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Drivers of fish biodiversity in a rapidly changing permafrost landscape

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Abstract

1. Rapid environmental change occurring in northern permafrost regions may have profound implications for fish biodiversity but remains poorly understood. Climate change, increasing human development, and resultant permafrost thaw may combine to alter the quality and quantity of fish habitat including reductions in preferred thermal habitat, changes in water quality, and modified drainage patterns.

2. Our study objective was to understand how lake fish communities residing on permafrost landscapes may be responding to climate change and land use disturbance. We investigated the drivers of freshwater fish community health in lakes of the lower Mackenzie River basin, an ice-rich permafrost region that is experiencing substantial warming, permafrost thaw, and new major highway development. We collected lake morphometry, water quality, and fish community data from 50 lakes and derived several indicators of aquatic health including fish species richness, relative abundance, and the occurrence of three culturally important fish species.

3. We found that water quality and lake size were significant co-drivers of fish community health whereas relationships with summer thermal habitat, as represented by July air temperature, were relatively negligible. Dissolved organic carbon (an indicator for lake browning) emerged as a particularly important driver of fish community structure, and fish community health steeply declined when dissolved organic carbon concentrations exceeded 17–18 mg/L. We suggest potential mechanisms for these declines including light inhibition during summer and a reduced capacity for overwintering in smaller and murkier lakes that may experience faster oxygen depletion rates.

4. Using a more expansive regional water quality database of 203 lakes, we observed potential supporting evidence that warming and new road development increased dissolved organic carbon and total phosphorus concentrations, possibly reducing fish habitat quality in this region.

5. Together, these results highlight how fishes relying on the numerous small and shallow lakes that dominate permafrost landscapes may be vulnerable to the combined effects of rapid warming and new infrastructure.

1 | INTRODUCTION

Rapid climate change in northern permafrost regions is leading to unprecedented ecological events, with far-reaching impacts on northern biodiversity and people (Knopp et al., 2020; Wrona et al., 2016). Growing concerns shared by northern Indigenous Peoples and scientists alike have resulted in an international call for more targeted conservation actions, including more protection for abruptly changing freshwater ecosystems (CAFF, 2013; Greaves, 2016; Heino et al., 2020). For northern Indigenous Peoples, traditional food activities such as hunting, fishing, and gathering are deeply tied to inter-generational knowledge transfer, which is being increasingly undermined by rapid environmental change (Meredith et al. 2019). However, predicting northern environmental change remains a great challenge in part due to inadequate monitoring combined with a backdrop of rapidly shifting baselines (Lento et al. 2019).

At high latitudes, warming rates are two to three times faster than global levels, leading to complex direct and indirect effects on freshwater ecosystems (IPCC, 2021; Meredith et al. 2019; Wrona et al., 2013). Much of the climate change research on northern aquatic biodiversity to-date has focused on anticipated changes in available thermal habitat, and it is expected that there will be a net loss of habitat for Arctic specialists whereas cold and cool water species will gradually expand their northern range limits as new habitats become thermally suitable (Lynch et al., 2016; Poesch et al., 2016; Reist et al., 2006). In addition to warmer lakes, climate change can produce marked changes in water quality including the eutrophication (*greening*) and brownification (*browning*) of subarctic lakes (Hayden et al., 2019), mirroring what has been observed for thousands of lakes at lower latitudes (Leech et al., 2018; Mahdiyan et al., 2020). As northern lakes become both warmer and more nutrient-rich it is expected that the diversity and productivity of many freshwater biological communities will increase (Brucet et al., 2013; Hayden et al., 2017; Heino, Virkkala, & Toivonen, 2009; Wrona et al., 2013). In contrast, increased carbon inputs and associated nutrients such as phosphorus or nitrogen may eventually reach and then surpass optimal states for northern fish communities due to resultant light inhibition, reduced oxygen levels, and altered lake thermal structure (Creed et al., 2018; Finstad et al., 2014; Karlsson et al., 2015; Stasko, Gunn, & Johnston, 2012).

Climate warming and increasing human development are contributing to widespread permafrost degradation in circumpolar regions, with potentially significant consequences for freshwater biodiversity including fish (Raynolds et al., 2014; Segal, Lantz, & Kokelj, 2016b; Thienpont et al., 2013; van der Sluijs et al., 2018; Vucic et al., 2020). Impacts to permafrost through active layer deepening and thermokarst (i.e., melting of ground ice) processes are leading to impacts on fish habitat quantity and quality including increased dissolved organic carbon and nutrient delivery to lakes, and altered catchment drainage patterns (Nitze et al., 2020; Vonk et al., 2015; Wauthy et al., 2018; Wrona et al., 2013). Although the effects of permafrost thaw on freshwater food webs can be varied and complex, many forms of thaw including retrogressive thaw slumping, active layer thickening, peat subsidence, and lakeshore erosion have been linked to water quality changes that may act to either strengthen or counteract lake greening and browning processes (Kokelj et al., 2005; Korosi et al., 2015; Morison et al., 2019; Vonk et al., 2015). These resultant physicochemical changes can be substantial (Houben et al., 2016; Kokelj et al., 2005), underscoring the need to understand how these complex and often opposing processes will impact fish biodiversity over broad spatial scales.

Our study objective was to understand how lake fish communities residing on sensitive permafrost landscapes may be responding to climate change and land use disturbance. We selected the lower Mackenzie River basin as our study area, an ice-rich permafrost region that is experiencing considerable environmental change including rapid warming, widespread permafrost thaw, and new major highway development (Burn & Kokelj, 2009; Tyson, Lantz, & Ban, 2016). Although there have been several previous studies examining lake water quality and lower trophic levels within the context of environmental change in the Mackenzie Delta region (e.g., Cohen et al., 2021; Houben et al., 2016; Kokelj et al., 2005; Thienpont et al., 2013; Vucic et al., 2020; Zhu et al., 2019), comparable work examining lake fishes remains a substantial data gap here and in other ice-rich permafrost regions worldwide (Heino et al., 2020; Laske et al., 2016; Raynolds et al., 2014). The importance of understanding changing fish biodiversity is echoed by Indigenous knowledge holders across the circumpolar north who have reported observations of environmental change directly relevant for their food security and cultural identity (Knopp et al., 2020).

To address our overall study objective, we divided our research questions into two interrelated parts. For part one, we asked: what are the current drivers of fish community health in lower Mackenzie River basin lakes? To answer this question, we collected standardised ecological data (lake morphometry, water quality, and fish community data) for 50 subarctic lakes along the forest–tundra transition. Since many of our sampled lakes appeared to have degraded water quality, we next decided to obtain more limnological data (lake morphometry and water quality) for the region to provide a broader context for ongoing environmental change (part two). Then, using available regional limnological data for 203 lakes with sampling dates spanning from 1990 to 2019 we asked: (1) is there any evidence for changes in regional lake water quality over time? and (2) can regional water quality patterns be attributed to climate change or road use?

2 | METHODS

2.1 | Study area

Supporting the second largest Arctic delta in the world, the lower Mackenzie River basin is an extremely dynamic ecosystem (Burn & Kokelj, 2009; Lesack & Marsh, 2010). In addition to providing extensive riverine and estuarine habitats for freshwater and anadromous fish species, the region contains tens of thousands of generally small and shallow lakes that receive varying inputs from river flooding each year (Lesack & Marsh, 2010). The historically cold and dry climate conditions of the region are classified as subarctic, but the region has experienced considerable warming (>3°C since 1970) that has led to widespread permafrost degradation including *mega* thaw slumps, disappearing (draining) lakes, and changes in freshwater biodiversity (Burn & Kokelj, 2009; Kokelj et al., 2015; Thienpont et al., 2013; Wrona et al., 2016). There are two major highways that intersect the study area, including the Dempster Highway, opened in 1979, which connects Inuvik to the Klondike Highway 740 km to the south, and the Inuvik-to-Tuktoyaktuk Highway, opened in 2017,

which joins Inuvik to the coastal hamlet of Tuktoyaktuk (Figure 1). The region is further characterised by its position along several steep ecozone gradients including the Peel Plateau located west of Fort McPherson, the intermediate northern taiga plains, and the tundra uplands north of Inuvik (Figure 1).

