Oecologia (2025) 207:82
https://doi.org/10.1007/s00442-025-05681-9

ORIGINAL RESEARCH

Rapid recovery of an arctic lake ecosystem from a pulse disturbance caused by thermokarst failure

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Received: 12 March 2024 / Accepted: 15 February 2025

Abstract

Due to rapid climate change, arctic ecosystems are experiencing an increase in disturbances including localized land-surface failures caused by melting ground ice (thermokarst failures). These failures result in the mass transport of sediment and organic materials into surface waters, with the potential to dramatically alter aquatic ecosystem function and biotic interactions. We coupled direct comparisons and long-term data of a suite of abiotic and biotic variables in a thermokarst-impacted lake and nearby reference lake to assess the impacts of thermokarst failure. After the thermokarst failure and relative to long-term averages, water transparency was substantially reduced. We hypothesized there would be subsequent changes to lower trophic levels and profound declines in fish foraging efficiency. However, these characteristics were within the range of natural variability and/or rapidly recovered to values within the range of long-term variability. In addition, although there was limited evidence of taxa-specific changes, we did not observe any strong changes in the total relative densities, growth rates, or composition of the bacterioplankton and zooplankton communities, benthic macroinvertebrates, or changes in fish diet, that could be attributed statistically to the thermokarst event. In sum, the thermokarst disturbance had substantial effects on water transparency and some lower trophic levels, which surprisingly were not manifested in higher trophic levels. Overall, the lake ecosystem appeared resistant to thermokarst disturbance with rapid recovery within two years after the disturbance.

Keywords Climate change · Warming · Fish · Zooplankton · Microbe · Water quality

Introduction

Climate change is altering aquatic ecosystems, and the climate is changing faster in the Arctic than in any place on Earth (Overland et al. 2015; Box et al. 2019; IPCC 2023). Consequently, arctic ecosystems have begun to change rapidly and are experiencing an increase in ecological pulse and press (e.g., climate change influenced) disturbances (e.g., Hobbie and Kling 2014; Kendrick et al. 2018). Pulse disturbances include tundra fires (Mack et al. 2011; Hu et al. 2010, 2015) and land-surface failures due to melting ground ice (termed thermokarst failures), which can persist in some

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Communicated by Robert O. Hall.

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instances long enough to be considered press disturbances (Bowden et al. 2008; Schurr et al. 2009; Bowden et al. 2014). Thermokarst failures typically result in reductions in water clarity and increased productivity via the mass transport of soil (e.g., sediment, carbon), vegetation, and dissolved constituents (including nutrients) into surface waters, with the potential to dramatically alter aquatic ecosystem function and biological interactions (Kokelj et al. 2005; Mack et al. 2011; Vonk et al. 2015).

Much prior research has focused on the effects of climate change on components of lake ecosystems via warmer waters (e.g., Baulch et al. 2005; Schneider and Hook 2010). However, in the Arctic, the effects of climate change via disturbances, such as thermokarst failure, may be more influential on lake ecosystem processes than the direct effects of warming (Luecke et al. 2014; Vasconcelos et al. 2019). The plug of suspended sediment and nutrients delivered to aquatic ecosystems after these pulse disturbances likely has a variety of effects on lake processes that vary both spatially (locally versus system-wide) and temporally (Budy et al. 2021). These thermokarst failures can range in size from small slumps (< 1 m^2) to > 1 km^2 and can be caused by climate change including warming and fire (Burn 2013). Thermokarst failures are increasing in arctic regions in response to increased air temperatures (Gooseff et al. 2011; Lewkowicz and Way 2019). Bowden et al. (2008) identified at least 34 arctic thermokarst features in the area near Toolik Lake using high-resolution aerial surveys, 67% of which were new since 1980, and most of which were associated with headwater streams or lakes.

Observations of thermokarst failures potentially impacting lakes suggest their impacts may vary depending on the type and duration of the disturbance (*this study*; Budy et al. 2021). Some thermokarst failures called “gurglers” occur from the apparent thaw of an ice wedge accompanied by upslope subsidence, which results in sediment and other organic material entering surface waters (i.e., ‘incipient gulley thermokarst’; Bowden et al. 2008). Decreased water clarity from increased suspended sediments can impact primary productivity via reduced light attenuation, which can then negatively affect zooplankton and other macroinvertebrates that feed on phytoplankton and periphyton (*reviewed in* Billota and Brazier 2008; Chapman et al. 2017). If suspended sediment concentrations are high enough, they can have direct physiological impacts on filter-feeding biota (e.g., many zooplankton species) because feeding structures become clogged and reduce feeding efficiency, with concordant impacts on vital rates (Hynes 1970; Billota and Brazier 2008). Conversely, thermokarst failures deliver nutrients that can stimulate the food web from the bottom up, if not negated by a reduction in light, as mentioned above (Donohue and Molinos 2009; Vasconcelos et al. 2019; Budy et al. 2021). For example, bacterioplankton density and growth rate responses to thermokarst failures are highly variable in direction and magnitude (Thompson et al. 2012; Roiha et al. 2015; Moquin and Wrona 2015; Deshpande et al. 2016). Finally, reduced water transparency can interrupt the foraging cycle of visually feeding fish predators (Endler 1991), dramatically decrease encounter rates (e.g., Turesson and Brönmark 2007), and even impair predator avoidance (Bollens et al. 1989), which ultimately could lead to lower foraging efficiency, growth, and survival (Byström et al. 2006; van Dorst et al. 2019, 2020).

Because the number of lakes impacted by thermokarst failures and the magnitude and duration of these disturbances appear to be increasing with warming air temperatures in the Arctic, it is important to compare current disturbance effects with long-term data on lake ecosystems. Long-term limnological studies of arctic lakes near Toolik Field Station (NSF Arctic Long Term Ecological Research [ARC LTER]), Alaska, USA, began in 1975, providing a long and necessary baseline against which to measure the limnological response of lakes to environmental change (Turner et al. 2003; Luecke et al. 2014). First detected in the summer of 2019, and possibly starting as early as late fall 2018, a thermokarst failure occurred at an LTER study lake (Lake I2) in the northern foothills of the Brooks Range, Alaska. Here we assess the effects of this thermokarst failure on an arctic lake ecosystem relative to before the disturbance and relative to an unimpacted, nearby LTER reference lake (Lake I1). Based on substantial and persistent reductions in water transparency, we hypothesized the thermokarst failure would reduce production by phytoplankton and bacterioplankton. In turn, we hypothesized that this reduction could impact higher trophic levels, including the availability of fish prey and declines in visibility that would lead to changes in fish feeding and diet composition. In other work, where the impacts on water transparency were less dramatic, we hypothesized the simultaneous increase in nutrients delivered by a thermokarst would stimulate phytoplankton growth with concordant effects up the food web (Budy et al. 2021).

Materials and methods

Study area

Our study occurred in lakes near Toolik Lake and the Toolik Field Station (68°37’ N, 149°36’W; https://toolik.alaska.edu), in the primary study area of the ARC LTER monitoring program (https://arc-lter.ecosystems.mbl.edu). Study lakes are surrounded by permafrost soils with summer soil active (thawed) layers less than 1 m thick (typically 30–40 cm); mean annual air temperature is – 7 °C, and mean July temperature is 12 °C (Hobbie and Kling 2014). The lakes are generally ice-free from mid-June to late September. For example, Toolik Lake had 109 ± 10 ice-free days from 2010 to 2021 (mean ± Standard Deviation, SD; Toolik Lake West camera; EDCT 2007).

