








LETTER

From clear lakes to murky waters – tracing the functional response of high-latitude lake communities to concurrent '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 across 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. Our data also revealed a convergence of the carbon isotope ratios of pelagic and benthic food web endmembers in the warmest, most productive lakes indicating that the incorporation of terrestrial derived carbon into aquatic food webs increases as land use intensifies. 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.

Keywords

cryptic energetic pathways, ecological stable states, habitat coupling, space-for-time, stable isotope analysis, trophic niche.

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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 Arctic and subarctic areas, where increases in temperature and precipitation exceed global averages, resulting in an extension of 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 catchments into watercourses (Payette *et al.* 2001). The co-occurrence of both stressors and their effect on biodiversity has long been recognized 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 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 about the mechanisms through which climate change will modify thermally stratifying 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

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Domis *et al.* 2013). The fish communities are comprised primarily of cold-water adapted salmonid species which forage on both benthic and pelagic prey, but predominantly assimilate carbon synthesized by benthic algae (Vander Zanden & Rasmussen 1996; Hampton *et al.* 2011). Increasing temperature and productivity in the region has led 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 fuelled by pelagic detritus (Docmac *et al.* 2017). Initial descriptions of coupling within lake food webs 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 focuses 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 primary consumers (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) synthesized 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 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 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 productivity 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

Field sampling

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 environmental variation (Figs. S2 and 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 Methods, Figs. S4 and 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.* 2014). 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 $\text{g net series}^{-1} \text{h}^{-1}$) 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, Arctic charr *Salvelinus alpinus*) and benthic niches (large burbot, pike *Esox lucius*) were also included in our analysis (Amundsen *et al.* 2003; Kahilainen & Lehtonen 2003).

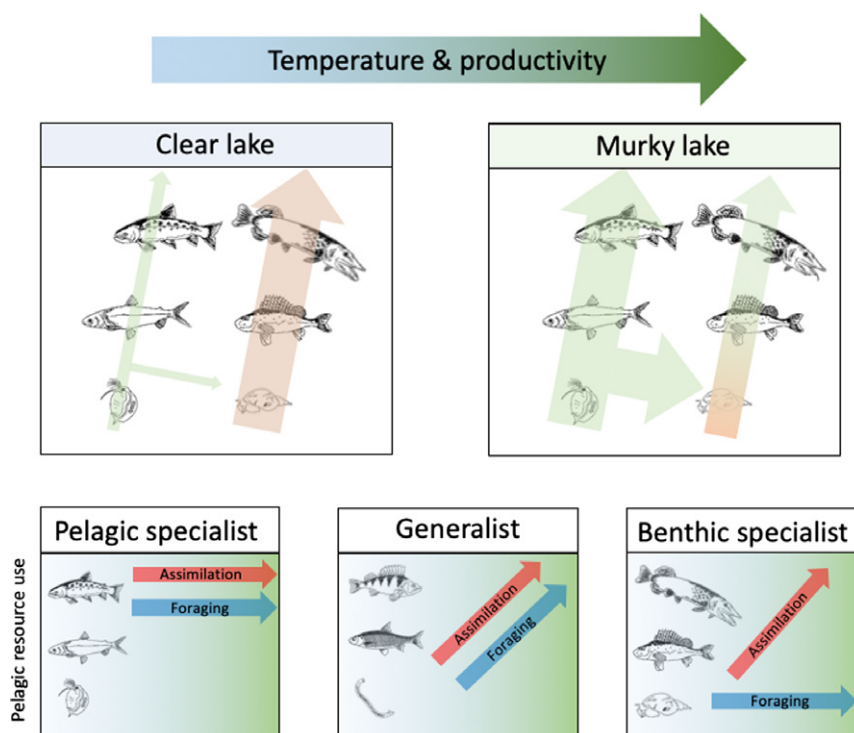


Figure 1 Conceptual model of the predicted changes in subarctic lake food webs in response to increasing temperature and productivity. Top row: lake food webs are fuelled by either pelagic (green arrows) or littoral benthic (brown arrows) production, with arrow size reflecting importance of each pathway.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

Laboratory analysis

Stable isotope analysis

We assessed the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios of benthic invertebrates and fishes and estimated pelagic resource reliance (SI_{Apel}) of each benthic invertebrate sample and individual fish using stable isotope mixing models (Post 2002). Benthic grazers (principally *Lymnaea* 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 (Supporting Information 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 (GCA_{pel}, measured on a 0-1 scale as the relative abundance of benthic and pelagic prey in fish stomach contents) 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 that forage on pelagic prey (Supporting Information Methods).

