Muddy Waters - tracing the functional response of high latitude lake communities to 'greening' and 'browning'

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Abstract

Climate change and the intensification of land use practices are causing widespread eutrophication of subarctic lakes. The implications of this rapid change for lake ecosystem function remain poorly understood. To assess how freshwater communities respond to such profound changes in their habitat and resource availability, we conducted a space-for-time analysis of food web structure in 30 lakes situated on a temperature-productivity gradient equivalent to the predicted future climate of subarctic Europe (temperature +3˚C, precipitation +30% and nutrient +45 µg L^{-1} total phosphorus). Along this gradient, we observed an increase in the assimilation of pelagic-derived carbon from 25 to 75% throughout primary, secondary and tertiary consumers. This shift was overwhelmingly driven by the consumption of pelagic detritus by benthic primary consumers and was not accompanied by increased pelagic foraging by higher trophic level consumers. These results, reflecting changes along a gradient characteristic of the predicted future environment throughout the subarctic, indicate that climate and land use driven eutrophication and browning are radically altering the function and fuelling of aquatic food webs in this biome.

Introduction

Climate change and intensification of land use practices are modifying ecosystem productivity across the globe (Vitousek 1994; Flynn *et al.* 2009). These changes are most pronounced in the Arctic and subarctic where increases in temperature and precipitation exceed global averages, resulting in an increase in the annual growth period (Bokhorst *et al.* 2008), an overall greening of the landscape (Xu *et al.* 2013) and the range expansion of warm adapted species (Rolls *et al.* 2017). Increased exploitation of natural resources e.g. infrastructure development, forestry and mining in these regions has increased supply of carbon, nitrogen and phosphorus from the catchment into watercourses (Payette *et al.* 2001). The co-occurrence of both stressors and their effect on biodiversity has been recognized for many years as a key driver of ecosystem level response to climate change in lakes (Post *et al.* 2009). Increases in temperature and nutrient availability in lakes intensifies pelagic productivity, leading to increased biomass of phyto- and zooplankton (de Senerpont Domis *et al.* 2013), and ultimately changing the fish community structure from large generalist taxa to smaller pelagic feeding fishes (Jeppesen *et al.* 2005, 2012; Hayden *et al.* 2017). However, the majority of data collected regarding these changes relates to shallow temperate lakes (Meerhoff *et al.* 2012), and considerably less is known regarding the mechanisms through which climate change will modify subarctic or Arctic lakes (Adrian *et al.* 2009).

Subarctic lakes are generally cold, clear, nutrient-poor ecosystems. Primary production in these systems is dominated by benthic algae with a seasonal plankton bloom in late summer (Vadeboncoeur *et al.* 2003; de Senerpont Domis *et al.* 2013). The fish communities are primarily comprised of cold-water adapted salmonid species which forage on both benthic and pelagic prey, but predominantly assimilate carbon synthesised by benthic algae (Hayden *et al.* 2014a). Increasing temperature and productivity in the region has lead to the eutrophication (Vadeboncoeur *et al.* 2003) and browning (Leech *et al.* 2018) of these lakes, increasing the duration and intensity of pelagic production and creating a habitat for warmer adapted consumers which occupy distinct benthic and pelagic niches (Hayden *et al.* 2017). Evidence from marine systems indicates that increased pelagic productivity may also result in an increase in pelagic-benthic coupling, whereby benthic communities are increasingly fuelled by pelagic detritus (Docmac *et al.* 2017). Initial descriptions of coupling within lake foods focussed on the degree to which ecological communities integrate resources produced in different habitats through "a set of processes that functionally link the ecological dynamics of benthic, riparian and pelagic habitats of lakes" (Schindler & Scheuerell 2002). Although this definition explicitly focusses on coupling of energy and resources which may be driven by sessile benthic organisms (e.g. Higgins & Vander Zanden 2010) most investigations of this phenomenon in lakes have focussed on foraging behaviour of fishes rather than nutrient pathways (Tunney *et al.* 2014; Guzzo *et al.* 2017), and comparatively few studies have detailed how changes in climate and productivity will affect pelagic-benthic coupling and lake ecosystem function across multiple trophic levels. Meerhoff *et al.* (2012) synthesised data from multiple space-for-time studies of shallow lakes revealing that the response of biota to climate change are often counterintuitive and nonlinear due to predator-prey dynamics within these ecosystems. Consequently, targeted research containing a range of different lake types is necessary to understand how lake communities in specific biomes will respond to environmental change. Such research is particularly relevant to subarctic lakes as freshwater fishes comprise a significant proportion of human diet in this region. Hence, changes to the quantity and quality of fishes are likely to impact subsistence fisheries and may be subsequently detrimental to human health.