Our study focused on a pair of lakes, Lake I1 and I2, hereafter referred to as the reference lake and thermokarst lake, respectively. These lakes are located about 5 km south of Toolik Lake, less than 350 m apart, and have many similarities including both are headwater lakes in a series of nine lakes connected by streams in the Toolik catchment, and they share similar water chemistry (Luecke et al. 2014). The fish assemblages in both lakes consist of arctic grayling (*Thymallus arcticus*), lake trout (*Salvelinus namaycush*), slimy sculpin (*Cottus cognatus*), round whitefish (*Prosopium cylindraceum*), and burbot (*Lota lota*). The lakes do differ in morphology, where the reference lake has a maximum depth of 10.4 m, average depth of 3.9 m, and surface area of 34.5 ha, and the thermokarst lake has a maximum depth of 18.2 m, average depth of 7.2 m, and surface area of 9.3 ha. At the beginning of the summer in 2019, a gurgler thermokarst was noted on the south shore of the thermokarst lake and the water color had changed dramatically (Fig. 1). We report on data from these lakes collected from 2010 to 2021; although, the temporal extent of data available differs among response variables (see below).

Sample collection and processing

We measured limnological and biotic variables at both lakes at least weekly during the summer of each year (July–August; Table S1) throughout the water column (every 0.5 – 1 m) using standard limnological techniques (e.g., Wetzel and Likens 2000; *additional sampling and analysis details are available* in Kling et al. 1992a, b, 2000; Luecke et al. 2014). Sampling and measurements were performed at the deepest part of the lakes, except where noted.

We classified samples as in the epilimnion, metalimnion, or hypolimnion based on sample depth relative to the thermocline based on summer temperature averages. Here, we focus on time series of summer data from the epilimnion for temperature, dissolved oxygen, water transparency, nutrients, chlorophyll *a*, bacterioplankton productivity and composition, zooplankton density and composition, littoral (< 5 m) and benthic macroinvertebrate density and composition, and fish abundance and diet composition. We also estimated primary productivity using uptake of ^{14}C labeled bicarbonate in the particulate fraction and conversion into carbon assimilation by incubating water samples at collection depth for 24 h (Miller et al. 1986; Wetzel and Likens 2000). Because of logistical constraints, water samples were incubated in nearby Toolik Lake. Samples collected at 1 m depth from both lakes were incubated at 1 m depth in Toolik Lake, meaning that the thermokarst lake samples received more light than if incubated *in-situ* in the thermokarst lake when the thermokarst failure had reduced light penetration. To assess the effects of the thermokarst on primary production and compare between lakes, we first calculated the depth in m to 1% of surface light using profiles of photosynthetically active radiation (PAR, 400–700 nm) on all dates in both lakes and then integrated the 1 m sample production values in mg C per m^3 per day to that depth (e.g., [mg C m^{-3} day^{-1}] * m = [mg C m^{-2} day^{-1}]). This provided a relative areal production adjusted for changes in light penetration in both lakes. These are maximum values because we could not correct for lower production rates with lower light (i.e., there are no consistent photosynthesis vs. irradiance curve data available), and we could not correct for the fact that the 1% light depth may be above the thermocline depth and thus phytoplankton would be circulated below the compensation point for photosynthesis in the epilimnion. Because of these upward biases of absolute primary production values (but still consistent treatment between sample dates and lakes), we instead set 2017, the year prior to any thermokarst failure, to a value of 100% and expressed the relative areal values after 2017 as a percentage change from 2017 (Fig. S1).

We measured temperature and dissolved oxygen (DO; mg L^{-1}) and calculated light extinction coefficients (K; m) using depth profiles of PAR measured with a Licor sensor on a multi-sonde probe (YSI or Hydrolab) following Kling (1988); the Licor sensor's minimum resolution was ~ 20 µmol m^{-2} s^{-1} for years 2018 and prior, and ~ 1 µmol m^{-2} s^{-1} for years 2019–2021. We also measured water transparency (m) with a 200 mm standard Secchi disk. We analyzed water samples for NH_4^+ with the *o*-phthalaldehyde (OPA) fluorometric method (Holmes et al. 1999, *with corrections in* Taylor et al. 2007), nitrate + nitrite using the cadmium reduction method, and SRP (soluble reactive phosphorus, an estimate of PO_4^{3-}) with the colorimetric method (Murphy and Riley 1962) using a Varian Cary 50 Scan UV–Vis Spectrophotometer (Agilent Technologies). We calculated dissolved inorganic N (DIN) as the sum of nitrate + nitrite and ammonium. We measured chlorophyll *a* (*µ*g L^{-1}) fluorometrically after extraction in acetone (Axler and Owen 1994) and correction for phaeophytin.

We estimated epilimnetic bacterial productivity from ^{14}C-leucine incorporation rate during 2–3 h incubations following Crump et al. (2003). Samples were collected from 1-m depth in July from 2010 to 2021. We collected bacterioplankton DNA from the epilimnion and hypolimnion (2014–2019) to analyze bacterial community composition using 16S rRNA gene amplicon sequencing following Kellogg et al. (2019). For bacterial community composition, PCR amplicons were sequenced on an Illumina MiSeq platform (San Diego, California, USA) using 2 * 150 bp paired-end reads at the Center for Quantitative Life Sciences