Data analysis

We used Generalized Linear Models (GLM) and Generalized 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 SI_{Apel} 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 Supporting Information Methods.

RESULTS

Carbon isotope ratios of food web endmembers and consumers displayed considerable variation across the dataset. The littoral endmember $\delta^{13}\text{C}$ values shifted from *c.* -25‰ to -28‰ , whereas the pelagic endmember increased from -33‰

to -30‰ with increasing CPI (Fig. 2). 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 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 pelagic-derived carbon displayed a positive relationship with CPI ($\beta = 0.1 \pm 0.02$; $P = 0.01$; Fig. 3, Table S3), despite there being no change in their consumption of pelagic prey.

The assimilation of pelagic-derived carbon (SI_{Apel}) by benthic macroinvertebrates was primarily explained by foraging guild, as pelagic specialists assimilated more pelagic-derived

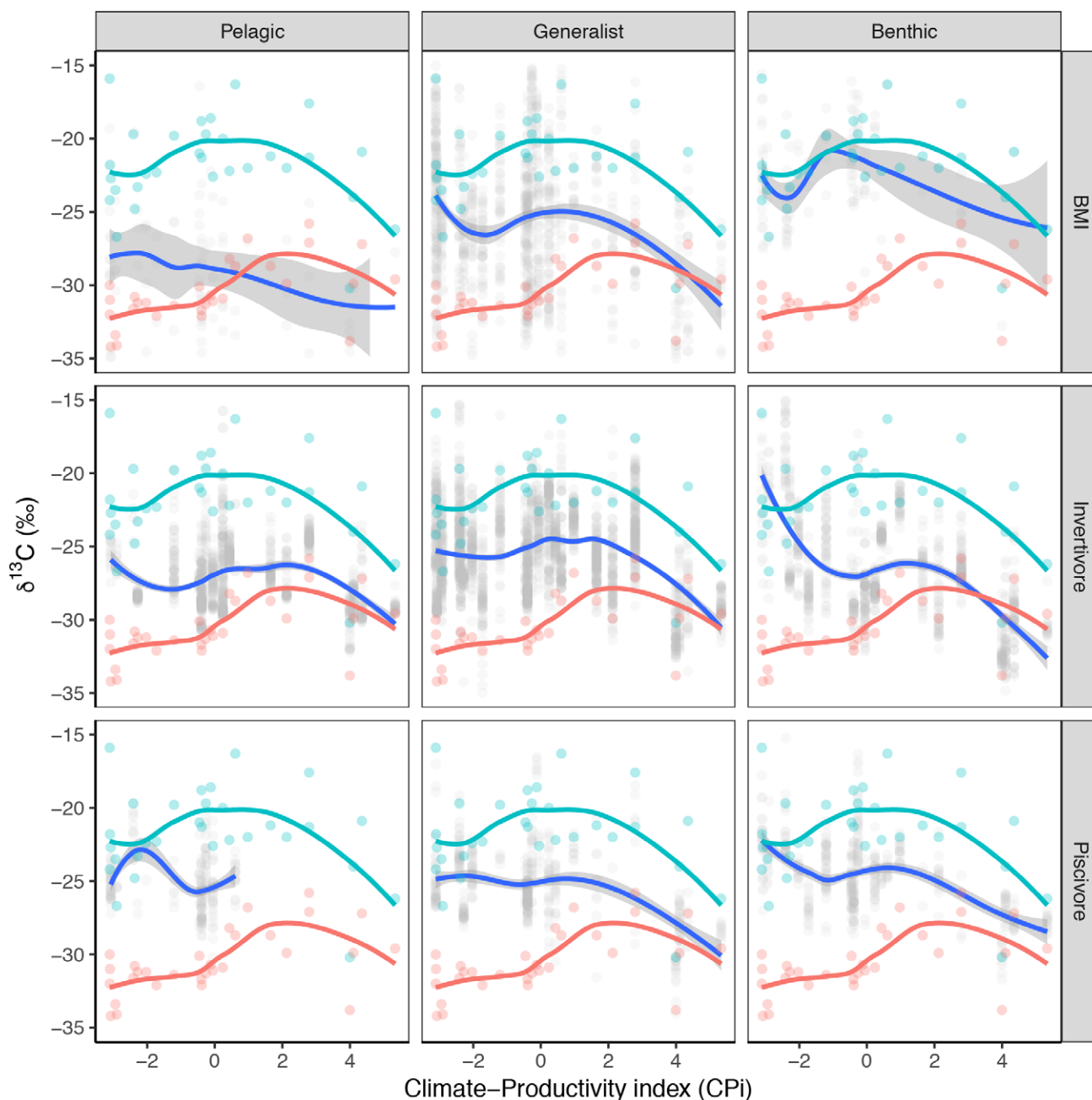