Our study area spans two traditional territories including the Gwich'in Settlement Area in the south and the Inuvialuit Settlement Region in the north (Figure 1). Since time immemorial, Gwich'in and Inuvialuit citizens have been stewards of their lands and have heavily relied upon healthy ecosystems for their food security, culture, and overall well being (Gwich'in Tribal Council and Government of Canada, 1992; Inuvialuit Regional Corporation, 2011). Some culturally important fish species for Gwich'in and Inuvialuit citizens in the lower Mackenzie River basin include broad whitefish *Coregonus nasus*, lake whitefish *Coregonus clupeaformis*, lake trout *Salvelinus namaycush*, Dolly Varden *Salvelinus malma*, burbot *Lota lota*, inconnu *Stenodus leucichthys*, northern pike *Esox lucius*, Arctic grayling *Thymallus arcticus*, Arctic cisco *Coregonus autumnalis*, and least cisco *Coregonus sardinella* (Inuvialuit Regional Corporation, 2011; Kavik-Stantec Inc., 2012).
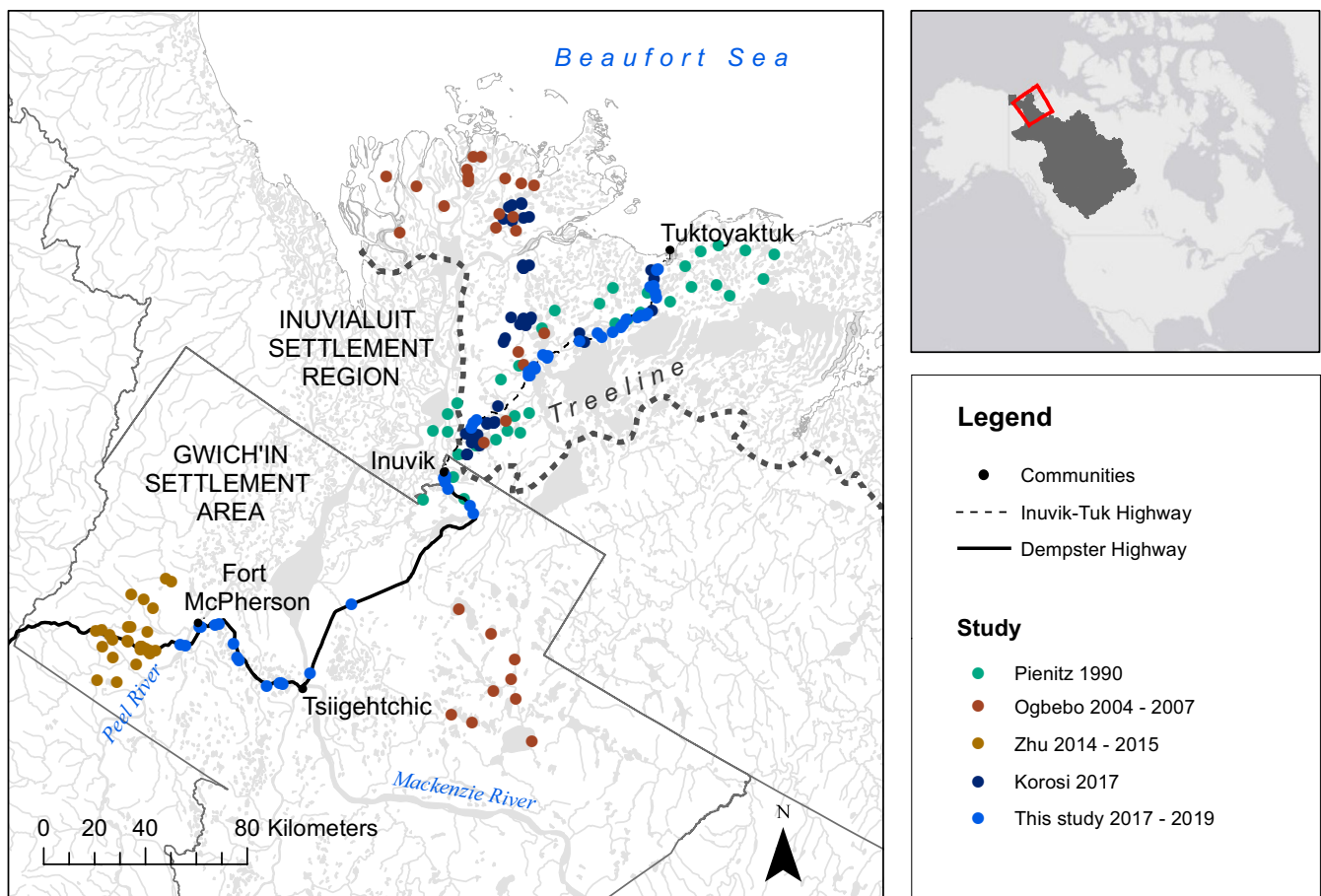
FIGURE 1 Study area in the lower Mackenzie River basin, Northwest Territories, Canada. The Mackenzie River drainage is shown in grey within the inset map. Sites used for the regional water quality analysis of 203 lakes are coloured by study source, with sampling years reported. Sampling lakes from this study include both water quality and fish sampling

2.2 | Examining drivers of fish community health

2.2.1 | Conceptual model development and predictions

We created a conceptual model to understand the potential relationships among variables indicative of environmental change (warming, changes in precipitation, permafrost thaw, and road development and use), physical environmental covariates (lake morphometry and hydrologic connectivity), lake water quality variables, and fish community indicators of health in lower Mackenzie River basin lakes (Figure 2, Table 1). We chose three fish species for investigation including northern pike, least cisco, and whitefish, due to their relatively high frequency of occurrence in our study lakes (captured in 22%–50% of lakes), and their noted importance to local Indigenous communities. We made specific directional predictions for the linkages between each fish community indicator and relevant physical, chemical, and thermal habitat variables, and these expected relationships were then used to inform variable selection for our analyses described below (Table S1). Briefly, we predicted that overall diversity and abundances would be positively related to warmer temperatures and greater nutrient availability, but that individual species would exhibit varied results (Brucet et al. 2013; Poesch et al. 2016; Hayden et al. 2017). Comparing known species thermal optima and preferences with summer water temperatures observed in lower Mackenzie River Basin lakes, we predicted that the two coldwater Coregonids (whitefish and least cisco) would decline with increased temperatures, whereas coolwater northern pike would increase (Christie & Regier, 1988; Harvey, 2009; Hasnain, Minns, & Shuter, 2010; Jacobson et al., 2012). Further, we predicted that northern pike would be sensitive to changes in water clarity due to the species' reliance on macrophyte habitats but would also demonstrate a preference for mesotrophic to eutrophic lakes (Casselman & Lewis, 1996; Harvey, 2009). In contrast, we expected that Coregonid species would prefer lower nutrient and chlorophyll levels as previous studies have linked declines to eutrophication-driven oxythermal habitat degradation (COSEWIC, 2005; Jacobson et al., 2012; Jacobson, Stefan, & Pereira, 2010). Lastly, we predicted that lakes with higher concentrations of dissolved organic carbon would support lower overall diversity and abundances given the evidence that lower Mackenzie River basin lakes may be naturally highly coloured and light limited (Finstad et al., 2014; Houben et al., 2016; Karlsson et al., 2015; Moquin & Wrona, 2015; Pienitz, Smol, & Lean, 1997). Further, we predicted that decreases in DOC associated with retrogressive thaw slumping on lake shorelines could benefit freshwater food web diversity including fish (Cohen et al., 2021; Houben et al., 2016; Moquin & Wrona, 2015).

2.2.2 | Field sampling methods

Our team sampled 48 lakes over a 3-year period (2017–2019) along the Dempster and Inuvik to Tuktoyaktuk Highways (Figure 1). Fish sampling followed a modified version of the Ontario Broadscale Monitoring protocol which incorporates a standardised study design using large and small mesh gillnets spread over representative lake depth strata (Sandstrom, Rawson, & Lester, 2013). We used Ontario broadscale monitoring nets which target fish over 20 cm with large mesh sizes ranging from 38 to 127 mm, and fish under 20 cm with mesh sizes ranging from 13 to 38 mm. We additionally acquired fish presence/absence data for two lakes from a sampling programme conducted by White Mountain Environmental in 2018 (White Mountain Environmental, 2018). Although different gillnets were used, the range of mesh sizes was similar for comparing presence/absence data of our focal species (25–76 mm and 76–127 mm).

In most lakes, gillnets were set for 1-hr periods with an average of 11 net-hours for lakes less than 500 ha and 37 net-hours for lakes over 500 ha (Table S2). However, we also used data collected using overnight sets for two lakes visited in 2017. The difference in lake sampling methods stemmed from community feedback following our 2017 field season, which resulted in moving to short 1-hr sets to reduce fish mortality during 2018 and 2019. While most 2017 lakes were re-sampled to ensure comparable data, we were unfortunately unable to revisit every lake. As a conservative measure, we removed these two lakes from analyses examining catch-per-unit-effort (CPUE) trends but retained them when looking at models relying on species presence/absence data, as these indicators are typically more robust to sampling methodology variation (Table S2).

