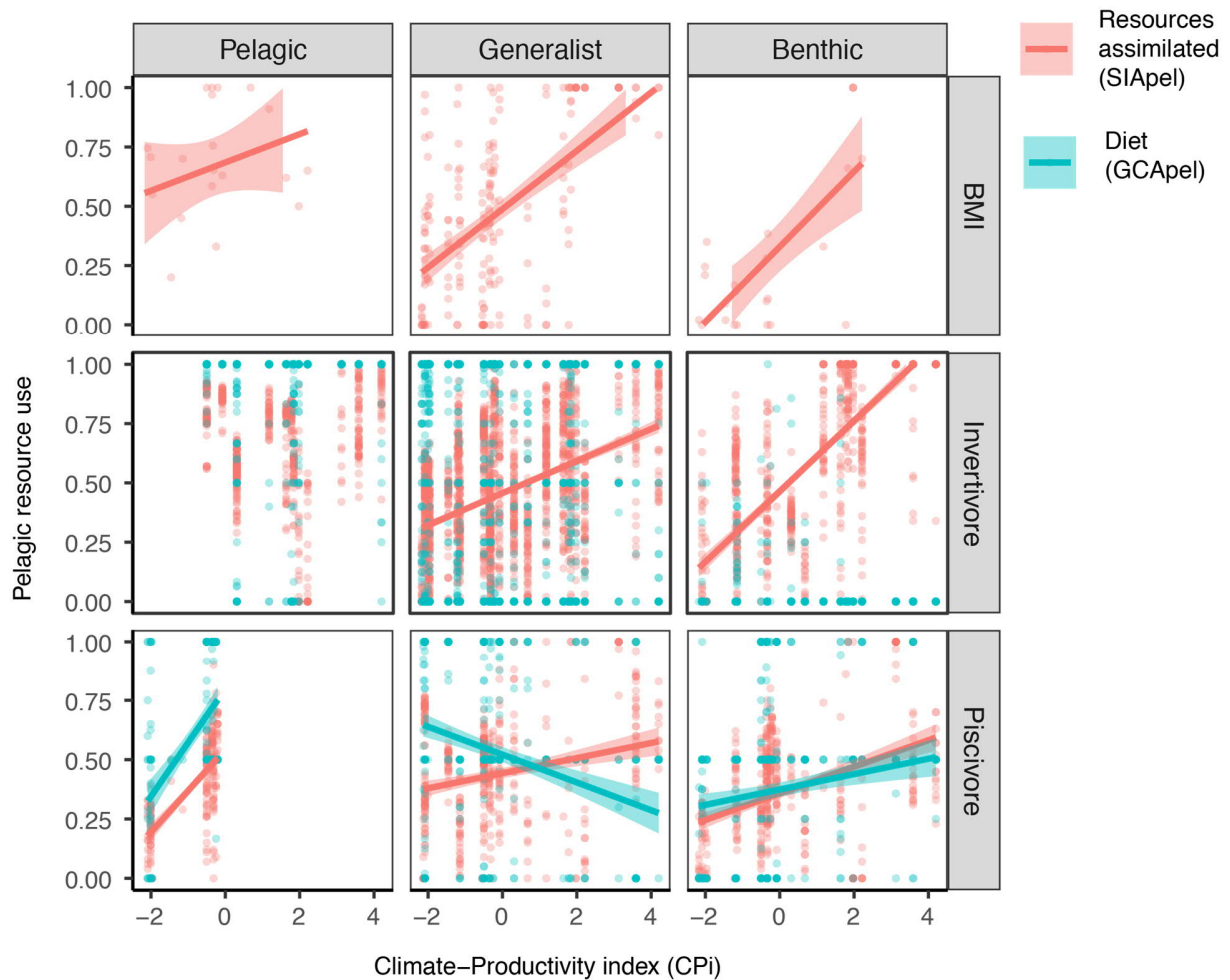


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562 **Fig. 3.** Scatter plots outlining the relationship between community-level pelagic resource use of
 563 benthic invertebrates (BMI), invertivores and piscivores and the Climate-Productivity index
 564 (CPI, a principal component explaining 80% of environmental variation among lakes). Each
 565 datapoint represents the mean assimilation of pelagic-derived carbon (red) or pelagic prey
 566 consumed (blue) weighted by population density (BMI) or biomass (fish) for a single lake.

567 Linear trendlines with 95% confidence intervals (shading) denote statistically significant
 568 relationships. Full model fits are provided in Table S2, S3 and S4.



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571 **Fig. 4.** Scatter plots outlining changes in individual pelagic resource use, inferred from stable
 572 isotope (red lines) and gut content (blue lines) analyses along a gradient of increasing lake
 573 temperature and productivity (CPI, a principal component explaining 80% environmental
 574 variation among lakes). Each datapoint represents an individual sample of benthic
 575 macroinvertebrates (BMI), invertivore or piscivore fish. Linear trendlines with 95% confidence
 576 intervals (shading) denote statistically significant relationships. Full model fits are provided in
 577 Table 1.