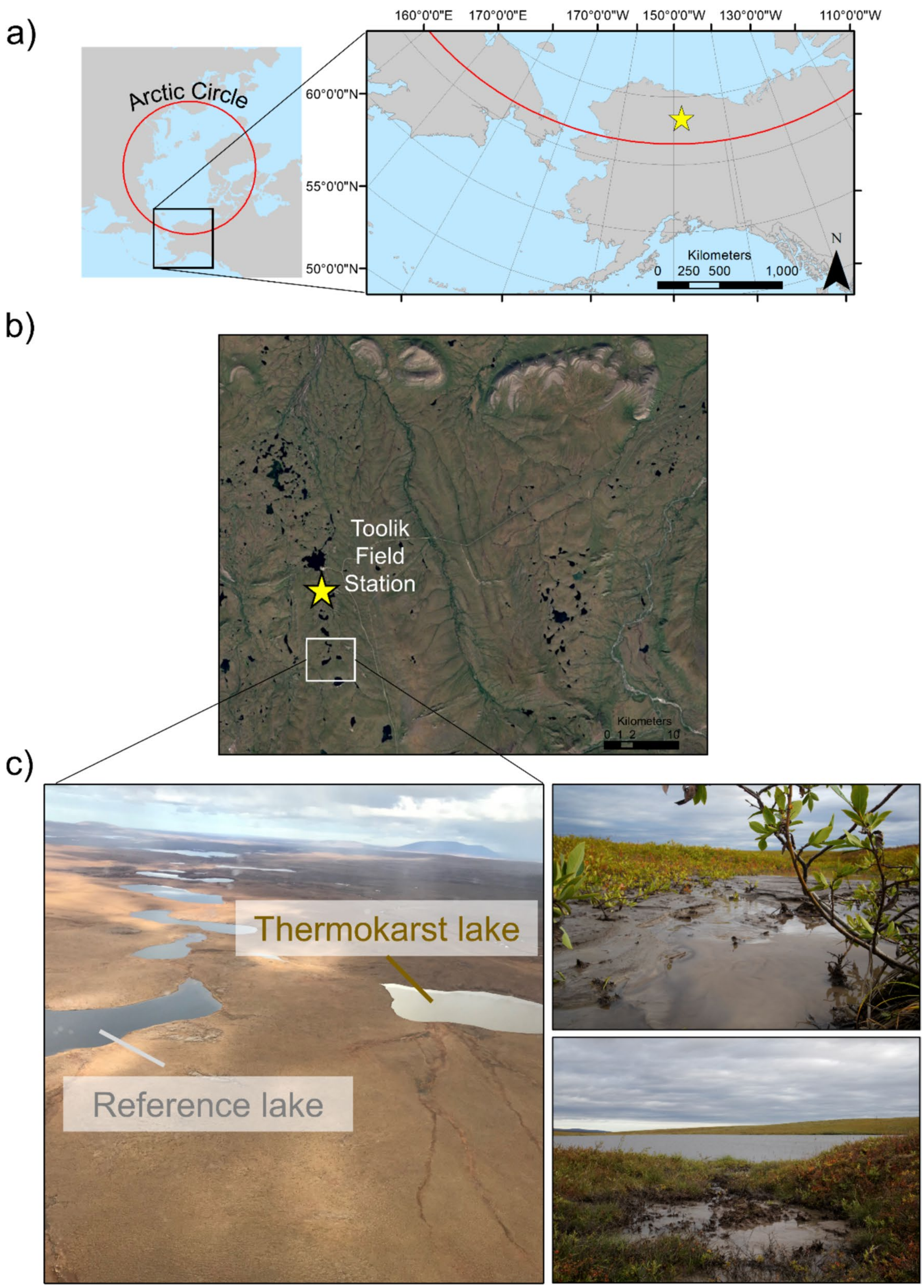


Fig. 1 Location of Toolik Field Station in Arctic Alaska (**a**). Our study lakes were two headwater lakes south of Toolik Field Station (**b**). One of the lakes was impacted by a gurgler thermokarst failure in 2019 (two photo panels beside [c]), while the other remained unimpacted and served as a reference in our analyses (**c**). Photos were taken by P. Budy

(CQLS) at Oregon State University. Forward reads from DNA sequences were demultiplexed and trimmed to 120 bp using the DADA2 pipeline within the QIIME2 2021.2 software package (Bolyen et al. 2019). Datasets were grouped into amplicon sequence variants using deblur, and representative sequences were classified with the SILVA 138 database of the 515F/806R region clustered at a 99% identity threshold (Quast et al. 2013). Sequences classified as chloroplasts, mitochondria, Eukaryota, and unclassified were removed from the dataset using the "phyloseq" R package (McMurdie and Holmes 2013).

We collected zooplankton via vertical tow (from ~ 1 m above the sediment to the surface) with a 243-µm mesh net in duplicate, preserved samples in sugar-buffered Lugol's solution, and identified zooplankton to species in the laboratory (Wetzel and Likens 2000). We collected benthic macroinvertebrates using an Ekman dredge (collection area of 0.023 m^2). Similar to zooplankton samples, we collected macroinvertebrates in duplicate and within 3 m depth throughout the littoral zone. We preserved samples in 95% ethanol and counted and sorted macroinvertebrates into major taxonomic groups in the laboratory. We sampled fishes mainly with angling, but occasionally used combinations of angling, short-set gill nets, and fyke nets. Along with measuring the total length (mm) and weight (g) of each captured fish, we performed gastric lavage on arctic grayling and lake trout of various sizes to determine total gut contents and diet composition. For fish that experienced mortality during capture or handling, we preserved the entire stomach and contents in 95% ethanol. In the laboratory, we counted, weighed, and categorized diet items into major taxonomic groups.

We qualitatively compared fish catch over time in the two lakes by calculating the annual average catch per unit effort (CPUE) of arctic grayling and lake trout. However, these metrics are somewhat confounded by water transparency and thus visibility for fishes, because we capture these fish largely via angling (visual lures) to minimize stress and mortality on very small populations. Therefore, fish sampling in the thermokarst lake was likely highly inefficient during the low water transparency years. In addition, the sampling for grayling is extremely variable across years depending on whether an invertebrate food hatch occurred during sampling.

Data analysis

To test for the effects of the thermokarst failure, we used a Before-After Control-Impact (BACI) design whereby the interaction term is of primary interest. We assessed the impacts of the thermokarst failure on epilimnetic temperature, dissolved oxygen, light, DIN, SRP, chlorophyll *a*, and bacterial productivity relative to long-term trends in both lakes. For temperature and oxygen profiles, we averaged data across depths and used the average epilimnetic temperature and oxygen in statistical models. We fit linear mixed-effects models (LMM) including the additive effects of time (before and after) and lake (reference and thermokarst) and their interactive effect. We also included the year as a random effect. For each response variable except bacterioplankton production, we included the categorical effect of the month as an additional fixed effect to control for intra-annual variation in response variables. We ensured model assumptions of normality and equal variance were reasonably met by inspecting residual plots. We also compared patterns in these metrics calculated for the metalimnion (versus the epilimnion) and observed the same general patterns (Fig. S3); therefore, we restrict the primary analyses herein to the epilimnion, which is also more meaningful given the emphasis on light and light penetration. We conducted all analyses in the R statistical language (version 4.1.3; R Core Team 2022).

We tested for changes in total densities of zooplankton ($n = 87$ samples total for both lakes), benthic macroinvertebrates ($n = 22$), and fish total gut content ($n = 92$) over time and between lakes. To test for the effects of the thermokarst failure on zooplankton densities, we used a BACI design with the same fixed and random effect structure as described above. We used a generalized LMM (GLMM) and assumed a negative binomial distribution to test for changes in zooplankton densities because data were counts, and included volume sampled as a covariate because the depth sampled varied among years. Since we only had benthic macroinvertebrate and fish diet samples from one year prior to the thermokarst failure, we used a Control-Impact design. To test for Control-Impact effects on benthic macroinvertebrates, we used a generalized linear model (GLM) and assumed a negative-binomial distribution with a log-link because data were counts and the area sampled was the same for both lakes and in each year. We included month as a categorical fixed effect, as above, and additive and interactive effects of year (categorical) and lake (Control-Impact). We fit a GLM with a gamma distribution and log-link for the total biomass of fish gut contents. Fish length was included as a covariate to account for differences in consumption due to fish size. We included the categorical effect of the month and all additive and interactive effects of the year (categorical), fish species, and lake (Control-Impact). We did not include a three-way interaction between year, fish species, and lake because of a lack of lake trout captures in the thermokarst lake in some years. The glmmTMB package was used for mixed effects modeling (Brooks et al. 2017). We determined the statistical significance of fixed effects using Walds tests ($\alpha = 0.05$). We used marginal and conditional R^2 to assess the proportion of variation explained by fixed effects (R^2_{m}) and fixed effects and random effects combined (R^2_{c}), respectively (Nakagawa et al. 2017). Coefficient estimates from univariate models are presented in supplemental materials (Table S2; Table S3).

Along with testing univariate responses, we also tested for effects of thermokarst failure on the composition of zooplankton, benthic macroinvertebrate, bacterioplankton, and fish diets using multivariate GLM using the same set of predictor variables used for univariate analyses described above, respectively. We used a Control-Impact design to test for changes in bacterioplankton composition because of similar constraints of samples as described for benthic macroinvertebrates. We included the additive and interactive effects of year (categorical) and lake in the model. For zooplankton, benthic macroinvertebrates, and bacterioplankton we used counts of each taxon as response variables and assumed a negative binomial distribution. We excluded three taxa of benthic macroinvertebrates from the analysis because they only occurred in one sample (e.g., Amphipoda, Ephemeroptera, and Simuliidae). We also excluded bacterioplankton taxa that occurred in <3 samples. Before analyzing fish diet composition, we transformed data to presence-absence because this approach provides a robust account of diet composition and is less influenced by common biases of reconstructing fish diets (Baker et al. 2014; Buckland et al. 2017). Because diet composition data were presence-absence, we fit a multivariate GLM assuming a binomial distribution with a complementary log–log link. Before analysis, we removed prey types that occurred in less than 10% of samples and unidentified insects. Using the mvabund package (Wang et al. 2012, 2019), we fitted individual models for each taxon using the same set of predictor variables. Test-statistics from each model were summed together, and this was used to test for an assemblage-level effect with *p*-values estimated via resampling (Wang et al. 2012). The statistical significance of individual taxa models was determined using permutation-based ANOVA with *p*-values corrected for multiple testing using PIT-trap resampling (permutations = 9999; Warton et al. 2017).