In addition to fish sampling, we collected lake morphometry and water quality data for each lake including mean and maximum lake depth (m), lake area (ha), water temperature (°C), Secchi depth (m), turbidity (NTU), specific conductivity (µS/cm), chlorophyll-*a* (Chl-*a*; µg/L), total phosphorus (TP; µg/L), total nitrogen (TN; mg/L), dissolved oxygen (mg/L), pH, and dissolved organic carbon (DOC; mg/L)(Table 2). Full sampling details have been described previously in Vucic et al. (2020) and Cohen et al. (2021). Briefly, we obtained lake bathymetry data using a Humminbird® Helix 5 chart plotter (Johnson Outdoors Marine Electronics, Inc.) and Reefmaster bathymetry software (Reefmaster Ltd.). Water quality data were collected using a Eureka Manta multiparameter probe (Eureka Water Probes) at a 1 m depth over the deepest point of the lake for water temperature, pH, conductivity, dissolved oxygen, and turbidity. Secchi depth was measured at the same location by lowering the disk over the shady side of the boat. A water sample was collected and analysed in the laboratory at Wilfrid Laurier University to measure TP, TN, Chl-*a*, and DOC. Chl-*a* measurements were obtained by filtering 250 ml of each sample through G4 glass fibre filters (Fisherbrand). We then used methanol to extract the Chl-*a* from the filters and measured the concentration dissolved in the methanol using a Turner TD700 fluorometer (Symons, Arnott, & Sweetman, 2012). While most water quality sampling and fish community surveying occurred during the same sampling season, sampling year differed for a few lakes when re-sampling was required (Table S2). Zooplankton data were also collected at each lake for an additional project, and we used one indicator species from this dataset (*Chaoborus americanus*) to infer fish absence in six of our study lakes (Table S2; Vucic et al., 2020).
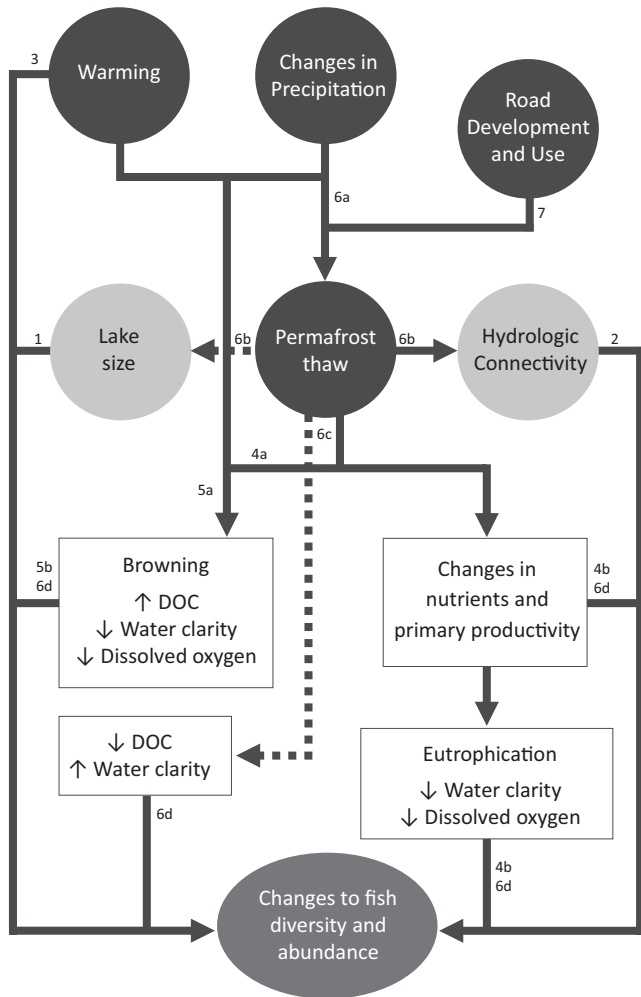
FIGURE 2 Conceptual model demonstrating the predicted linkages between variables of environmental change (black circles), physical environmental covariates (light grey circles), lake water quality (white boxes), and fish diversity and abundance in lower Mackenzie River basin lakes. Dashed lines are used to illustrate linkages that do not connect to overlaying solid lines. Refer to Table 1 for further details behind each numbered linkage. DOC = dissolved organic carbon

2.2.3 | Additional data acquisition

We used mean July air temperature as a surrogate for mean summer water temperature (Sharma et al., 2007). In situ water temperatures measured during the cooling period in August were significantly related to both Julian date and August air temperature during the year of sampling in our dataset, indicating that air temperature was a suitable proxy for mean summer water temperature ($r^2_{adj} = 0.84$). July air temperature was obtained from the ClimateNA program, which uses a 4-km grid spatial resolution (version 6.3; Wang et al., 2016).

Hydrologic connectivity to major perennial habitats was also investigated as a potential binary predictor variable for fish species richness, catch per unit effort, and the presence of migratory Coregonid (whitefish and cisco) species (Table 1). Because we were unable to visit our lakes during spring freshet to assess potential

seasonal connections, we instead used a conservative approach and only indicated connectivity if the lake had a close and stable connection that we verified in the field or using a combination of Google Earth imagery and stream crossing assessment information (IMG Golder Corporation, 2012). As a result, we noted a total of six lakes that had close and seasonally stable connections to large, perennial habitats.

2.2.4 | Fish community data analyses

Fish community analyses followed a sequential framework that included deriving indicators of fish community health, identifying potentially important environmental drivers of fish community health (Figure 2, Table 1), isolating environmental gradients using a principal component analysis (PCA), performing model selection, interpreting final models, and identifying individual effect contributions using hierarchical partitioning (Figure 3). Details of each step are provided below.

We calculated three community-level metrics including species richness, CPUE with large mesh nets and CPUE using small mesh nets. In addition, we used three species-level metrics based on the detected presence of northern pike, least cisco, and whitefish species in our study lakes. CPUE was calculated as the total number of fish caught per net per hour (*net-hours*) and was only calculated for lakes with comparable sampling methods and gillnet mesh sizes (*n* = 46 lakes, Table S2). One extreme outlier lake (>90 times the median value and >5 times the next highest value) that was greatly impacting trends was removed for the small mesh CPUE analysis, reducing the sample size to 45 lakes. Lake and broad whitefish were combined into one category due to small samples sizes and similar expected lake habitat preferences (Richardson, Reist, & Minns, 2001; Scott & Crossman, 1985).

Prior to running analyses, we examined variable distributions and applied log-transformations to improve normality for several predictor variables including lake area, turbidity, DOC, and Chl-*a*. In addition, we applied a log(*x* + 1) transformation to two response variables including large mesh CPUE and small mesh CPUE. We discovered that the effect of sampling date was significantly and negatively related to Chl-*a* (*r* = 0.7), so we detrended this variable prior to analyses. In addition, DOC appeared to display a wedge-shaped response, i.e., an abrupt and nonlinear response (Baker & King, 2010), with several fish community indicators, making its effect potentially less detectable using linear statistical methods. To help further explore these relationships, we performed threshold change-point analyses between DOC and all fish indicators plus overall fish presence using the *TITAN2* package (Baker & King, 2010).

Principal component analysis
We chose a PCA approach as many of the environmental variables were related (Figure S1), and PCA facilitated an effective separation of key environmental gradients while maintaining the overall variability. All environmental variables that were expected to influence fish

community health were retained in this step (Table 1). PCA scores from the first four axes were used as predictor variables for each fish community indicator. Four axes were selected following the Kaiser–Guttman stopping criterion (Borcard, Gillet, & Legendre, 2011), and due to clear gradients with individual environmental variables (Table S3). Results from the PCA are reported in Section 3.1.1 below.

Linear and logistic regression models

We ran linear regression models for three community-level metrics (species richness, large mesh CPUE, and small mesh CPUE) and logistic regression models for the presence of three species (whitefish, least cisco, and northern pike). All predictor variables were standardised onto a unitless comparable scale prior to model selection

TABLE 1 Background information describing the predicted linkages in our conceptual model between variables of environmental change (warming, changes in precipitation, permafrost thaw, and road development and use), physical environmental covariates (lake morphometry and hydrologic connectivity), lake water quality (chl-*a*, dissolved oxygen, DOC, TN, TP, and water clarity), and indicators of fish community health. Relevant environmental variables used in fish community indicator models are listed below each section heading