To determine how climate and productivity influence pelagic-benthic coupling in lake food webs, we quantified the food web structure in 30 lakes situated on a space-for-time gradient reflecting the predicted future climate and land use scenarios for Northern Fennoscandia (Kovats *et al.* 2014, Fig. S1). We hypothesized that increased primary production associated with higher temperature and nutrient availability would incrementally shift food webs from a ‘clear’ to a ‘murky’ state (Leech et al. 2018), whereby consumers would increasingly be supported by pelagic production (Fig. 1). We predicted that a) increased pelagic-benthic coupling at the primary consumer level (i.e. benthic macroinvertebrates) would propagate pelagic-derived resources upwards through lake food webs to invertivorous and ultimately piscivorous fishes; and b) consumers with different foraging strategies would display distinct functional responses to this change, i.e. pelagic specialists would forage on pelagic prey throughout the gradient, generalist consumers would switch from benthic to pelagic foraging, and benthic specialists would feed on benthic prey, but assimilate an increased proportion of pelagic resources due to strengthened pelagic-benthic coupling by primary consumers (Fig. 1).

Methods

<u>Field sampling</u>

Environmental variables

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

Benthic macroinvertebrates

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

Fish

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

Laboratory analysis

Stable isotope analysis

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

Diet analysis

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

Data analysis

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

Results

Carbon isotope ratios of food web endmembers and consumers displayed considerable variation across the dataset. The littoral endmember values shifted from approximately -25‰ to -28‰, whereas the pelagic endmember increased from -33‰ to approximately -30‰ (Fig. 2). Commensurate with this, most consumers became depleted in ^{13}C with increasing CPi. Mixing models performed on this dataset revealed a major shift in the productivity pathways fuelling subarctic lake food webs along a climate and productivity gradient. The proportion of pelagic-derived carbon assimilated by benthic macroinvertebrates displayed a strong positive relationship with lake temperature and productivity (i.e. CPi). The assimilation of pelagic-derived carbon by benthic macroinvertebrates increased from approximately zero to over 90% across the CPi gradient (GLM: $\beta = 0.5 \pm 0.2$ SE; $p < 0.001$; Fig. 3, Table S2). The proportion of invertivorous fish biomass supported by pelagic-derived carbon increased from approximately 25% to 75% with increasing CPi ($\beta = 0.1 \pm 0.02$ SE; $p < 0.01$; Fig. 3, Table S3). However, this could not be explained by increased pelagic productivity, as CPi was not included among the best fitting models describing invertivore diet (Table S4, Fig. S6). Similar, albeit weaker, relationships were observed in piscivorous fishes (Fig. 3), whose integration of phytoplankton derived carbon displayed a positive relationship with CPi ($\beta = 0.1 \pm 0.02$; $p = 0.01$; Fig. 3, Table S3), despite their being no change in their consumption of pelagic prey.

The assimilation of phytoplankton-derived carbon (SIApel) by benthic macroinvertebrates was primarily explained by foraging guild, as pelagic specialists assimilated more pelagic-derived carbon than benthic specialists, whilst generalists were intermediate (Fig. 4, Table 1).

Assimilation of pelagic-derived carbon by benthic specialist macroinvertebrates was positively related to CPi ($\beta = 1.5 \pm 0.2$ SE, $p < 0.001$, Fig. 3, Fig. S6) and sampling depth ($\beta = 3.1 \pm 0.3$ SE, $p < 0.01$) and negatively related to Lake Area ($\beta = -0.3 \pm 0.1$ SE, $p < 0.05$, Fig. S4, Table 1). Despite occupying benthic habitats, generalist and benthic specialist invertebrates mainly integrated phytoplankton-derived carbon in lakes with high CPi scores (Fig. 4, Table S2).