Results

Water transparency (Secchi depth; m), light extinction coefficient (K; m^{-1}), and chlorophyll *a* in the thermokarst lake measured after the thermokarst failure were some of the most extreme values observed over the long-term sampling of these lakes (Figs. 2, 3), but only water transparency displayed a statistically significant BACI effect ($p < 0.001$; Table 1; Fig. 2). After the thermokarst failure in 2019, water transparency declined by over 3.5 SD of the long-term average before the thermokarst failure, was 2.9 SD below the average in 2020, but had recovered by 2021 (i.e., reached values within the long-term SD) in the thermokarst lake (Table S4; Fig. 2, left). In the reference lake, water transparency varied but remained consistent with the long-term average and SD (Table S4; Fig. 2, left). Light extinction coefficients (K) similarly increased due to the thermokarst failure in 2019 (Fig. 2, right). Starting in 2019, values of K between the lakes diverged and the average K in 2019 was 3.8 times higher in the thermokarst lake than in the reference lake (Fig. 2).

These higher K values were associated with a dramatic reduction in the depth at which 1% of surface light remained ($Z_{1\%}$, a general estimate of no net phytoplankton growth), and in the thermokarst lake this depth dropped from a high of 14.7 m in 2017 to 0.8 m in 2019 (Fig. S2). In the reference lake, the $Z_{1\%}$ also dropped in 2019 compared to 2017 but was similar to 2016 values and still much greater than in the thermokarst lake (up to 6.4 times greater depth of 1% light on 20 August 2019; Fig. S2). Areal primary production relative to 2017 (100%),

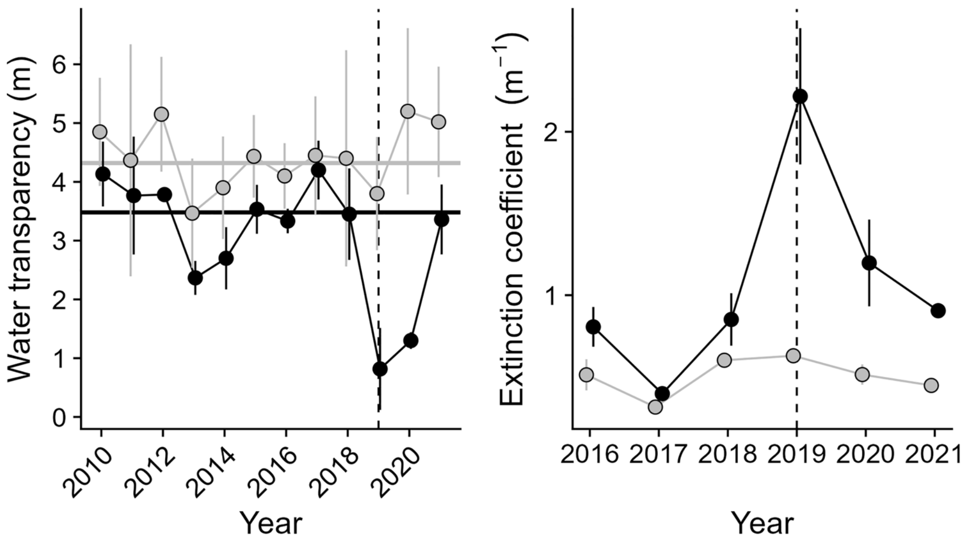


Fig. 2 Time series of Secchi depth (left panel; $n = 77$) and light extinction coefficient (K) (right panel; $n = 44$) in two arctic lakes before (2010–2018) and after (2019–2021) a thermokarst failure (denoted by the dashed vertical line) occurred in the thermokarst lake (black circles). A nearby lake served as a reference lake (grey circles). Values represent means (± Standard Error, SE) of data collected in summer during ice-off (June–August). Horizontal lines are means calculated before the thermokarst failure across the time series for the thermokarst (black) and reference (grey) lakes