Figure 2 Scatter plots outlining the variation in littoral (light blue) and pelagic (red) food web endmembers, benthic macroinvertebrates (BMI) and fishes (grey circles and dark blue smoother) along the climate – productivity gradient. Loess smoothers (shaded area denotes 95% confidence interval) are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

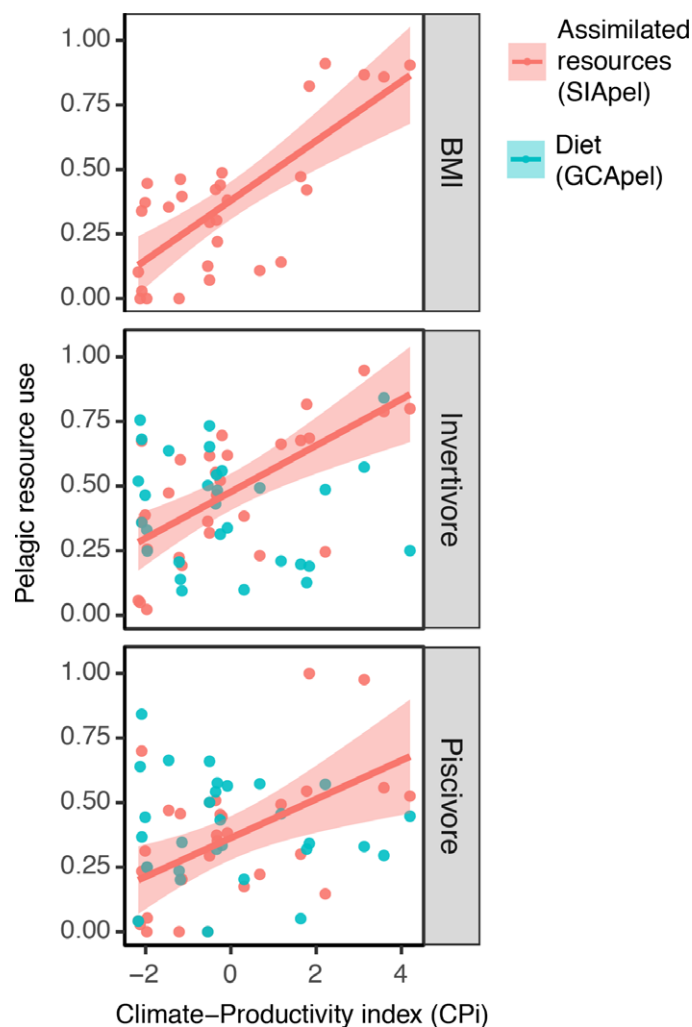


Figure 3 Scatter plots outlining the relationship between community-level pelagic resource use of benthic invertebrates (BMI), invertivores and piscivores and the Climate-Productivity index (CPI, a principal component explaining 80% of environmental variation among lakes). Each datapoint represents the 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 with 95% confidence intervals (shading) denote statistically significant relationships. Full model fits are provided in Table S2, S3 and S4.

carbon than benthic specialists, whilst generalists were intermediate in their use of the two resources (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 pelagic-derived carbon in lakes with high CPI scores (Fig. 4, Table S2).