The level of assimilation of phytoplankton-derived carbon (SIApel) by invertivorous fishes was positively related to CPi ($\beta = 1.1 \pm 0.2$ SE, $p < 0.001$) and Lake Area ($\beta = 0.5 \pm 0.2$ SE, $p < 0.05$), and differed between foraging guilds (Table 1). SIApel of pelagic specialist invertivorous fishes was consistently high (approximately 65%) throughout the study region, whereas SIAα of benthic specialist invertivores increased from 25% to 100% with increasing CPi. A similar, though less-pronounced increase (approx. 35% to 70%) was observed in generalist invertivores (Fig. 4, Table 1). Strikingly, pelagic prey consumption of all invertivore feeding guilds (GCApel) was unrelated to CPi, indicating that fishes did not change their foraging behaviour along the gradient. However, variation in pelagic foraging associated with CPi was evident in certain species (Fig S7). Perch, a cool-water generalist, and whitefish, a cold-water generalist, integrated more pelagic derived carbon in high CPi lakes, however, pelagic foraging by perch increased with increasing CPi, whereas pelagic foraging by whitefish decreased (Table S4).

Broadly similar patterns were observed in piscivorous fishes, though the strength of the relationship was slightly lower than in invertivores (Fig. 4, Fig. S6). Across guilds, piscivore 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, $p < 0.01$), while the slope of regression for benthivores was slightly lower than for generalists or pelagic specialists (Fig. 4). Interestingly, piscivore pelagic foraging (GCApel) was not related to CPi, but was primarily associated with Lake Area ($\beta = 0.5 \pm 0.1$ SE, $p < 0.01$) and Fish Species Richness ($\beta = -0.3 \pm 0.1$ SE, $p < 0.01$, Fig. 4, Table 1).

Discussion

Elevated temperature and productivity was associated with a profound shift from benthic to pelagic fuelled food webs in the 30 subarctic lakes analysed. The disconnect between pelagic resource assimilation and pelagic foraging across all consumer communities indicates that this shift was driven by pelagic-benthic coupling, i.e. a functional link between the ecological dynamics of benthic, riparian and pelagic habitats of lakes (sensu Schindler & Scheuerell 2002), at low trophic levels rather than increased pelagic foraging by higher trophic level consumers. Our results highlight the establishment of an indirect ‘green’ food chain following eutrophication of subarctic lakes. Phytoplankton synthesise organic carbon in the pelagic zone, and then settle on the lake bed, where they are consumed by benthic macroinvertebrates and ultimately fuel a benthic food chain. These results derived from a subarctic climate-productivity gradient are likely relevant to lakes globally as temperature, light and nutrient availability determines the dominant primary production pathway in all lakes (Adrian *et al.* 2009).

Our results show that pelagic-benthic coupling by benthic invertebrates is capable of shifting an entire lake food web towards a reliance on pelagic-derived carbon. A similar mechanism of pelagic-benthic coupling by primary consumers is responsible for pelagic fuelled littoral food chains in productive marine habitats (Docmac *et al.* 2017). Although Vadeboncoeur *et al.* (2003) demonstrate that the contribution of pelagic primary production to zoobenthos scales with lake productivity, evidence of this pathway in freshwater systems is mostly limited to a small number of taxa specific examples of diatom blooms fuelling deep-water chironomid communities and fluvial snails feeding on phytoplankton (Goedkoop & Johnson 1996; Kathol *et al.* 2011). Comparable coupling has been recorded in lake food webs following the establishment of invasive bivalves, e.g. Dreissenid mussels. These mussels filter phytoplankton and pelagic detritus from the water column and transfer it to the lake bed in the form of pseudofaeces, where it becomes a resource for benthic consumers (Higgins & Vander Zanden 2010). The majority of studies analysing this dynamic report an increase in benthic production due to increased water clarity following invasion (Madenjian *et al.* 2013; Fera *et al.* 2017), which is a reversal of the shift detailed in our results. It would be extremely interesting to assess the degree to which benthic consumers in those systems are fuelled by pelagic derived energy. In contrast to littoral invertebrates, both marine (France 1995) and freshwater profundal communities are known to be fuelled by pelagic detritus. Our results reveal that this trait is also characteristic of benthic consumers within the photic zone of subarctic lakes. This mechanism may also explain a widely observed phenomenon whereby benthic and pelagic invertebrates have distinct $\delta^{13}C$ isotope values in oligotrophic lakes, but comparatively similar values in more productive systems (Vadeboncoeur *et al.* 2003). The $\delta^{13}C$ values of littoral grazers are regularly used as a proxy for benthic algal primary production in stable isotope mixing models (Post 2002). However, in productive lakes these values are often identical to those of pelagic consumers, negating the ability to distinguish between pelagic and benthic resource use using $\delta^{13}C$ alone (Phillips *et al.* 2014). Indeed, in this study we were forced to omit data from one eutrophic lake as we could not accurately determine the $\delta^{13}C$ values of the littoral baseline (Supplemental Methods). The widespread integration of pelagic derived carbon by the littoral invertebrate community is commensurate with the convergence of $\delta^{13}C$ values between pelagic and benthic endmembers in eutrophic lakes (Vadeboncoeur *et al.* 2003).