Conceptual model link ID	Description of linkage in conceptual model
(1) Lake morphometry Lake area and depth	Larger lakes provide more diverse habitat types and facilitate zonation, allowing more species to survive at greater abundances (Jackson et al., 2001; Mathias & Barica, 1980); species presence in small high latitude lakes is related to maximum lake depth and resultant overwintering capacity (Haynes et al., 2014; Hershey et al., 2006), and mean depth is important for determining overall fish productivity (Christie & Regier, 1988; Ryder, 1965).
(2) Hydrologic connectivity	Close hydrologic connections to larger habitats increase the probability of species establishment (Haynes et al., 2014; Hershey et al., 2006; Laske et al., 2016) and allow for seasonal use of small lakes by migratory species (Lesack & Marsh, 2010; Richardson et al., 2001).
(3) Warming July air temperature	Fish biodiversity and productivity are positively related to warmer temperatures (Brucet et al., 2013; Hayden et al., 2017; Heino et al., 2009; Wrona et al., 2013); individual species exhibit optimal temperatures for growth and reproduction, and are constrained by thermal limits that dictate survival (Magnuson et al., 1979).
(4) Changes in nutrients and primary productivity Chl-*a*, TN, TP	(4a) Climate—water quality link: Warmer temperatures may enhance terrestrial runoff into lakes as well as increase internal nutrient cycling due to a longer growing season, expected shifts in vegetation, and shorter ice cover; more precipitation can increase catchment mineral weathering and delivery of nutrients (Gregory-Eaves et al., 2000; Huser et al., 2018; Jeppesen et al., 2009; Ruhland et al., 2003; Wrona et al., 2016); in contrast, lake nutrient declines may be expected in association with warmer and/or drier climates due to increases in nutrient sequestration by growing terrestrial vegetation, or increased evapotranspiration (Huser et al., 2018; Jeppesen et al., 2009).
Eutrophication (sub-category) Dissolved oxygen, Secchi depth, turbidity	(4b) Water quality—fish link: Effects of changing nutrients and primary productivity can vary depending on the original lake trophic state and individual species preferences (Heino et al., 2009; Wrona et al., 2013); prolonged nutrient increases may lead to lake eutrophication including substantial reductions in water clarity that can alter fish community structure (Jeppesen et al., 2010); increased eutrophication of lakes may facilitate hypoxic or anoxic conditions either during the open water season or under ice, lowering fish survival (COSEWIC, 2005; Jacobson et al., 2012, 2010; Mathias & Barica, 1980).
(5) Browning Dissolved oxygen, DOC, Secchi depth, turbidity	(5a) Climate—water quality link: Recent lake browning trends have been observed across the northern hemisphere with suggested mechanisms including recovery from acidification, land use change, warming, and changes in hydrology (Creed et al., 2018; Kritzberg et al., 2020; Leech et al., 2018; Mahdiyan et al., 2020); although trends are complex and there is substantial regional variation, projected warming and increases in precipitation are generally expected to lead to additional browning of northern lakes due to longer growing seasons, changes in vegetative cover, and resultant increases in terrestrial runoff (Creed et al., 2018; Kritzberg et al., 2020; Leech et al., 2018; Stasko et al., 2012); latitudinal studies in northern regions provide additional insight into browning trends, as lakes situated within relatively warmer, more vegetated areas with greater wetland coverage typically have higher DOC concentrations that lakes located further north (Gregory-Eaves et al., 2000; Pienitz et al., 1997; Ruhland et al., 2003). (5b) Water quality—fish link: Higher concentrations of DOC may provide beneficial nutrient subsidies to fish communities until optimal levels are surpassed, and light levels become compromised (Creed et al., 2018); reduced water clarity can lower food availability, fish feeding efficiency, growth, and survival, leading to altered community composition and eventual productivity declines once high concentrations are reached (Finstad et al., 2014; Karlsson et al., 2015; Stasko et al., 2012); increases in DOC can enhance oxygen depletion and increase toxic methane production under ice which could limit fish survival in small, northern lakes (Clilverd et al., 2009; Cunada et al., 2018).

(Continues)

TABLE 1 (Continued)

Conceptual model link ID	Description of linkage in conceptual model
(6) Permafrost thaw	(6a) Climate—permafrost link: Warmer and wetter conditions have led to increased permafrost degradation over the past several decades (Kokelj et al., 2015; Segal et al., 2016b).
Chl-*a*, DOC, lake area, lake depth, Secchi depth, TN, TP, turbidity	(6b) Permafrost—water quantity link: Permafrost degradation may lead to changes in lake size including declining water levels or entire lake drainage, lake subsidence, lake expansion, or changes in hydrologic connections between habitats (Lantz & Turner, 2015; Nitze et al., 2020; Wrona et al., 2016). (6c) Permafrost—water quality link: Lakes with shoreline retrogressive thaw slumps are linked to lower DOC, nutrients, and Chl-*a* in the Mackenzie Delta uplands region; other types of permafrost thaw including active layer thickening, peat subsidence, and other forms of lake shoreline erosion have been associated with variable changes including increases in nutrients and DOC in freshwaters (Burn & Kokelj, 2009; Houben et al., 2016; Kokelj et al., 2005; Korosi et al., 2015; Reyes & Lougheed, 2015; Vonk et al., 2015; Wauthy et al., 2018; Wrona et al., 2016). (6d) Water quality—fish link: Dependent on thaw type and resultant water quality changes. Link to sections on browning and changes in nutrients and primary productivity for further detail.
(7) Road development and use	Roads and other infrastructure development over ice-rich permafrost have been associated with increased flooding, road dust deposition, and thermokarst (Raynolds et al., 2014; van der Sluijs et al., 2018; Walker & Everett, 1987; Zhu et al., 2019). Link to permafrost thaw section for relationship with fish.

TABLE 2 Summary statistics of predictor variables used to model indicators of fish community health in 50 lower Mackenzie River basin lakes

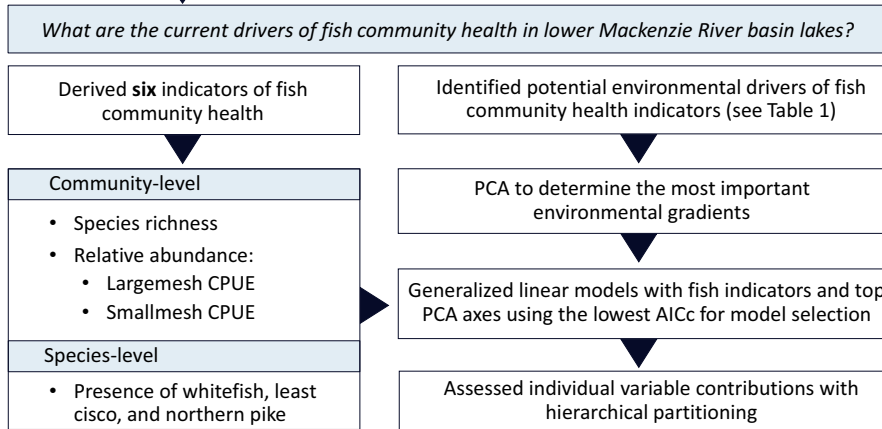| Variable Type	Variable	Units	Mean	Min	Max	SD
Temperature	mean July air temperature	°C	13.1	10.8	15.3	1.6
Lake morphometry	lake area	ha	126	0.4	1,310	285
	maximum lake depth	m	4.8	0.6	13.1	2.8
	mean lake depth	m	1.6	0.6	3.1	0.5
Water quality	dissolved organic carbon	mg/L	21.2	6.0	54.5	12.0
	total phosphorus	µg/L	59	0	165	37
	total nitrogen	mg/L	0.7	0.1	1.8	0.4
	chlorophyll-*a*[*]	µg/L	4.4	0.3	24.2	5.0
	dissolved oxygen	mg/L	10.2	8.0	12.6	1.1
	Secchi depth	m	1.7	0.5	3.7	0.8
	turbidity	NTU	5.9	0.1	38.3	6.0

*Chlorophyll-*a* values are uncorrected raw data and may not reflect maximum summer values (see methods)

using the *arm* package (Gelman et al., 2018). Standardisation allowed inference of the relative strength of each predictor variable within models. For model selection, we used the *dredge* function from the multi-model inference (MuMIn) package to identify the most parsimonious model with the lowest corrected Akaike information criterion (Barton, 2018). To assess model performance for the logistic regression models we computed classification success, sensitivity (proportion of true positives) and specificity (proportion of true negatives) using 70% of the data as a training dataset and the remaining 30% as a testing dataset. We employed receiver operating characteristic curves to determine the most accurate threshold points for assigning probabilities to either *present* or *absent* (Fielding & Bell, 1997).
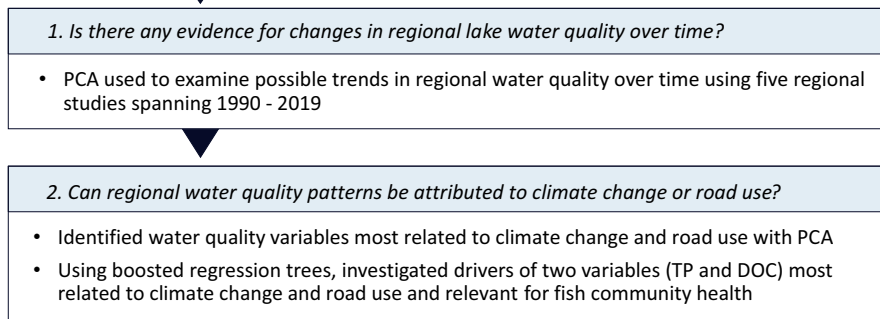
Assessing and controlling for differences in fish community sampling effort

We took several steps to account for the potential influence of differing sampling effort among our study lakes. We included the potential for a model offset (log-transformed total net-hours) to be retained in the top species richness model and in the three species presence models. As six fishless lakes were not sampled (Table S2), we estimated sampling effort based on the mean net-hour values from similarly sized lakes (<500 ha) in order to maintain our full sample sizes for analyses. Following model selection, only one model (least cisco) retained the sampling effort offset within the most parsimonious model, and its inclusion resulted in a model with slightly improved model performance (Table S4). To further illustrate how

Part 1: Examining drivers of fish community health

What are the current drivers of fish community health in lower Mackenzie River basin lakes?