The level of assimilation of pelagic-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 (c. 65%) throughout the study region, whereas SIApel of benthic specialist invertivores increased from 25% to 100% with increasing CPI. A similar, though less-pronounced increase (c. 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 were 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' trophic pathway following eutrophication of subarctic lakes. Phytoplankton synthesize 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 determine the dominant primary production pathway in 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

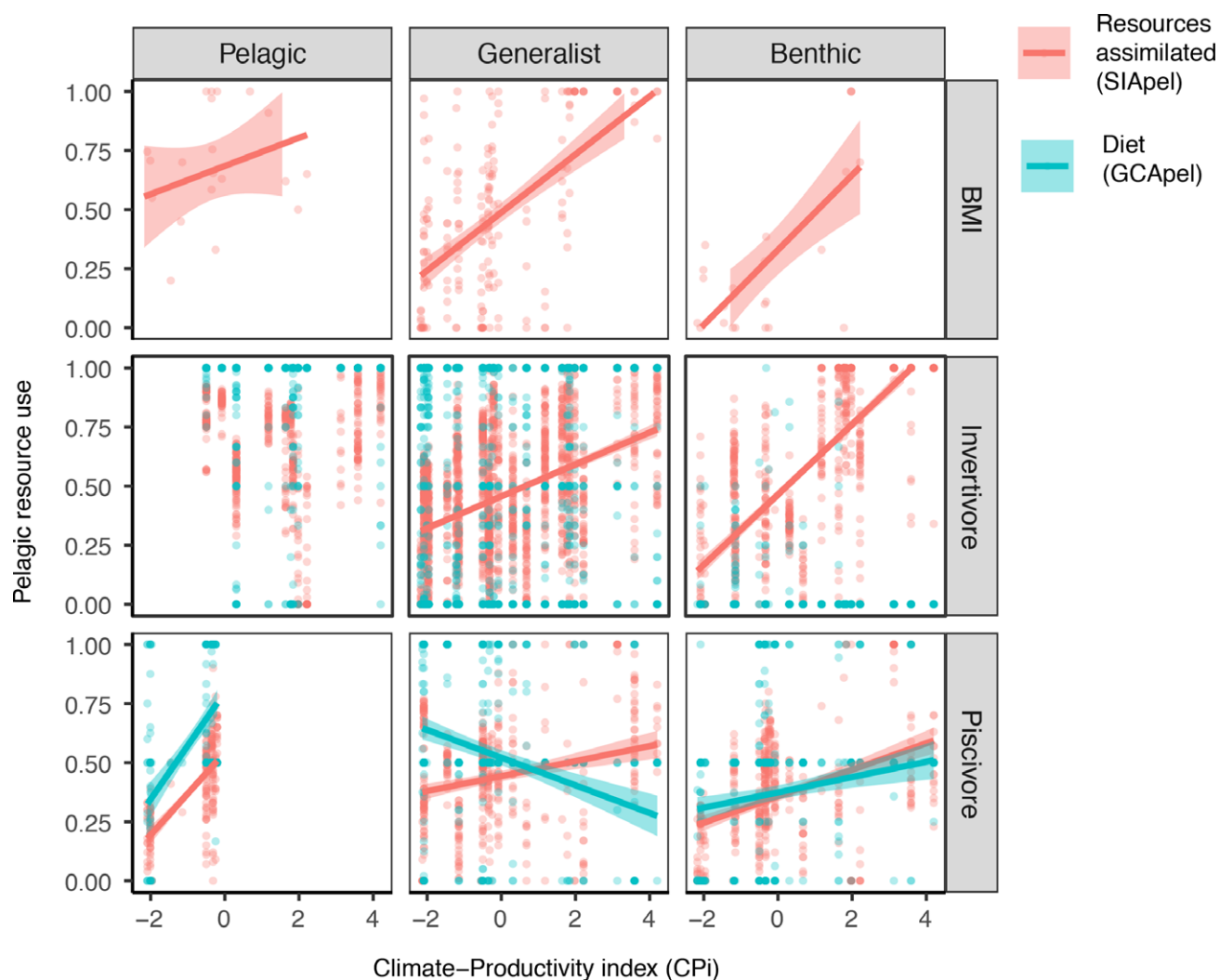


Figure 4 Scatter plots outlining changes in individual pelagic resource use, inferred from stable isotope (red lines) and gut content (blue lines) analyses along a gradient of increasing lake temperature and productivity (CPI, a principal component explaining 80% environmental variation among lakes). 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.

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 highly interesting to assess the degree to which benthic consumers in those invaded systems are fuelled by pelagic-derived energy. In contrast with littoral invertebrates, both marine (France 1995) and freshwater profundal communities are known to be fuelled by pelagic detritus (Goedkoop & Johnson 1996). 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 $\delta^{13}\text{C}$ values in oligotrophic

lakes, but comparatively similar values in more productive systems (Vadeboncoeur *et al.* 2003). The $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ values of the littoral baseline (Supporting Information Methods). The widespread integration of pelagic derived carbon by the littoral invertebrate community is commensurate with the convergence of $\delta^{13}\text{C}$ values between pelagic and benthic endmembers in eutrophic lakes (Vadeboncoeur *et al.* 2003).