The conversion of carbon isotope ratio values in our data also indicate that terrestrial derived carbon is increasingly important in eutrophic lakes as land use intensifies with increasing CPi. Low CPi lakes are associated with ecotourism and reindeer herding, this shifts first to mild and then intensive forestry at the high CPi extreme of the gradient (Hayden *et al.* 2017). This shift in land use leads to increased terrestrial carbon entering the water system resulting in lower light penetration and brownification of the waterbody (Graneli 2012). Primary consumers, pelagic zooplankton, may utilise poor quality terrestrial carbon, especially when phytoplankton is not available (Taipale *et al.* 2016). Carbon isotope ratios of the pelagic and benthic primary consumer end-members in our study system showed some evidence of this phenomenon. Littoral endmembers became depleted in ^{13}C, shifting from approximately -22 to -25‰, whereas pelagic zooplankton became ^{13}C-enriched, shifting from -32 to -29‰. Terrestrial primary consumers in this region typically have $\delta^{13}C$ values of approximately -28 to -27‰ (Milardi *et al.* 2016), and convergence of both endmembers towards this value is commensurate with brownification of the food web. The degree to which aquatic primary producers and consumers utilise terrestrial derived carbon has been a topic of considerable debate in the limnological literature (Brett *et al.* 2017) and while our data cannot resolve that debate it does indicate increasing terrestrial carbon along intensification of land use will change the base of lake food webs, adding a further dimension the pelagic-benthic convergence detailed by Vadeboncoeur *et al* (2003).

The space-for-time approach we used to assess the relationship between environmental drivers and ecosystem function allowed us to observe and record changes in the actual environment rather than extrapolating from micro- or mesocosm studies. However, it also conferred several disadvantages; collinearity between our key predictor variables, namely temperature and productivity, negates our ability to determine the effects of climate and land use change independently, along with any characterisation of synergistic or additive effects associated with these variables (Thomaz *et al.* 2012; Blois *et al.* 2013). As land use intensification occurs in conjunction with climate change across the globe, it is challenging to identify locations where these factors may be disentangled in the field. Further investigation on this topic may require additional mesocosm based studies. In addition, though we consider lakes as independent replicates in our models, variation in lake morphometry in conjunction with light availability may alter the relative abundance of pelagic, littoral and profundal habitat amongst lakes with clear implications for the relative contribution of pelagic and benthic primary production to the food web (Hayden *et al.* 2014b). In our study, lake area had a positive association with the degree to which fishes foraged on pelagic prey and assimilated pelagic-derived carbon. Though these effects were weaker than the shift associated with CPi, they do raise interesting questions regarding the interaction between lake productivity change and morphometry. In larger lakes the 'greening' of the food web extends an already existing pathway, whereas in small lakes it could potentially create novel pelagic niches, facilitating the encroachment of warm water adapted taxa adapted to foraging in such conditions (Hayden *et al.* 2017). Additional studies in a controlled environment or specifically comparing large and small lakes would necessary to test this conclusively.