Derived **six** indicators of fish community health

Identified potential environmental drivers of fish community health indicators (see Table 1)

Community-level

- Species richness
- Relative abundance:
  - Largemesh CPUE
  - Smallmesh CPUE

Species-level

- Presence of whitefish, least cisco, and northern pike

PCA to determine the most important environmental gradients

Generalized linear models with fish indicators and top PCA axes using the lowest AICc for model selection

Assessed individual variable contributions with hierarchical partitioning

Part 2: Examining regional water quality patterns within the context of environmental change

1. Is there any evidence for changes in regional lake water quality over time?

- PCA used to examine possible trends in regional water quality over time using five regional studies spanning 1990 - 2019

2. Can regional water quality patterns be attributed to climate change or road use?

- Identified water quality variables most related to climate change and road use with PCA
- Using boosted regression trees, investigated drivers of two variables (TP and DOC) most related to climate change and road use and relevant for fish community health

FIGURE 3 Stepwise framework used to investigate drivers of fish community health (Part 1), and to investigate regional water quality patterns in the lower Mackenzie River basin (Part 2). AICc = corrected Akaike information criterion; CPUE = catch per unit effort; DOC = dissolved organic carbon; PCA = principal component analysis; TP = total phosphorous

our results were robust to sampling differences, a cross comparison of models with and without the offset forced into the final models were provided in Table S4. Although there were some changes in coefficient significance between analyses, we note that model performance remained near identical and overall interpretation of individual coefficients were consistent.

As the two CPUE models already included sampling effort in the response variable, we employed a different strategy to test the robustness of our results. We created alternate models using a negative binomial distribution with fish counts as the response variable and sampling effort included as an offset term (either large mesh net-hours or small mesh net-hours; Table S4). The results of these alternate models provided further confidence to our CPUE models as they demonstrated identical interpretation of coefficient direction and significance, as well as comparable performance metrics using a likelihood-ratio based pseudo-r^2 metric from the *MuMIn* package (Barton, 2018). Because CPUE models are commonly used in fisheries literature, we retained them in our main study presentation for ease of comparability.

Finally, we compared fish community data from five lakes that were sampled using more standard overnight gill net sets in August 2017 followed by our short-set method in August 2019. These lakes ranged in size from 5 to 54 ha (mean = 21 ha) and received

an average of 123 net-hours during overnight sampling versus 13 net-hours during short-set sampling. Despite our limited sample size, a comparison of the results provided some preliminary support for the ability of short-sets with lower overall net-hours to adequately characterise fish communities in our study lakes. Spearman correlation coefficients between species richness, large mesh CPUE, and small mesh CPUE using the two methods ranged from 0.7 to 0.9 (Figure S2). Further, northern pike and whitefish species had identical presence detection in all five lakes. In contrast, least cisco presence differed in two of the five lakes sampled, although the results were not biased toward one method. We note that all five lakes had known connections to larger waterbodies and therefore differences in interannual movement timing for least cisco could have also contributed to the discrepancy between sampling periods.

Hierarchical partitioning

To provide insight into the relative contribution of individual environmental variables and fish sampling effort to final linear and logistic models, we completed hierarchical partitioning analyses using the package *hier.part* (Table S1; Walsh & Mac Nally, 2013). Hierarchical partitioning was selected as it alleviates the issue of multicollinearity between predictor variables by isolating the sum of the individual and joint effects of related variables through an exhaustive model

search. The model output provides the average contribution of each individual variable to the overall explained variance across all models (Mac Nally, 2000), allowing a better understanding of the strongest variables driving relationships in our linear and logistic regression models. However, because there is no reporting of relationship direction, we additionally completed pairwise correlation tests between each predictor variable and fish community indicator for improved interpretation of the hierarchical partitioning results. We calculated Pearson correlations for community-level indicators and non-parametric Spearman correlations for species presence–absence indicators.

While all predictor variables with potential importance to fish community indicators were included in the PCA step, we used indicator-specific variable combinations based on empirical relationships found in previous studies for the hierarchical partitioning step (Table S1). All models included the following variables: mean July air temperature, lake area, lake depth, fish sampling effort, and select water quality variables (Chl-*a*, TN, TP, dissolved oxygen, Secchi depth, and turbidity). We used maximum lake depth for the species richness and three species presence models and mean lake depth for the two CPUE models (Christie & Regier, 1988; Haynes et al., 2014; Hershey et al., 2006; Jackson, Peres-Neto, & Olden, 2001; Mathias & Barica, 1980; Ryder, 1965). DOC was included as a variable for species richness, CPUE, and northern pike presence (Casselman & Lewis, 1996; Clilverd, White, & Lilly, 2009; Creed et al., 2018; Cunada, Lesack, & Tank, 2018; Harvey, 2009; Stasko et al., 2012). Connectivity was included as a variable for species richness, CPUE, and the two Coregonid species due to their migratory life histories (Haynes et al., 2014; Hershey et al., 2006; Laske et al., 2016; Lesack & Marsh, 2010; Richardson et al., 2001).

2.3 | Regional water quality patterns

2.3.1 | Data sources

We compiled water quality data from five different studies, including our own, that resulted in a database of 203 lakes spanning several ecoregions (Figure 1; Table 3). Of these lake water quality studies, one examined the effects of retrogressive permafrost thaw slumps

(contributed data from coauthor Dr Korosi and colleagues; Appendix B), two focused on potential road-related effects (This study and Zhu et al. 2019), and two had no known landscape stressors (*reference studies*; Pienitz et al. 1997; Ogbebo et al. 2009). In addition to these differences in study design, sampling years greatly varied with the earliest study occurring in 1990 and the remaining studies occurring between 2004 and 2019. Another consideration is that the month of sampling varied from late June to August, which could result in water quality differences as solutes may become more concentrated over the course of the open-water season (Houben et al., 2016). Although field sampling methodology was similar across studies, the noted variation in survey year, geographic location, and study design means that we can not fully eliminate potential study-related effects (i.e., unknown variables relating to study differences), and we are therefore cautious with our inferences in the following results and discussion sections.

Using our compiled database, we identified lake morphometry and water chemistry parameters that were measured among the majority of studies and that were of potential interest to structuring fish communities. These included lake area, maximum depth, TP, DOC, specific conductivity, and pH (Table S5). To account for potential differences in sampling timing over the season, we assigned each project to broad sampling time categories including early (late June–early July), early–mid (July), mid–late (late July–mid August), and late (mid–late August). Maximum depth values were missing from one study (Ogbebo et al., 2009), however we estimated them using a quadratic model between mean depth and maximum depth for 105 lakes across northern Canada ($r^2 = 0.95$). Depth data for 50 lakes were from this study in the lower Mackenzie Delta, and from an additional 55 lakes spanning northern Canada (Campana et al., 2020).

We derived four climate variables including mean annual air temperature, mean annual precipitation, and the long-term change in mean annual air temperature and precipitation from the ClimateNA program (Table S5; Wang et al., 2016). Mean annual air temperature and mean annual precipitation were extracted for each lake location over the 5-year period prior to sampling. We chose a conservative 5-year period calculated back from the most recent sampling year as some multi-year studies did not report which samples were collected in which years. To confirm our choice, we ran all models using

TABLE 3 Regional water quality studies compiled into a database of 203 lakes

Study	Year(s) sampled	Month(s) sampled	Ecoregion(s)	Reference lakes	Thaw lakes	Road lakes
Pienitz et al. 1997	1990	July	taiga, tundra	36	0	0
Ogbebo et al. 2009	2004, 2006, 2007	July–August	taiga, tundra, delta	30	0	0
Zhu et al. 2019	2014, 2015	August	Peel Plateau	12	4	12
Korosi et al. contributed data	2017	June–July	tundra	29	26	4
This study	2017, 2018, 2019	July–August	taiga, tundra, delta	0	0	50
			Totals	107	30	66

Note: Eight lakes from this study were assigned to being thaw lakes in addition to road lakes (see methods). Information from an additional source, Gunter (2017) was used to assign thaw lakes for Zhu et al. 2019.

either 1-year or 5-year averages, which allowed us to verify that all models using the 5-year period had greater model fit (increased variation explained and predictive cross validation). The two long-term climate change variables were calculated as the difference between mean annual air temperature from the most recent 30-year period and the previous 30-year period. The site locations reported in one study that used older geospatial technology (Pienitz et al., 1997) were georeferenced for accuracy using their published study map, and we used these new estimated locations for climate extraction. Georeferencing was completed in ArcMap Desktop 10.7.1.