The conversion of pelagic and benthic carbon isotope ratio values in our data also indicates that terrestrial derived carbon is increasingly important in eutrophic lakes as land use intensifies with increasing CPI. Land use in the catchment of

Table 1 Summary of Generalized 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 in pelagic-derived carbon (SIA) and pelagic foraging (GCA) of benthic macroinvertebrates (BMI), invertivorous and piscivorous fishes. The values present Parameter Estimates ($\beta \pm$ 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 the assumption that fishes move between depths.

Variable	BMI		Invertivores		Piscivores	
	SIA		SIApel	GCApel	SIApel	GCApel
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)

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

low CPi lakes predominantly consists of ecotourism and reindeer herding, but 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, e.g. pelagic zooplankton, may utilize poor quality terrestrial carbon, especially when phytoplankton is not available (Taipale *et al.* 2016). Carbon isotope ratios of the pelagic and benthic primary consumer endmembers in our study system showed some evidence of this phenomenon. Littoral endmembers became depleted in ^{13}C , shifting $\delta^{13}\text{C}$ from -22 to -25‰ , whereas pelagic zooplankton became ^{13}C -enriched, shifting $\delta^{13}\text{C}$ from -32 to -29‰ . Terrestrial primary consumers in this region typically have $\delta^{13}\text{C}$ values of -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 utilize terrestrial-derived carbon has been a topic of considerable debate in the limnological literature (Brett *et al.* 2017). While our data cannot resolve that debate, they do indicate that an increased availability of terrestrial carbon due to the intensification of land use will change the base of lake food webs, adding a further dimension to 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 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 characterization 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.* 2014). 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 under such conditions (Hayden *et al.* 2017). Additional studies in a controlled environment, or specifically comparing large and small lakes, would be 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 are 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 suggesting 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 characterized 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 an additional 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 subarctic lakes 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 shift from benthic to pelagic productivity pathways may correspond to a negative shift in nutritional capacity of food webs and has major bottom-up effects by reducing the quality of local fish catches (Hayden *et al.* 2017). In addition, the reduction in 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 (Jeppesen *et al.* 2003) suggests that the mechanisms outlined in this study have relevance to freshwater ecosystems across the globe.

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AUTHORSHIP

All authors made a substantial intellectual contribution to this work. BH and KKK designed the study; all authors conducted field sampling; BH, APE and CH conducted stable isotope analysis; BH, KKK and APE conducted dietary analysis, BH and SMT conducted data analysis, all contributed to writing and editing the manuscript.

DATA ACCESSIBILITY STATEMENT

Summary data supporting all analyses and plots are provided in the supporting material. The data supporting the results are available on Figshare (<https://doi.org/10.6084/m9.figshare.7611557.v1>).

REFERENCES

- Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., *et al.* (2009). Lakes as sentinels of climate change. *Limnol. Oceanogr.*, 54, 2283–2297.
- Amundsen, P.-A., Bøhn, T., Popova, O.A., Staldvik, F.J., Reshetnikov, Y.S., Kashulin, N.A., *et al.* (2003). Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. *Hydrobiologia*, 497, 109–119.
- Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T. & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *Proc. Natl Acad. Sci.*, 110, 9374–9379.
- Bokhorst, S., Bjerke, J.W., Bowles, F.W., Melillo, J., Callaghan, T.V. & Phoenix, G.K. (2008). Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Glob. Change Biol.*, 14, 2603–2612.
- Brett, M.T., Bunn, S.E., Chandra, S., Galloway, A.W.E., Guo, F., Kainz, M.J., *et al.* (2017). How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? *Freshw. Biol.*, 62, 833–853.
- Docmac, F., Araya, M., Hinojosa, I.A., Dorador, C. & Harrod, C. (2017). Habitat coupling writ large: pelagic-derived materials fuel benthivorous macroalgal reef fishes in an upwelling zone. *Ecology*, 98, 2267–2272.
- Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., *et al.* (2016). Navigating the complexity of ecological stability. *Ecol. Lett.*, 19, 1172–1185.
- Fera, S.A., Rennie, M.D. & Dunlop, E.S. (2017). Broad shifts in the resource use of a commercially harvested fish following the invasion of dreissenid mussels. *Ecology*, 98, 1681–1692.
- Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., *et al.* (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.*, 12, 22–33.