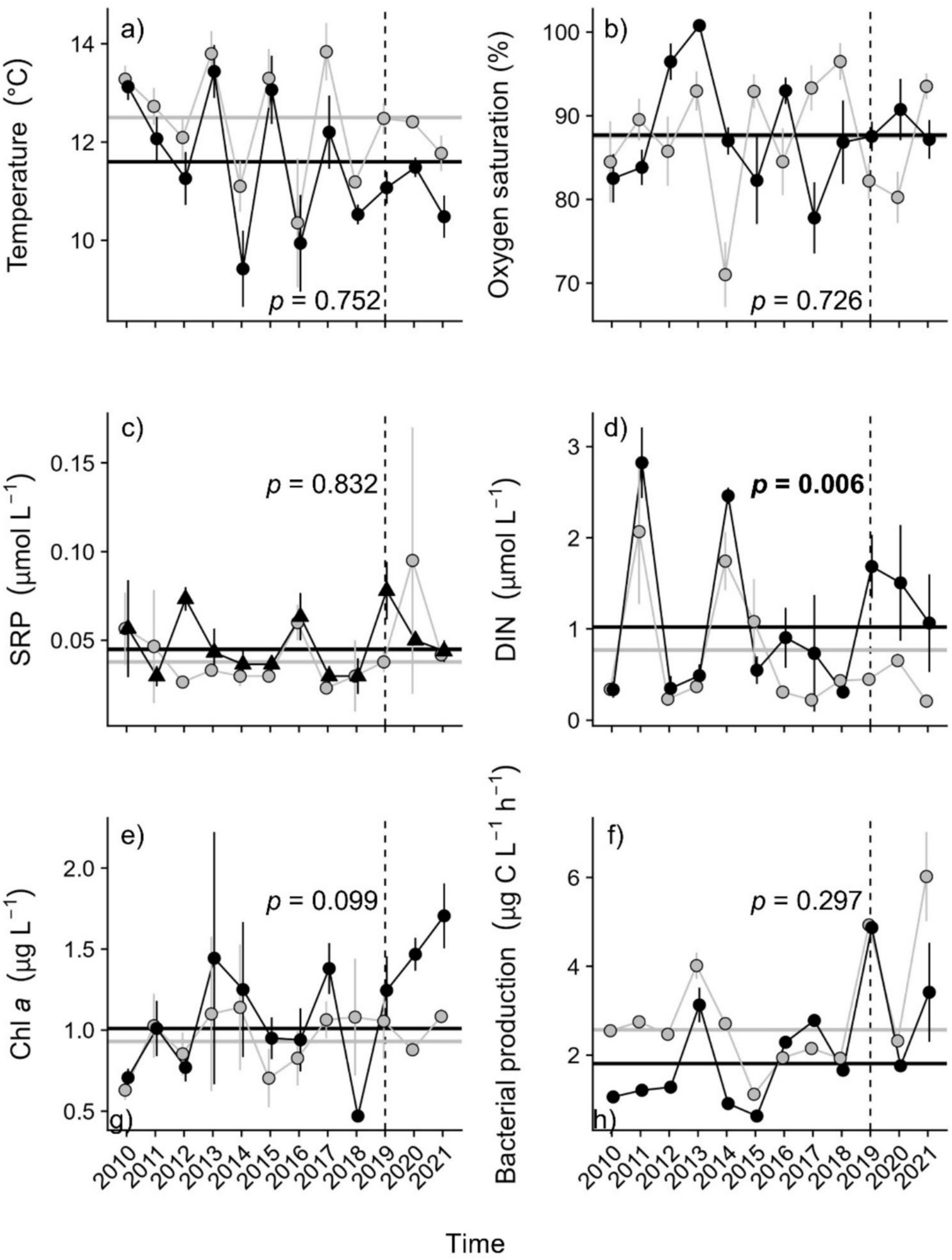


Fig. 3 Time series of epilimnetic temperature (**a**; *n* = 82), dissolved oxygen saturation (**b**; *n* = 82), soluble reactive phosphorus (**c**; *n* = 76), DIN (**d**; *n* = 76), chlorophyll *a* (**e**; *n* = 76), and bacterial production (**f**; *n* = 28) in two arctic lakes before (2010–2018) and after (2019–2012) a thermokarst failure (dashed vertical line, **a**–**f**) occurred in the thermokarst lake (black circles). The reference lake is denoted by grey circles. Values in panels a–f represent means (± SE) of data collected in summer during ice-off (June–August). Horizontal lines are means calculated before the thermokarst failure across the time series for the thermokarst and reference lakes. *P*-values from linear mixed effects models are presented for the potential BACI interactive effect (Table 1)

adjusted for the depth of 1% surface light, was initially relatively high in the thermokarst lake compared to the following years (Fig. S1). The primary production values dropped in 2018 to 25–26% of the values in 2017 in both lakes, but in the following year (2019), presumably the reduction in light in the thermokarst lake resulted in lower production values, while in the reference lake production values increased (Fig. S1).

Epilimnetic temperature (Fig. 3a) and DO (Fig. 3b) varied over time in both the thermokarst and reference lakes, but did not appear to be strongly affected by the thermokarst disturbance (Table 1; Fig. 3). Both SRP and DIN were 1.4 SD and 0.7 SD greater than the long-term average in 2019

Table 1 Statistical output from Wald tests for significance of fixed effects from LMM of water transparency (measured as Secchi depth), temperature, dissolved oxygen, nutrients, chlorophyll *a*, and bacterioplankton production

Response	Effect	χ^2	p	R^2_m	R^2_c
Water transparency ($n=77$)	Month	3.42	0.181	0.47	0.64
	Time	3.11	0.078		
	Lake	**62.37**	**<0.001**		
	Time*Lake	**19.45**	**<0.001**		
Temperature ($n=82$)	Month	72.67	<0.001	0.45	0.55
	Time	0.89	0.346		
	Lake	3.31	0.069		
	Time*Lake	0.10	0.752		
Dissolved oxygen ($n=82$)	Month	2.47	0.291	0.03	0.03
	Time	0.40	0.526		
	Lake	0.03	0.871		
	Time*Lake	0.12	0.726		
DIN ($n=76$)	Month	**6.14**	**0.046**	0.15	0.62
	Time	0.01	0.906		
	Lake	**14.81**	**<0.001**		
	Time*Lake	**7.57**	**0.006**		
SRP ($n=76$)	Month	5.04	0.081	0.13	0.15
	Time	2.95	0.086		
	Lake	1.91	0.167		
	Time*Lake	0.05	0.832		
Chlorophyll *a* ($n=76$)	Month	1.30	0.523	0.16	0.19
	Time	**5.20**	**0.023**		
	Lake	3.72	0.054		
	Time*Lake	2.72	0.099		
Bacterial production ($n=28$)	Time	**9.78**	**0.002**	0.46	0.71
	Lake	**9.95**	**0.002**		
	Time*Lake	1.09	0.297		

R^2_m is the variance explained by the fixed effects and R^2_c is the variance explained by the fixed effects and random effect of year combined. Bold text denotes statistically significant effects ($\alpha=0.05$)

in the thermokarst lake, respectively (Table S4; Fig. 3c, d). Phosphorus and DIN remained elevated in 2020, SRP was 0.2 SD and DIN was 0.5 SD greater than the long-term average in 2020 before lowering in 2021 (Table S4; Fig. 3c, d). In the reference lake, SRP was equivalent to the long-term average in 2019, increased to 2.4 SD above the long-term mean in 2020, and returned towards the long-term mean in 2021 (Table S4). Nitrogen remained below the long-term mean after the thermokarst in the reference lake. Relatively high values of DIN were observed in both the thermokarst lake and reference lake in 2011 and 2014.

Chlorophyll *a* concentrations varied little and were similar to the long-term average in the thermokarst lake in 2019, but subsequently increased to 1.4 times the long-term average in 2020 and remained relatively high in 2021 (1.7 times; Fig. 3e). In contrast, chlorophyll *a* in the reference lake varied but remained consistent with the long-term average over time, and there was no statistically significant BACI effect (Fig. 3e; Table 1). Bacterial production generally increased over time in both lakes; however, the pattern did not change dramatically in 2019 in the thermokarst lake relative to the beginning of the time series (Fig. 3f). The two lakes varied similarly over time with no statistically significant BACI effect ($p=0.297$; Table 1). Results from samples in the metalimnion were similar to those from the epilimnion (Fig. S3).

There were no statistically significant interactions between time and lake for total densities of zooplankton, macroinvertebrates, or total gut contents of fishes, indicating the thermokarst failure did not have strong impacts on these higher trophic levels (Table 2). Total zooplankton density (Fig. 4a) was higher on average in the reference lake before the thermokarst failure ($p<0.049$; Table 2), yet this was largely driven by a single high sample in 2018 in the reference lake (Fig. 4a). Total benthic macroinvertebrate density was highly variable over time (Fig. 4b) and was particularly low in 2021 in both lakes (Fig. 4b).

Total biomass of fish gut contents generally declined over time, more so for lake trout than for arctic grayling (Fig. 5), but did not differ among lakes ($p=0.585$; Table 2). Relative to the long-term average, fish catch generally declined in the reference lake over time from a high of near 1 fish h^{-1} in 2017 to 0.42 fish h^{-1} in 2021 (Fig. S4). In the thermokarst lake, CPUE (which is compounded by water transparency) varied around the long-term mean, but was 2.4 times the long-term average in 2021, two years after initiation of the thermokarst (Fig. S4).

Similar to the univariate responses, there were no multivariate effects of the thermokarst on lower trophic level community composition measured as bacterioplankton composition, zooplankton composition, and benthic macroinvertebrate composition (Table 3). Zooplankton, benthic macroinvertebrate, and bacterioplankton composition all differed between lakes (all $p\leq 0.024$; Table 3), but no interactive effect between time (Before-After or Year) and lake was significant for any group (all $p\geq 0.09$; Table 3). Bacterioplankton community composition varied with depth and was different between lakes ($p=0.001$) but was not strongly affected by the thermokarst ($p=0.098$; Table 3; Fig. 6). The first axis of the PCoA explained 31.2% of the variance in composition and mainly represented differences between the epilimnion and hypolimnion within lakes. The second axis explained 15.6% of the variance in composition and represented differences between lakes. Finally, none of the two-way interactive effects on fish diet composition were statistically significant (all $p\geq 0.090$; Table 4). Fish diet composition differed among fish species ($p=0.001$), among

Table 2 Statistical output from Wald tests for significance of fixed effects from a GLMM of total zooplankton counts and a GLM of total benthic macroinvertebrate counts and total gut content