To account for other potential sources of variability among studies, we added variables to indicate survey year, road type (0 = no road, 1 = representing the older, pre-existing Dempster Highway, 2 = representing the newly constructed Inuvik to Tuktoyaktuk Highway), and presence of shoreline retrogressive permafrost thaw. Lakes situated within 1 km of the road were considered *road lakes* following Zhu et al. (2019). Data for shoreline thaw slump presence were provided directly by thaw studies, and we additionally identified that eight of our fish sampling study lakes had shoreline retrogressive thaw slumps using the Northwest Territories Inventory of Landscape Change map viewer, five of which were currently active (Segal et al. 2016a).

2.3.2 | Data analyses

We recognise that differences in study design pose limitations to our regional water quality analysis, and that an *ideal* study would have had a more equal distribution of study lakes across ecoregions, sampling years, impact categories, and morphometric gradients. However, given the lack of historical data to conduct such a study in this region, and the careful analytic framework proposed below, we suggest that useful conclusions may still be drawn surrounding water quality patterns in our study region.

We followed a stepwise analytical framework to address our water quality research questions, which is detailed below (Figure 3). First, we performed a PCA to examine any evidence for changes in water quality over time, and to identify water quality variables that were potentially related to climate and road use in our study area. A data subset (n = 198 lakes) was used because depth data were missing for five lakes from Korosi et al. (contributed data). All variables were inspected for normality which resulted in log-transforming lake area, lake depth, DOC, and conductivity, and square-root transforming TP.

After inspecting the first two PCA axes we chose two variables, DOC and TP, which were potentially related to road use and/ or climate as well as fish community health for further analyses. To examine the potential environmental drivers of DOC and TP we developed boosted regression tree models using previously identified candidate variables (Table S6). We selected boosted regression trees for this step as our data had many strongly correlated predictor variables ($r > 0.7$) and exhibited nonlinear data relationships (Elith, Leathwick, & Hastie, 2008). The boosted tree method uses boosting,

which builds on each successive model output, in combination with regression tree analyses, which aim to group data following a recursive binary partitioning algorithm (Elith & Leathwick, 2017). We were able to use the entire lake database for this step, as the algorithm can accurately impute missing data (Elith & Leathwick, 2017). For each tree model, we initially tested 10 predictor variables including two morphometric variables (lake area and maximum depth), four climate variables (mean annual temperature, change in mean annual temperature, mean annual precipitation, change in mean annual precipitation), and other potential contributing factors (road type, ecoregion, the presence of thaw slumps, and sampling month). We added DOC as a predictor variable for TP, as it can be a useful metric for inferring the amount of external dissolved organic matter loading to lakes, which includes TP (Eimers et al., 2009; Huser et al., 2018). Models were simplified to remove variables that did not contribute to predictive performance using the gbm.simplify function in the package *dismo* (Elith & Leathwick, 2017).

3 | RESULTS

3.1 | What are the current drivers of fish community health in lower Mackenzie River basin lakes?

3.1.1 | Environmental variability

A PCA was completed as an initial step to determine the main environmental gradients structuring our study lakes that were then used as model predictors for fish community health indicators (Section 3.1.2). Results from the PCA indicated that our fish sampling study lakes had two main environmental gradients, with PC1 representing a DOC and temperature gradient, *browning-warming gradient* (axis variation explained = 30%), and PC2 representing a nutrient and water clarity gradient, *eutrophication gradient* (axis variation explained = 17%; Figure S3, Table S3). We labelled each axis using the variables with the highest loadings while also maintaining simplicity of interpretation. Lakes with positive PC1 scores were colder, larger, deeper, more oxygenated, and had lower DOC and TN concentrations, whereas lakes with positive PC2 scores were deeper and less eutrophic (clearer lakes with low TP and Chl-*a*). In addition, lake area was strongly and positively related to PCA axis three (axis variation explained = 13%), and lake connectivity was positively related to PCA axis four (axis variation explained = 11%; Figure S1).

3.1.2 | Fish community

Water quality variables collectively explained the most variation in fish community indicators (44%), followed by lake size (31%), connectivity (11%), sampling effort (10%), and July temperature (5%), averaged across all six hierarchical partitioning models (Figure 4). Larger,

deeper, clearer, and colder lakes with direct access to larger perennial habitats supported more fish species and higher abundances overall (Figures 4, 5, Table 4). Water quality variables including DOC and Secchi depth emerged as important predictors for many fish community indicators. Using change-point threshold analyses, it was found that lakes exceeding 17–18 mg/L of DOC demonstrated reduced species richness, CPUE, and overall fish presence (Figure 6; Table S7).

Overall, more species were present in larger, deeper, clearer, colder, and well-connected lakes with low DOC and nutrient concentrations (Figure 5, Table 4). The top multiple linear regression model for species richness contained all four PCA axes, with the browning-warming gradient (std. effect size = 0.5) and eutrophication gradient (std. effect size = 0.4) demonstrating the strongest relationships with richness (r^2_{adj} = 57%; Table 4). Using the hierarchical partitioning results, we observed that lake area, maximum depth, DOC, connectivity, and Secchi depth had the highest individual contributions of the environmental variables, collectively making up 63% of the explained variance. When divided by variable type, it was found that water quality had the largest contribution to the explained variance (42%), followed by lake size (33%), connectivity (12%), sampling effort (9%), and July temperature (4%; Figure 4).

Similar to species richness, larger, deeper, and colder lakes with lower DOC and nutrient values supported the highest relative abundances of both large and small-bodied fish (Figure 5, Table 4). Water quality variables were the most important drivers of overall abundance as they made up 48% and 58% of the explained variance for large mesh and small mesh abundances, respectively (Figure 4). The next most important drivers included lake size (20%–31%, for small and large mesh abundances, respectively), sampling effort (9% for both), connectivity (7%–8%), and July temperature (5% for both). Relative abundances were best explained in our multiple regression

models by the browning-warming gradient (std. effect sizes = 0.6), followed by the eutrophication gradient (std. effect sizes = 0.3–0.4; large mesh model r^2_{adj} = 58%; small mesh model r^2_{adj} = 37%; Table 4). Both models had the same top four environmental variables identified by hierarchical partitioning, including mean depth, Secchi depth, lake area, and DOC; however, depth was the primary determinant for large-bodied fish whereas DOC was the top predictor for small-bodied fish.

Water quality variables including DOC, Secchi depth, and TP, were collectively the most important drivers of whitefish and pike presence, but not for least cisco presence (Figures 4, 5). Both whitefish and pike were more likely to be present in larger and clearer lakes with lower trophic states, whereas cisco were found in larger, colder, and well-connected lakes with varying water quality. All three species were significantly related to the browning-warming gradient, with smaller, warmer, and browner lakes having lower species occurrences (logistic regression classification success 79%–100%; Table 4). However, there were some key differences as northern pike and whitefish were positively related to the eutrophication gradient (=more occurrences in less eutrophic lakes) whereas least cisco was unrelated.