- France, R.L. (1995). Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar. Ecol. Prog. Ser.*, 124, 307–312.
- Goedkoop, W. & Johnson, R.K. (1996). Pelagic-benthic coupling: profundal benthic community response to spring diatom deposition in mesotrophic Lake Erken. *Limnol. Oceanogr.*, 41, 636–647.
- Graneli, W. (2012). Brownification of Lakes. In *Encyclopedia of Lakes and Reservoirs* (eds Bengtsson, L., Herschy, R.W., Fairbridge, R.W.). Springer, Netherlands, Dordrecht, pp. 117–119.
- Guzzo, M.M., Blanchfield, P.J. & Rennie, M.D. (2017). Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator. *Proc. Natl Acad. Sci.*, 114, 9912–9917.
- Hampton, S.E., Fradkin, S.C., Leavitt, P.R. & Rosenberger, E.E. (2011). Disproportionate importance of nearshore habitat for the food web of a deep oligotrophic lake. *Mar. Freshw. Res.*, 62, 350–358.
- Hayden, B., Harrod, C. & Kahilainen, K.K. (2014). Lake morphometry and resource polymorphism determine niche segregation between cool- and cold-water adapted fish. *Ecology*, 95, 538–552.
- Hayden, B., Myllykangas, J.-P., Rolls, R.J. & Kahilainen, K.K. (2017). Climate and productivity shape fish and invertebrate community structure in subarctic lakes. *Freshw. Biol.*, 62, 990–1003.
- Higgins, S.N. & Vander Zanden, M.J. (2010). What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecol. Monogr.*, 80, 179–196.
- Hilt, S., Köhler, J., Adrian, R., Monaghan, M.T. & Sayer, C.D. (2013). Clear, crashing, turbid and back – long-term changes in macrophyte assemblages in a shallow lake. *Freshw. Biol.*, 58, 2027–2036.
- Jeppesen, E., Jensen, J.P., Jensen, C., Faafeng, B., Hessen, D.O., Søndergaard, M., et al. (2003). The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate zone to the arctic. *Ecosystems*, 6, 313–325.
- Jeppesen, E., Søndergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., et al. (2005). Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.*, 50, 1747–1771.
- Jeppesen, E., Mehner, T., Winfield, I.J., Kangur, K., Sarvala, J., Gerdeaux, D., et al. (2012). Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia*, 694, 1–39.
- Kahilainen, K.K. & Lehtonen, H. (2003). Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. *J. Fish Biol.*, 63, 659–672.
- Kathol, M., Fischer, H. & Weitere, M. (2011). Contribution of biofilm-dwelling consumers to pelagic-benthic coupling in a large river. *Freshw. Biol.*, 56, 1160–1172.
- Kovats, R.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D. & Martin, E., et al. (2014). Europe. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change* (eds Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J. & Bilir, T.E., et al.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, pp. 1267–1326.
- Leech, D.M., Pollard, A.I., Labou, S.G. & Hampton, S.E. (2018). Fewer blue lakes and more murky lakes across the continental U.S.: Implications for planktonic food webs. *Limnol. Oceanogr.*, 63, 2661–2680.
- Madenjian, C.P., Rutherford, E.S., Stow, C.A., Roseman, E.F. & He, J.X. (2013). Trophic Shift, Not Collapse. *Environ. Sci. Technol.*, 47, 11915–11916.
- McMeans, B.C., McCann, K.S., Humphries, M., Rooney, N. & Fisk, A.T. (2015). Food web structure in temporally-forced ecosystems. *Trends Ecol. Evol.*, 30, 662–672.
- Meerhoff, M., deTeixeira-Mello, F., Kruk, C., Alonso, C., González-Bergonzoni, I., Pacheco, J.P., et al. (2012). Environmental Warming in Shallow Lakes: A Review of Potential Changes in Community Structure as Evidenced from Space-for-Time Substitution Approaches. *Advances in Ecological Research*, 46, pp. 259–349.
- Merritt, R.W., Cummins, K.W. & Berg, M.B. (2008). *An Introduction to Aquatic Insects of North America*, 4th edn. Kendall/Hunt Publishing Co., Dubuque.
- Milardi, M., Thomas, S.M. & Kahilainen, K.K. (2016). Reliance of brown trout on terrestrial prey varies with season but not fish density. *Freshw. Biol.*, 61, 1143–1156.
- Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., et al. (2011). Allied attack: climate change and eutrophication. *Inland Waters*, 1, 101–105.
- Müller-Navarra, D.C., Brett, M.T., Park, S., Chandra, S., Ballantyne, A.P., Zorita, E., et al. (2004). Unsaturated fatty acid content in seston and tropho-dynamic coupling in lakes. *Nature*, 427, 69–72.
- Payette, S., Fortin, M.-J. & Gamache, I. (2001). The Subarctic Forest-Tundra: the Structure of a Biome in a Changing Climate The shifting of local subarctic tree lines throughout the forest-tundra biome, which is linked to ecological processes at different spatiotemporal scales, will reflect future global changes in climate. *Bioscience*, 51, 709–718.
- Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., et al. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.*, 92, 823–835.
- Post, D.M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83, 703–718.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., et al. (2009). Ecological Dynamics Across the Arctic Associated with Recent Climate Change. *Science*, 325, 1355–1358.
- Przytułska, A., Bartosiewicz, M. & Vincent, W.F. (2017). Increased risk of cyanobacterial blooms in northern high-latitude lakes through climate warming and phosphorus enrichment. *Freshw. Biol.*, 62, 1986–1996.
- Rolls, R.J., Hayden, B. & Kahilainen, K.K. (2017). Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecol. Evol.*, 7, 4109–4128.
- Rooney, N. & McCann, K.S. (2012). Integrating food web diversity, structure and stability. *Trends Ecol. Evol.*, 27, 40–45.
- Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.*, 18, 648–656.
- Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B. & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends Ecol. Evol.*, 8, 275–279.
- Schindler, D.E. & Scheuerell, M.D. (2002). Habitat coupling in lake ecosystems. *Oikos*, 98, 177–189.
- de Senerpont Domis, L.N., Elser, J.J., Gsell, A.S., Huszar, V.L.M., Ibelings, B.W., Jeppesen, E., et al. (2013). Plankton dynamics under different climatic conditions in space and time. *Freshw. Biol.*, 58, 463–482.
- Sierszen, M.E., McDonald, M.E. & Jensen, D.A. (2003). Benthos as the basis for arctic lake food webs. *Aquat. Ecol.*, 37, 437–445.
- Sjölander, P. (2011). What is known about the health and living conditions of the indigenous people of northern Scandinavia, the Sami? *Glob. Health Action*, 4, 8457.
- Swynnerton, G.H. & Worthington, E.B. (1940). Note on the Food of Fish in Haweswater (Westmorland). *J. Anim. Ecol.*, 9, 183–187.
- Taipale, S.J., Galloway, A.W.E., Aalto, S.L., Kahilainen, K.K., Strandberg, U. & Kankaala, P. (2016). Terrestrial carbohydrates support freshwater zooplankton during phytoplankton deficiency. *Sci. Rep.*, 6, 30897.
- Thomaz, S.M., Agostinho, A.A., Gomes, L.C., Silveira, M.J., Rejmánek, M., Aslan, C.E., et al. (2012). Using space-for-time substitution and time sequence approaches in invasion ecology. *Freshw. Biol.*, 57, 2401–2410.
- Tunney, T.D., McCann, K.S., Lester, N.P. & Shuter, B.J. (2014). Effects of differential habitat warming on complex communities. *Proc. Natl Acad. Sci.*, 111, 8077–8082.
- Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup, H.-H., Christoffersen, K. & Lodge, D.M. (2003). From Greenland to green

- lakes: cultural eutrophication and the loss of benthic pathways in lakes. *Limnol. Oceanogr.*, 48, 1408–1418.
- Vander Zanden, M.J. & Rasmussen, J.B. (1996). A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecol. Monogr.*, 66, 451–477.
- Vitousek, P.M. (1994). Beyond global warming - ecology and global change. *Ecology*, 75, 1861–1876.
- Xu, L., Myneni, R.B., Iii, F.S.C., Callaghan, T.V., Pinzon, J.E., Tucker, C.J., *et al.* (2013). Temperature and vegetation seasonality diminishment over northern lands. *Nat. Clim. Change*, 3, 581–586.

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