The range of trophic states evident along this gradient of lakes mirrors the alternative stable states of shallow temperate lakes, in which a regime shift from 'clear' water, macrophyte-dominated state to a turbid, phytoplankton-dominated state is initiated by changes to lake productivity and maintained by a shift in the functional community structure of the consumers

(Scheffer & Carpenter 2003). Previously documented ‘regime shifts’ are often associated with a critical tipping point and may be reversed when one or both of these forcing mechanisms is relaxed (Scheffer & Carpenter 2003). However, our data show that climate-productivity induced shifts in subarctic lakes are incremental and it is therefore likely that a much stronger environmental forcing is needed to return these lakes to their original ‘clear’ state (Scheffer *et al.* 1993). Our data are commensurate with a considerable body of work from temperate, shallow lakes that such regime shifts in response to climate change occur slowly and are only reversed following considerable forcing spanning multiple trophic levels (Moss *et al.* 2011; Hilt *et al.* 2013). Earlier studies of subarctic lakes in the region have shown that the CPi gradient is characterised by an increase in fish biomass, a decrease in mean fish size and a change in community structure from dominance by few large-bodied generalists, to functionally diverse communities of intermediate-sized specialists, and finally to communities dominated by small-sized pelagic foraging fishes (Hayden *et al.* 2017). Despite these changes in functional diversity, the degree to which fishes foraged on pelagic prey remained remarkably consistent along the CPi gradient, diminishing the chances of return to ‘clear’ state through a modification of the ecological community alone.

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

In conclusion, we detail a major regime shift from benthic- to pelagic-fuelled food webs, driven not only by an increased prevalence of pelagic consumers (Hayden *et al.* 2017), but also by the amplification of a pelagic-fuelled, benthic food chain following eutrophication. Such a profound change in the basis of food webs along a 3˚C temperature and land use gradient reveals that the eutrophication of subarctic lakes is radically altering lake ecosystem function. Furthermore, the fundamental importance of temperature, light and nutrient availability to primary production pathways in lakes (Erik *et al.* 2003) suggest that the mechanisms outlined in this study have relevance to freshwater ecosystems across the globe.

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

	BMI	Invertivores		Piscivores	
Variable	SIA	SIA	GCA	SIA	GCA
Fixed Effects					
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)**
Random Effects					
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)