The contribution of July air temperature in the two Coregonid species models was greater than what was observed at the community level, or for northern pike, but was still relatively small (Figure 4). Temperature was the sixth most important variable for both Coregonid species, making up 7%–8% of the explained variance in hierarchical partitioning (Figure 5). While cisco demonstrated a clearer decline in warmer lakes, whitefish presence displayed a more complicated relationship as its occurrence was more consistently distributed across the July temperature gradient (Figure S4) and was not significantly correlated (Figure 5).
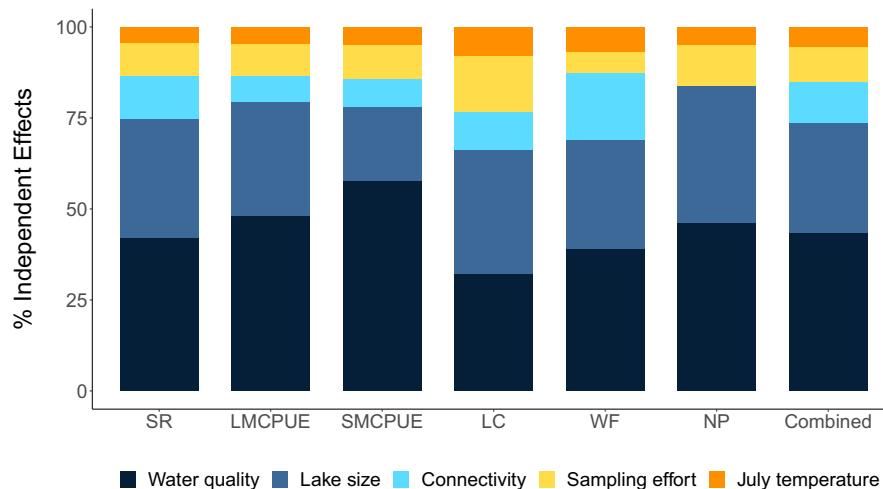
FIGURE 4 Hierarchical partitioning results summarised by variable category for all six indicators of fish community health. Indicator codes include: SR = species richness; LMCPUE = large mesh catch per unit effort; SMCPUE = small mesh catch per unit effort; LC = least cisco; WF = whitefish; and NP = northern pike. The water quality category includes the total sum of independent effects for chlorophyll-a, dissolved organic carbon, dissolved oxygen, total nitrogen, total phosphorus, and Secchi depth. The lake size category includes the sum of independent effects for lake area and lake depth. The combined total does not add up to 100% because different models had different variable inputs (see methods)
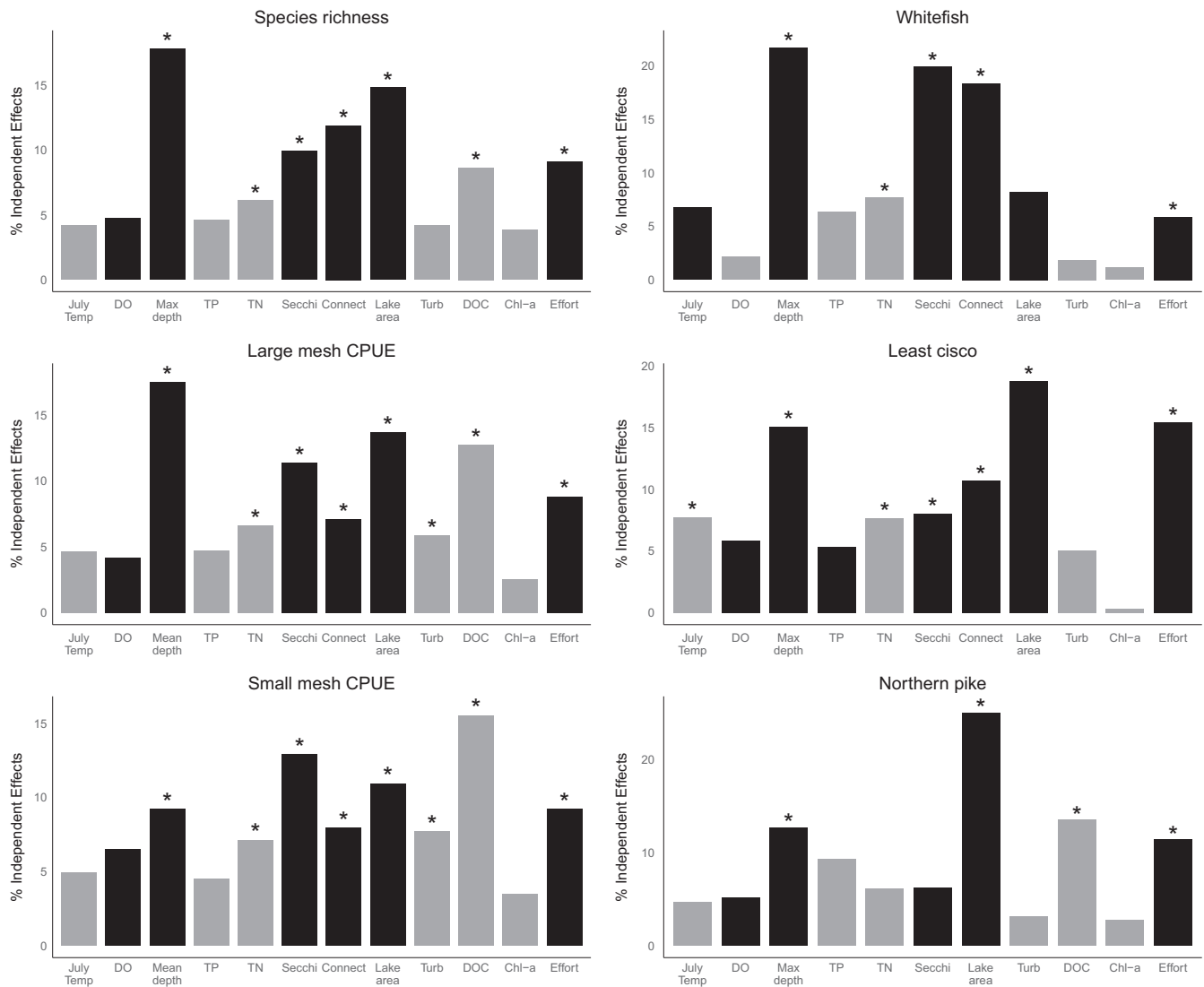
FIGURE 5 Hierarchical partitioning results for species richness, large mesh catch per unit effort (CPUE), small mesh CPUE, and the presence of whitefish species, least cisco, and northern pike. Black bars indicate positive relationships and grey bars indicate negative relationships using pairwise correlation tests. DO = dissolved oxygen; TP = total phosphorus; TN = total nitrogen; Secchi = Secchi depth; Connect = lake connectivity; Turb = turbidity; DOC = dissolved organic carbon; Chl-*a* = chlorophyll-*a*; Effort = sampling effort. Significant pairwise correlations are indicated with asterisks

3.2 | Examining regional water quality within the context of environmental change

3.2.1 | Is there any evidence for changes in regional lake water quality over time?

The positioning of lake sites on the PCA biplot was strongly related to survey year, with more recently sampled lakes having the highest DOC, TP, and conductivity values (Figure 7). The two older studies which occurred during a colder period (1990–2004) and without any road influence are clustered in the bottom left quadrant (Ogbebo et al., 2009; Pienitz et al., 1997), the 2015 Peel Plateau road study is located on the bottom right in association with lower latitude and a warmer and wetter climate (Zhu et al., 2019), and the two most recent studies from 2017 to 2019 that occurred during the warmest period with many sites along

the highway corridor are located mainly in the upper half (this study and Korosi et al.). Notably, our fish sampling lakes that were visited most recently in 2018–2019 were associated with the highest TP and DOC concentrations. Although the separation on the biplot also suggested that lake sizes (area and depth) were smaller in recent years, we note that our fish sampling lakes were generally larger in area but had similar depths to all other studies with the exception of Ogbebo et al. 2009 (Table S5).

3.2.2 | Can regional water quality patterns be attributed to climate change or road use?

PCA
A few water quality variables emerged as being potentially related to climate change and road use including DOC, TP, and conductivity

TABLE 4 Top model results for fish community and species indicators. The first three metrics were examined with multiple linear regression whereas species presence metrics were examined with logistic regression

| Biological indicator	Classification Success[*]	Adjusted r^2	Predictor variable	Standardised coefficient	SE	p-value
Species richness	n/a	57	PC1 (Browning–warming)	0.51	0.09	<0.01
			PC2 (Eutrophication)	0.42	0.09	<0.01
			PC3 (Lake area)	0.25	0.09	0.01
			PC4 (Connectivity)	0.32	0.09	<0.01
Large mesh CPUE	n/a	58	PC1 (Browning–warming)	0.62	0.10	<0.01
			PC2 (Eutrophication)	0.46	0.10	<0.01
			PC4 (Connectivity)	0.19	0.10	0.06
Small mesh CPUE	n/a	37	PC1 (Browning–warming)	0.56	0.12	<0.01
			PC2 (Eutrophication)	0.31	0.12	0.01
Least Cisco presence	93 (100, 80)	n/a	PC1 (Browning–warming)	6.27	2.26	<0.01
			PC3 (Lake area)	3.60	2.02	0.07
			PC4 (Connectivity)	2.39	1.10	0.03
Northern pike presence	79 (86, 71)	n/a	PC1 (Browning–warming)	2.68	1.01	<0.01
			PC2 (Eutrophication)	1.63	0.81	0.04
			PC3 (Lake area)	1.93	0.92	0.04
			PC4 (Connectivity)	2.23	1.32	0.09
Whitefish species presence	100 (100, 100)	n/a	PC1 (Browning–warming)	3.23	1.37	0.02
			PC2 (Eutrophication)	5.55	2.10	0.01
			PC4 (Connectivity)	3.25	1.57	0.04