Response	*n*	Effect	χ^2	*p*	R^2_m	R^2_c
Zooplankton	88	Volume sampled	0.08	0.778	0.21	0.42
		Month	4.48	0.106		
		Before-After	3.80	0.051		
		Lake	0.06	0.805		
		Before-After*Lake	0.17	0.677		
Benthic macroinvertebrates	22	Month	0.99	0.319	0.48	
		Year	**6.71**	**0.010**		
		Lake	0.29	0.593		
		Year*Lake	1.44	0.230		
Total gut content	91	Month	**8.46**	**0.015**	0.73	
		Year	**16.95**	**0.001**		
		Fish length	**33.33**	**< 0.001**		
		Fish species	1.77	0.184		
		Lake	0.11	0.743		
		Year*Lake	0.99	0.803		
		Year*Fish species	**12.67**	**0.005**		
		Lake*Fish species	2.61	0.106		

R^2_m is the variance explained by the fixed effects and R^2_c is the variance explained by the fixed effects and random effects combined, in the case of zooplankton. Bold text denotes statistically significant effects ($\alpha = 0.05$)

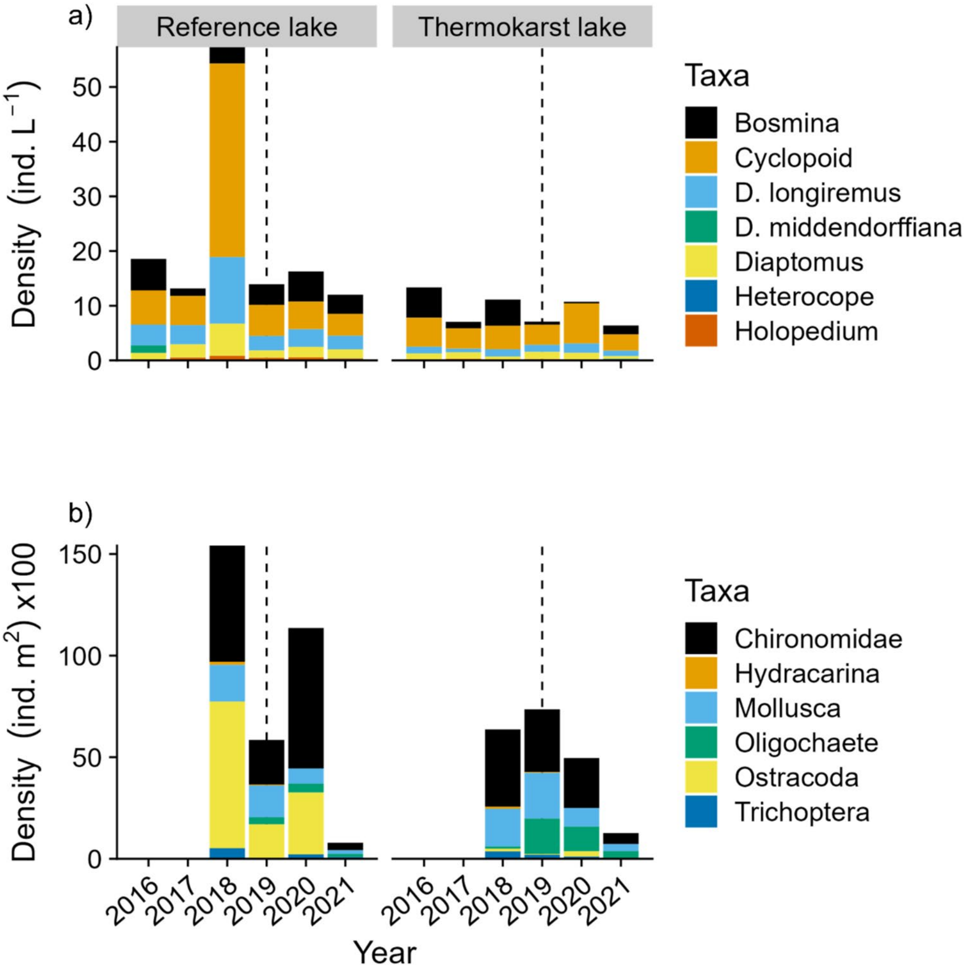


Fig. 4 Zooplankton (**a**; $n = 88$) and benthic macroinvertebrate (**b**; $n = 22$) assemblage composition and densities in the reference lake (left panels) and thermokarst lake (right panels). Values are average yearly densities for each taxon. The dashed vertical line represents the thermokarst failure event in 2019. We did not sample benthic macroinvertebrates prior to 2018

Fig. 5 Per capita biomass (mean ± SE) consumed by arctic grayling ($n = 63$) and lake trout ($n = 28$) in the thermokarst (black circles) and reference (grey circles) lakes. The dashed vertical line denotes the thermokarst failure event in 2019

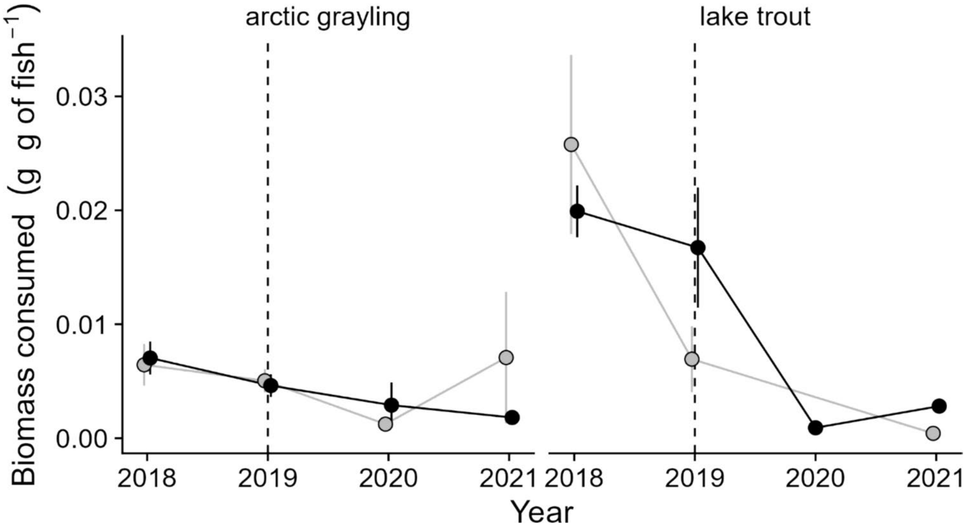
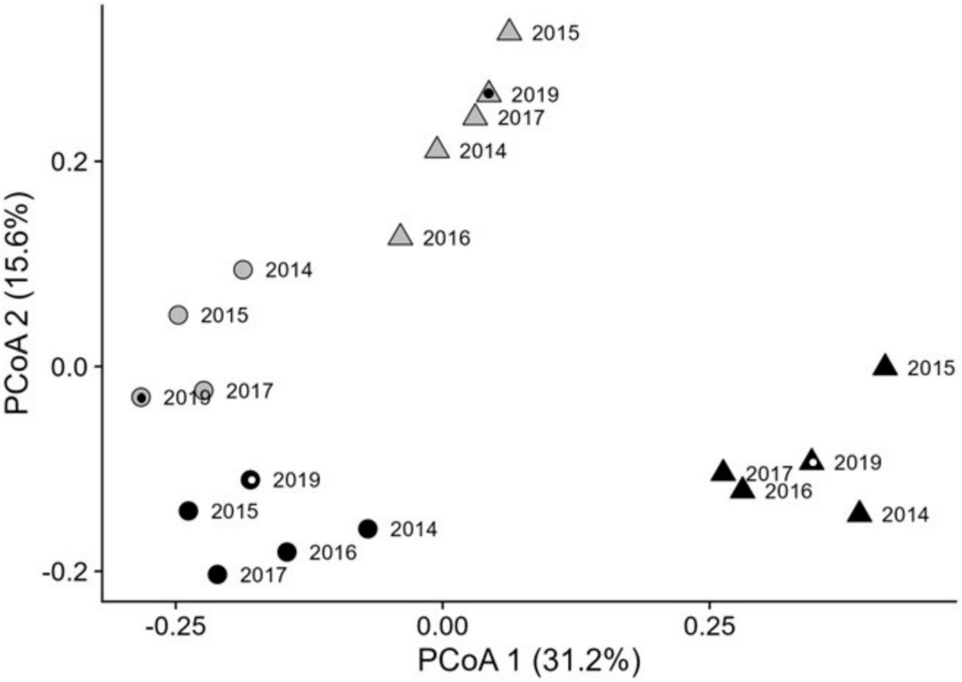


Fig. 6 PCoA explaining the variance in bacterioplankton community composition composition



years ($p < 0.001$), and as a function of fish length ($p < 0.001$; Table 4).