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

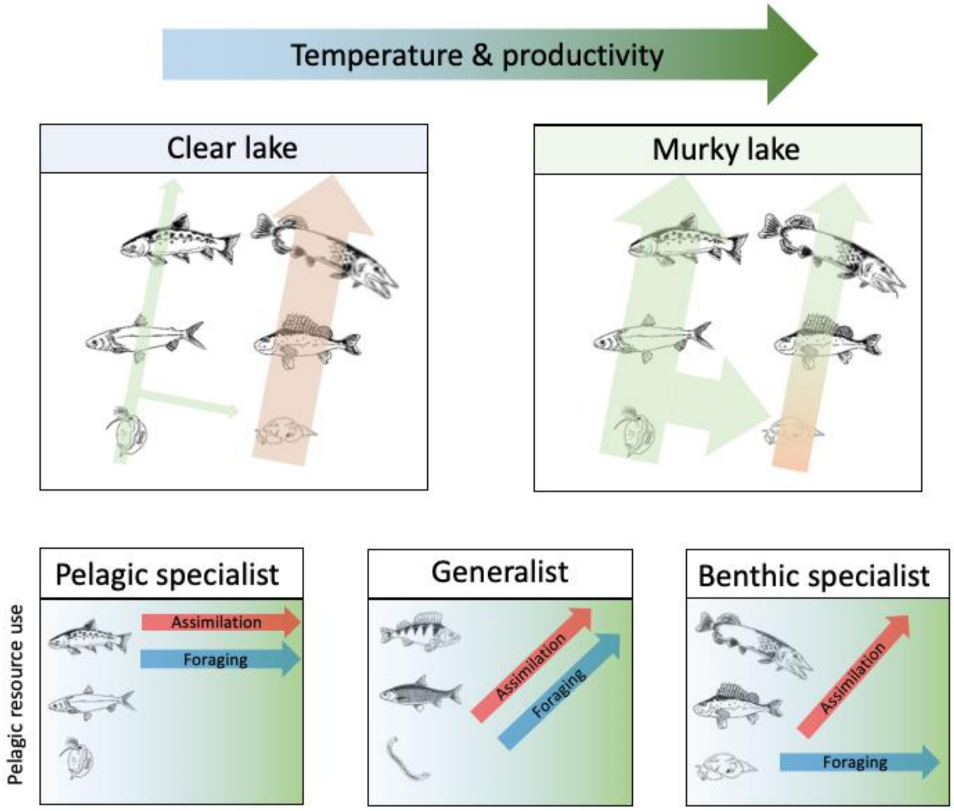

Fig. 1. Conceptual model of the predicted changes in subarctic lake food webs in response to increasing temperature and productivity. Top row: lake food webs are fuelled by either pelagic (green arrows) or littoral benthic (brown arrows) production, with arrow size reflecting importance of each pathway.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

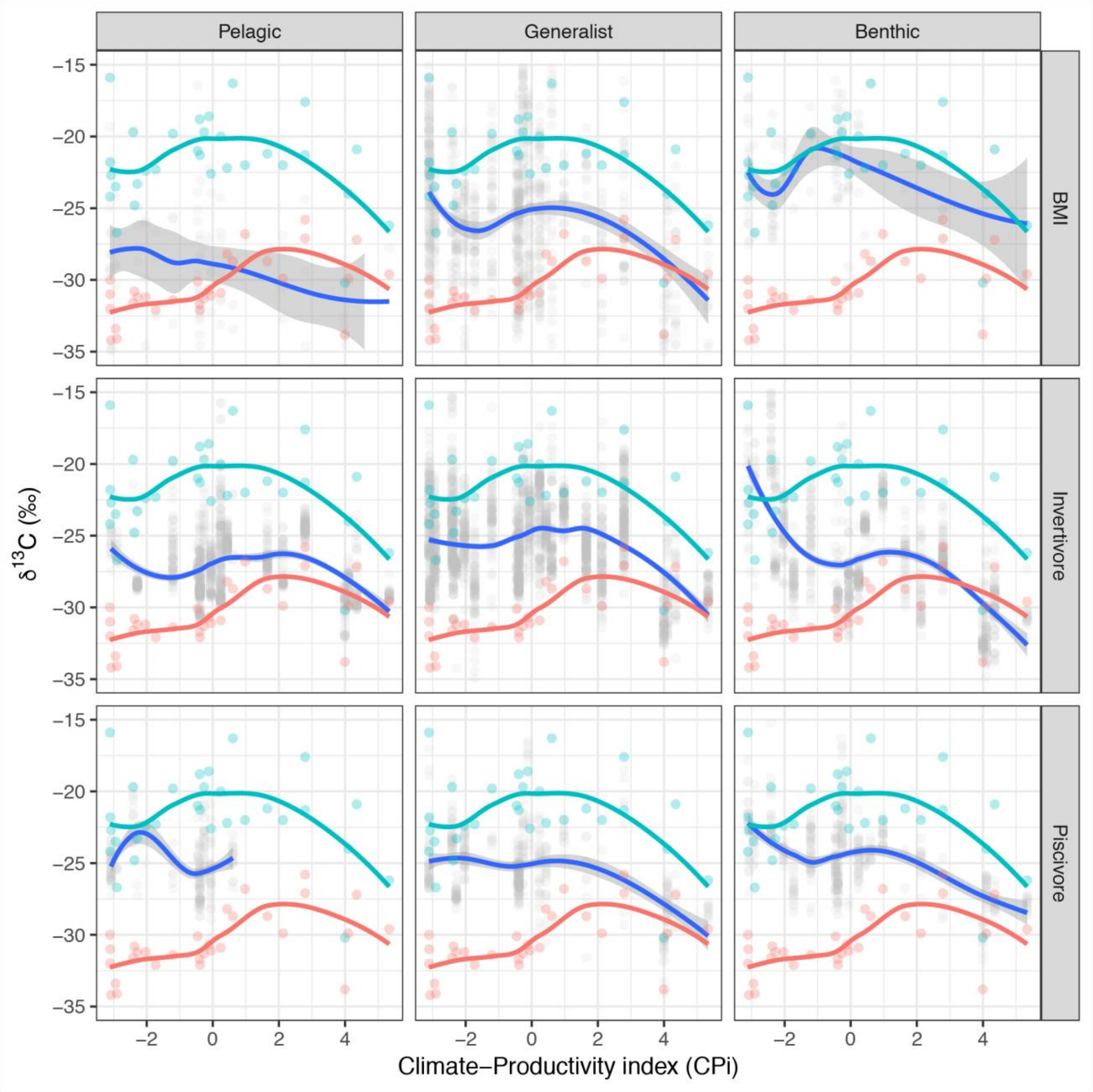

Fig 2. Scatter plots outlining the variation in littoral (light blue) and pelagic (red) food web endmembers and consumers (grey circles and dark blue smoother) along the climate - productivity gradient. Loess smoothers (shaded area denotes 95% confidence interval) are fitted to the data for illustrative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

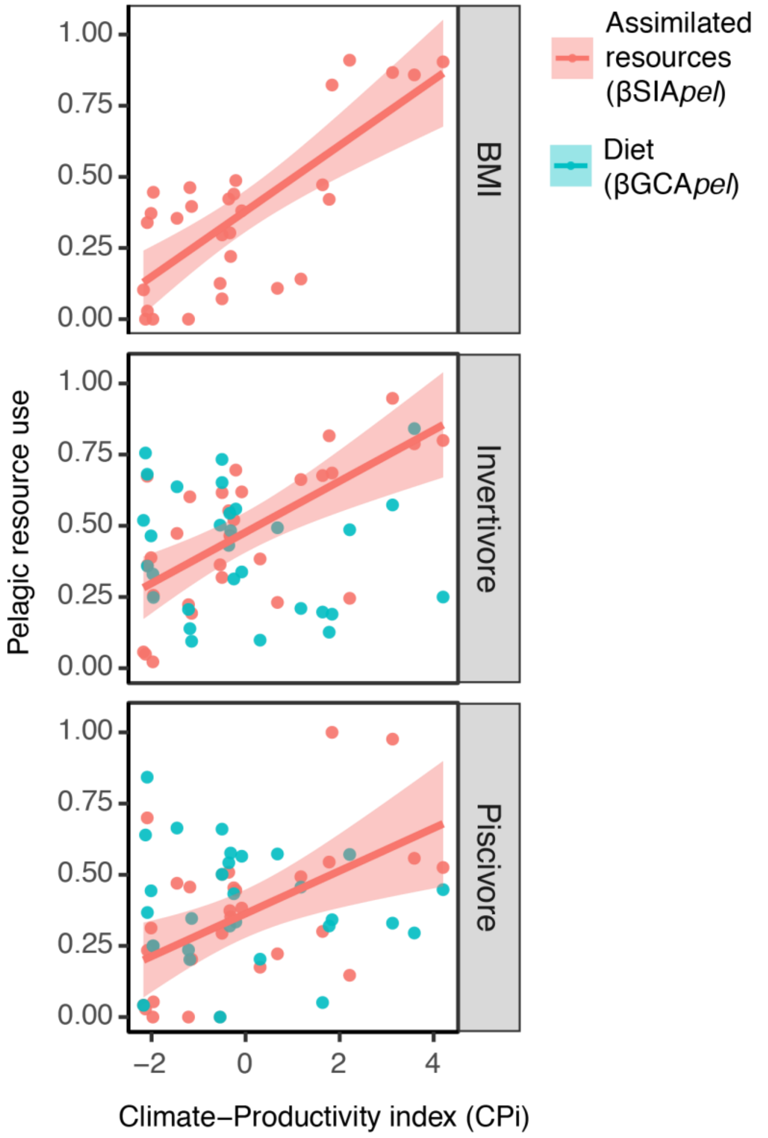

Fig. 3. Scatter plots outlining the relationship between community-level pelagic resource use of benthic invertebrates (BMI), invertivores and piscivores and the Climate-Productivity index (CPi, a principal component explaining 81% of environmental variation among lakes). Each datapoint represents the mean assimilation of pelagic-derived carbon (red) or pelagic prey consumed (blue) weighted by population density (BMI) or biomass (fish) for a single lake. Linear trendlines lines with 95% confidence intervals (shading) denote statistically significant relationships, full model fits are provided in Table S2, S3 and S4.