Discussion

Due to a rapidly changing climate, disturbances are increasing in frequency and magnitude in the Arctic, including thermokarst failures (Bowden et al. 2008; Gooseff et al. 2011; Lewkowicz and Way 2019). These disturbances result in the mass transport of sediment and organic materials into surface waters. This process is analogous to processes occurring across the globe, such as lake browning, with substantial changes to lake ecosystem function (e.g., Donohue and Molinos 2009; Williamson et al. 2015). We evaluated the whole-lake response of a long-term monitored lake (reference lake) to a nearby lake impacted by a gurgler thermokarst disturbance (thermokarst lake). Notably, we do not know exactly when the thermokarst began in 2019, we only know the effects were first observed in the summer of that year (i.e., it could have started in the autumn of 2018), which could explain some unexplained variance in trends. Despite a substantial reduction in water transparency (– 62%) that lasted for two years in the thermokarst lake, and some substantial increases in chlorophyll *a* after the thermokarst failure, biota from the lower and higher trophic levels

Table 3 Statistical results from multivariate generalized linear models testing for effects of a thermokarst failure near an arctic lake on zooplankton assemblage composition (counts) relative to a reference lake that did not experience a thermokarst failure using a Before-After Control-Impact design

Response	Effect	df	Deviance	p
Bacterioplankton	Lake	**1.17**	**1787.0**	**0.001**
	Year	4.13	3948.0	0.101
	Year*Lake	4.9	2741.0	0.098
Zooplankton	Volume sampled	1.85	10.4	0.375
	Month	**2.83**	**42.1**	**0.022**
	Before-After	1.82	18.6	0.064
	Lake	**1.81**	**27.8**	**0.024**
	Before-After*Lake	1.80	19.0	0.173
Benthic macroinvertebrates	Month	**1.20**	**26.4**	**0.013**
	Year	**3.17**	**75.6**	**< 0.001**
	Lake	**1.16**	**25.0**	**0.011**
	Year*Lake	3.13	18.7	0.661

Bold text denotes statistically significant effects ($\alpha = 0.05$)

were resistant to change from this disturbance. We originally predicted the thermokarst failure would lead to reduced light availability and thus less production at the base of the food web, and that this impact would also affect the zooplankton and macroinvertebrates and in turn fish diet composition and feeding, due to reductions in visual fish foraging (given Williamson et al. 2015; Hayden et al. 2019; and Urruta-Cordero et al. 2021). Although we initially observed substantial changes in some abiotic factors, most of these factors rapidly returned to within the range of long-term average conditions before the thermokarst disturbance with a relatively small variance. In addition, these short-term changes to the limnology of the impacted lake did not transfer up the food web to secondary trophic levels, and even more surprising, we observed no effects on the biomass of food consumed by visually feeding fish. These results suggest these arctic lakes are resistant to thermokarst disturbance and can recover quickly after disturbances subside; this suggestion is consistent with a similar, rapid recovery to experimental fertilization in a nearby lake as described in Budy et al. (2021).

Table 4 Statistical results from a multivariate generalized linear model testing for effects of a thermokarst failure near an arctic lake on fish diet composition (presence-absence) relative to a reference lake that did not experience a thermokarst failure using a Control-Impact design

Parameter	df	Deviance	p
Fish length	**1.90**	**75.21**	**< 0.001**
Month	**2.88**	**34.97**	**0.030**
Year	**3.85**	**76.13**	**< 0.001**
Lake	1.84	8.14	0.671
Fish species	**1.83**	**39.11**	**0.001**
Year*Fish species	3.80	27.42	0.152
Lake*Fish species	1.79	11.94	0.142
Year*Lake	3.76	22.32	0.629

Bold text denotes statistically significant effects ($\alpha = 0.05$)

Strong, natural temporal variation in limnological variables made it difficult to attribute the observed changes unequivocally to the thermokarst disturbance. Nonetheless, water transparency (Secchi depth), chlorophyll *a*, DIN, and SRP in the thermokarst lake measured soon after the thermokarst disturbance began were some of the most extreme values measured over the long-term sampling (12 years) of these lakes; however, the thermokarst lake appeared to recover rapidly. Relative to the long-term averages, we observed initial or early increases of > 150% in chlorophyll *a*, DIN, and SRP in the thermokarst lake, while water transparency decreased to a low of 0.8 m Secchi depth. Notably, the most extreme values of DIN observed occurred in both lakes (2011, 2014) before the thermokarst, again presumably due to natural variation; however, 2011 was a relatively dry year in terms of precipitation while 2014 was near average, offering no explanation for those extreme values (https://www.uaf.edu/toolik/edc*)*. Chlorophyll *a* concentrations increased after the thermokarst event in 2019–2021, but areal primary production decreased substantially in the thermokarst lake and remained low likely due to the reduction of available light in the water column. Moreover, as soon as 3 years after the thermokarst began, all factors except chlorophyll *a* had returned to values near the long-term average and within the range of long-term variability. In these oligotrophic lakes, it is possible that the increase in nutrients from the thermokarst disturbance led to more chlorophyll *a* in the lake surface (1 m depth), even though total, depth-integrated areal primary production rates likely declined and stayed low, due in part to a poor light climate deeper in the thermokarst lake (e.g., Daniels et al. 2015). In a nearby lake, a low-level, long-term fertilization experiment meant to mimic inputs of nutrients as permafrost thawed led to a > 200% increase in chlorophyll *a* concentration, but water transparency declined slowly over years and to a lesser degree (< 1 m; Budy et al. 2021) than observed here. However similarly in that study, despite changes during fertilization, most lower trophic level response variables also recovered rapidly after just 2–4 years post-fertilization, further supporting our conclusion that these lakes appear to be resilient to thermokarst or nutrient disturbance.

Interestingly, we did not observe a substantial change in epilimnetic water temperature in the thermokarst lake. However, even small (2 °C) changes in lake epilimnetic temperature can have large effects on almost all rates of productivity and on all ectothermic biota including zooplankton and fishes (e.g., Klobucar et al. 2018; Pennock et al. 2020). An increase in mineral turbidity can alter the heat budget of a lake by (a) increased reflection of sunlight (depending on sediment composition), thus causing surface temperatures to decrease (*reviewed in* Donohue and Molinos 2009), (b) causing changes to thermal stratification (e.g., Kling 1988; Williamson et al. 2015), or (c) via greater absorption of solar radiation causing temperatures to increase (Kling et al. 1989). Apparently, these different impacts of turbidity on temperature were either too small to have an effect or the net effect of these processes was too low to alter lake surface temperatures beyond natural variations. We similarly observed no consistent changes to oxygen concentrations throughout the water column, in contrast to other studies that have generally observed oxygen depletion and biogeochemical anoxia feedback loops (*reviewed in* Blanchet et al. 2022). Notably however, these arctic lakes have temperatures that are colder than most lakes studied for impacts of lake browning, which makes them more resilient to changes in dissolved oxygen (Luecke et al. 2014).