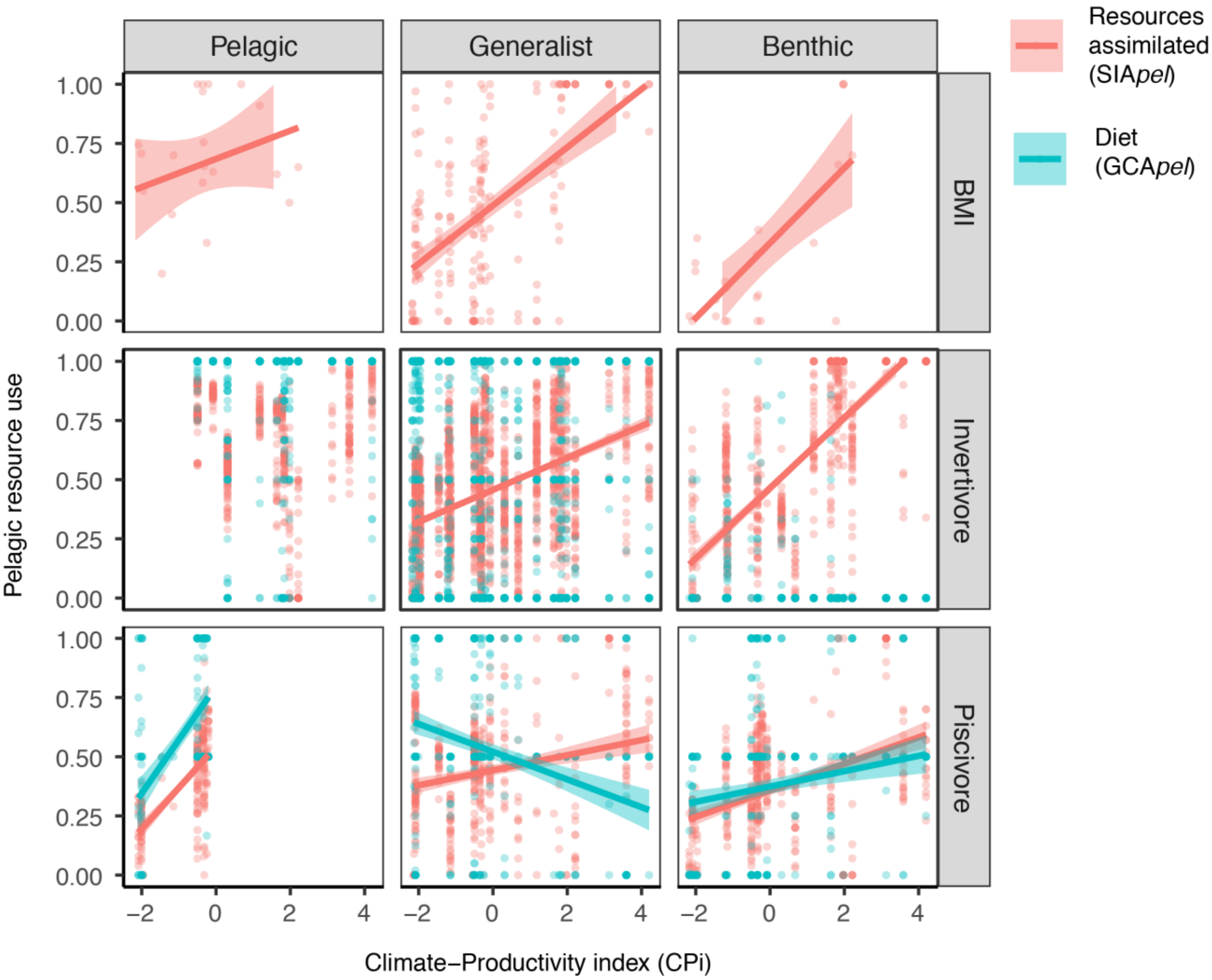

Fig. 4. Scatter plots outlining changes in individual pelagic resource use, inferred from stable isotope (red lines) and gut content (blue lines) analyses along a gradient of increasing lake temperature and productivity (CPi, a principal component explaining 81% environmental variation among lakes). Each datapoint represents an individual sample of benthic macroinvertebrates (BMI), invertivore or piscivore fish. Linear trendlines with 95% confidence intervals (shading) denote statistically significant relationships, full model fits are provided in Table 1.