Despite short-term changes in some abiotic factors and primary productivity, we observed no statistically significant changes in higher trophic levels. There were no statistically significant changes in bacterial productivity or in bacterioplankton, zooplankton, or benthic macroinvertebrate assemblage composition. Although similar studies are lacking regarding macroinvertebrate data, these results are counter to other observations of lake browning which include actual state changes and shifts toward heterotrophic metabolism (Ask et al. 2009, 2012), nutritional declines in the zooplankton community (e.g., Keva et al. 2021), and decreases in the primary grazing zooplankters and changes in the zooplankton community trophic structure (i.e., simplification, Williamson et al. 2015). In those studies, primary production decreased with reduced light penetration as it did in the impacted thermokarst lake herein. Further, not all suspended sediment has the same composition, and thus its effect on biota can be influenced by its chemical composition, concentration, duration of exposure, and particle size (Billota and Brazie 2008). Finally, the provision of refuge for zooplankton or macroinvertebrates from fish predation under low light conditions provides an indirect positive effect of suspended sediment for zooplankton (Donohue and Molinos 2009). While we did observe some species-specific changes in the zooplankton communities across time and between the two lakes, they were apparently not linked to the thermokarst disturbance. In other related work, we observed arctic zooplankton assemblages to be quite dynamic over time and particularly sensitive to the top-down effects of fish predation (O'Brien et al. 2004; Budy et al. 2021).

Perhaps most surprising and counter to our predictions, visually foraging fish diet composition and consumption did not change substantially, despite dramatic declines in water transparency in the thermokarst lake. For example, Beauchamp et al. (1999) observed a 30-fold difference in maximum depth-specific diel encounter rates of similar predators among three lakes of varying water transparency (Secchi depth ranging 2.5–19 m). In our study, all dominant pelagic fishes in these lakes are believed to be predominantly visual feeders (Wight et al. 2023). Using arctic grayling as an example (the most abundant fish), based on visual foraging models and changes in water transparency (e.g., Beauchamp et al. 1999; Klobucar and Budy 2016), we estimated reaction distance to prey would decline from 1.0 m before the thermokarst to < 0.25 m after the thermokarst effect. We assumed this potentially dramatic decline in reaction distance would translate to declines in the total biomass of food consumed or changes in diet composition. However, we observed no change in the composition or biomass of diet items consumed attributed to the thermokarst disturbance. There are several possible explanations for this unexpected observation. First, both arctic grayling and lake trout (the two most dominant fish species present) consumed predominantly snails and caddisflies (Mollusca and Trichoptera), and both prey species are largely littoral in their distribution in the lake. The effects of the decline in water transparency for fish feeding on relatively larger prey like snails and caddisflies (versus relatively smaller zooplankton prey) would be considerably less, and thus may not have limited fish foraging. Second, fish feeding in the shallow littoral zone compared to the lower-light environments deeper in the lake may be less affected. Third, in other related work we demonstrated that arctic char (*Salvelinus alpinus*) are largely opportunistic, feeding on prey found in relatively high density at fine spatial scales, such that if they encounter a "ball" of *Bosmina* or a nest of sculpin eggs or juveniles, they will eat a large portion at once with little foraging time (Björn Björnsson 2001; Klobucar and Budy 2020; Wight et al. 2023). Similarly, although for a stream environment, Sweka and Hartman (2001) determined that although turbidity significantly decreased the probability of a fish reacting to a prey item, it did not influence foraging success following reaction to the prey. Fourth, visual foraging models might be too simple for these fishes in these systems. Because these models were developed primarily for a limited number of stream drift-feeding fishes, they assume all foraging is targeted and visual (e.g., not considering smell or hearing; Pavlov and Kasumyan 1990), that vision is based only on body size and water transparency, and they may underestimate starvation as motivation (e.g., Colgan 1973; Croy and Hughes 1991). And finally, these lakes are open (i.e., connected to other lakes), so fishes captured in the impacted thermokarst lake could have been foraging in that lake or elsewhere in this connected string of open lakes, inlets, and outlets. In related ARC LTER work, we observed tagged grayling moving between these two lakes and many fishes moving into the shared outlet channel, and preliminary genetic analyses indicated no differentiation between the genetic structure of the fish captured in the two lakes (*unpublished data*, ARC LTER). In addition, as discussed above, due to sampling limitations, unfortunately the CPUE data are not very informative with regard to total fish density or site fidelity in either lake.

Because the number of lakes impacted by thermokarst failure and the frequency of thermokarst failures both appear to be increasing with warming air temperatures in the Arctic (Bowden et al. 2008; Gooseff et al. 2011), and more generally many lakes are "greening" or "browning" globally (e.g., Leech et al. 2018), there is a need to better understand the potential outcomes of these impacts using comparisons with long-term data. Despite very dramatic changes in some limnological factors in response to the thermokarst, these arctic lakes appear to be quite resistant to short-term disturbance and resilient in their recovery once disturbances subside (*see also* Budy et al. 2021). However, the magnitude and duration of inputs of exogenous materials from thermokarst disturbances vary widely. In addition, as discussed above, the lakes in this study are "open" lakes connected via inlets and outlets to each other and a series of downstream lakes, such that mobile organisms, such as fishes, have the option to leave if conditions become unsuitable after a disturbance, and ensuring meta-food web stability (Laske et al. 2019). There are many other arctic lakes in the area that are completely "closed" with no connectivity to other lakes, and in these lakes biota such as fish must endure the conditions during a disturbance. Thus, there are likely many local and watershed-scale factors that determine how a lake ecosystem will react to a thermokarst failure or a similar pulse disturbance (e.g., wildfire). Nonetheless, evidence suggests that these arctic lake ecosystems are ecologically more robust to disturbance than was previously thought and may recover to pre-disturbance conditions relatively quickly (e.g., Luecke et al. 2014).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-025-05681-9.

Acknowledgements We thank J. Dobkowski and L. Rossi who helped collect the limnological data, and a long list of volunteers who helped collect the fish data including S. Klobucar, R. Al-Chokhachy, and P. MacKinnon. National Science Foundation Research Experience for Undergraduates (REUs) who completed their tenure on the project included L. Simmons, T. Hafen, R. West, and D. Weedop. We thank J. Nielson, one anonymous peer reviewer, and the handling editors for constructive comments that greatly improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contribution statement PEB, CAP, BCC, AEG, and GWK conceived and designed the study. SM, HP, EA, GPT, and NRC conducted the bulk of the data collection and laboratory analyses. CAP analyzed most of the data. PEB, CAP, BCC, AEG, and GWK wrote the manuscript; other authors provided intellectual and editorial advice and formatting.

Funding This research was funded and supported by National Science Foundation (NSF) grants DEB 1026843, 0423385, 0508570, 1026843, 1637459, and 2224743, OPP 9911278, and by the Toolik Field Station, managed by the Institute of Arctic Biology at the University of Alaska Fairbanks with cooperative agreement support from the Division of Arctic Sciences of the Office of Polar Programs at NSF. Additional support was provided by the U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit (in-kind), and The Ecology Center at Utah State University.

Data availability All raw data and metadata are available through the ARC LTER website. DNA sequence data can be found in the NCBI Short Read Archive BioProject# PRJNA356108 under accessions listed in Supplementary Materials, Table S5.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval All applicable institutional and national guidelines for the care and use of animals were followed. This study was performed under the auspices of the USU Institutional Animal Care and Use Committee protocol number 1539 and annual permits to the ARC LTER from the Alaska Department of Fish and Game and the U.S. Bureau of Land Management.

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