Abbreviation: CPUE = catch per unit effort

*Model sensitivity (%) and specificity (%) indicated in brackets

FIGURE 6 Species richness, fish presence, log-transformed total large mesh catch per unit effort (CPUE), and log-transformed total small mesh CPUE with dissolved organic carbon (mg/L). Grey shading indicates 95% confidence interval using the loess method
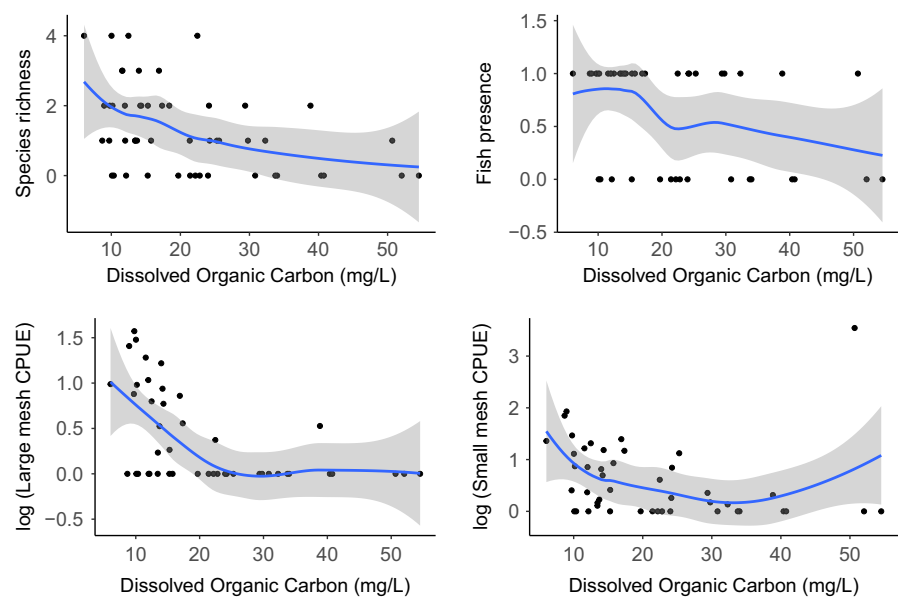
(Figure 7). The first PCA axis (38%) was correlated with geographic location, mean annual air temperature, mean annual precipitation, long-term change in precipitation, lake size, and DOC. The second PCA axis (17%) was related to survey year, climate warming, road type, TP, and conductivity. Smaller, warmer, and wetter taiga lakes that had experienced higher warming rates had the highest DOC values, whereas colder and larger lakes with lower warming rates had the lowest DOC values. Lakes with high phosphorus levels had similarly experienced greater warmer rates. High phosphorus lakes were also more likely to be located along the newly constructed Inuvik-to-Tuktoyaktuk Highway. Both pH and conductivity were greater in lakes at higher latitudes, with conductivity values being positively correlated with road presence.
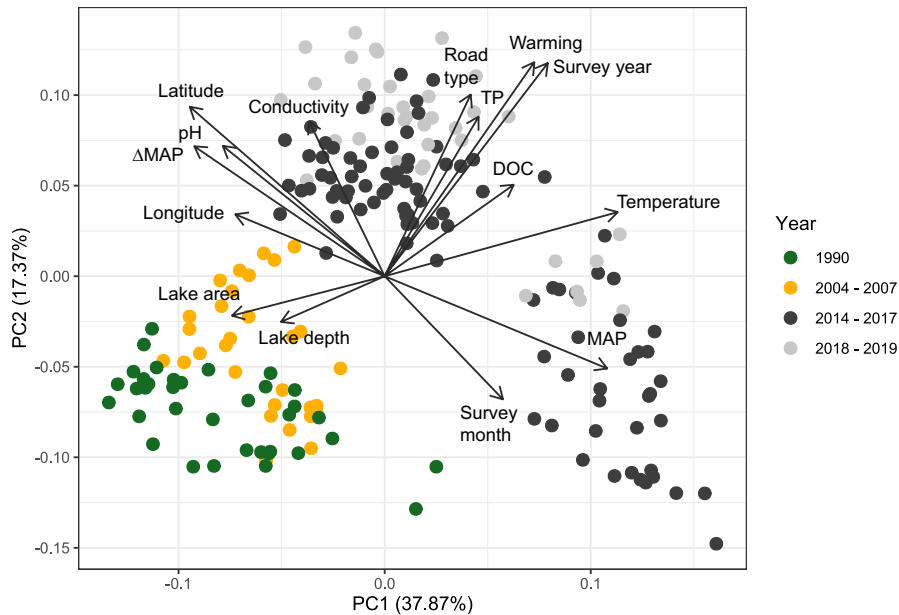
FIGURE 7 Principal component analysis (PCA) biplot demonstrating the relationship between water quality variables (dissolved organic carbon [DOC], total phosphorus [TP], specific conductivity, pH), geographic location (latitude, longitude), climate (mean annual air temperature [temperature], mean annual precipitation [MAP], warming rate [warming], change in mean annual precipitation [ΔMAP]), lake size (maximum depth [lake depth], lake area), sampling timing (water quality survey year and survey month), and road type (0 = no road, 1 = old highway, 2 = new highway)

Boosted regression tree analyses

Dissolved organic carbon values were highest in smaller and warmer lakes that received more annual precipitation and had experienced higher rates of climate warming (Figure S5; $r^2 = 0.68$, CV $r^2 = 0.39$). Lake area and depth were the most important variables, representing approximately 50% of the explained variability. Other variables such as the presence of thaw slumps, road type, designated ecoregion, survey month, and changing precipitation were less important for understanding DOC variability across the entire study area, as their inclusion did not decrease model prediction error.

Total phosphorous values were elevated in shallower lakes that had experienced more external loading (increased DOC) and higher rates of warming (Figure S6; $r^2 = 0.50$, CV $r^2 = 0.33$). In addition, road type emerged as an important predictor, with lakes along the new highway having the highest TP values relative to lakes along the old highway, and relative to lakes situated away from the road. Variables that did not contribute to lowering model prediction error included mean annual precipitation, mean annual temperature, change in mean annual precipitation, the presence of thaw slumps, survey month, and ecoregion.

4 | DISCUSSION

Water quality and lake size emerged as the leading co-drivers of fish community health in lower Mackenzie River basin lakes. Smaller lakes with poorer water quality (high DOC, low water clarity) were less likely to support healthy fish communities, and we found that lakes exceeding a DOC threshold of 17–18 mg/L had much lower fish diversity, abundance, and overall fish presence. In contrast, temperature had a relatively negligible direct effect on fish communities in our study lakes. Lake DOC and water clarity may be influenced by multiple interacting pathways of environmental change in this ice-rich permafrost landscape, and we provided

potential evidence for increases in regional lake browning (DOC) and nutrient enrichment (TP) over time that were related to current and changing climate variables and road use. Together, these results highlight the potential vulnerability of freshwater fish diversity within the rapidly changing lower Mackenzie River landscape as lakes may become increasingly degraded with additional warming, permafrost loss, and human development. Our finding that water quality effects may be driving northern fish diversity has important implications for guiding future research at the global scale, as much of the work on climate change to-date has focused on thermal habitat limitations alone rather than incorporating a more comprehensive view of possible outcomes (e.g., Reist et al. 2006; Lynch et al. 2016; Poesch et al. 2016).

4.1 | Water quality and lake size co-driving fish community health in lower Mackenzie River basin lakes

Fish diversity and abundances were lower in smaller, browner, and more eutrophic lakes, underscoring the importance of water quality and lake size for co-driving fish community health. The environmental PCA of our fish sampling sites revealed that water quality was closely related to lake size, with smaller and shallower lakes generally having lower water clarity and higher concentrations of DOC, nutrients, and Chl-*a*. This observed relationship between lake size and water quality is an important consideration for understanding fish community health in lower Mackenzie River basin lakes, as many of our study lakes were small, shallow lakes that may be disproportionately sensitive to changes in their catchments including warming, altered runoff, and permafrost thaw (Ogbebo et al., 2009; Prowse et al., 2006; Stasko et al., 2012). Moreover, climate-induced permafrost degradation surrounding lakes is anticipated to accelerate lake

drainage trends occurring in regions of the western North American Arctic (Lantz & Turner, 2015; Nitze et al., 2020), which may further reduce the availability of larger lakes that currently provide important fish diversity refuges. Notably, water quality degradation may be enhanced in shallow lakes dominating the lower Mackenzie River basin as they are prone to periodic wind mixing, which can prohibit stratification and facilitate the resuspension of nutrients in the water column (Dranga, Hayles, & Gajewski, 2018; Ogbebo et al., 2009). This potential for increased mixing suggests that typical effects expected via lake browning or eutrophication, such as lowered oxythermal habitat in deeper waters (Jacobson et al., 2010; Stasko et al., 2012), are less relevant in our study lakes which maintain relatively high dissolved oxygen levels (mean = 10 mg/L) throughout the water column during summer. Instead, we suggest that the interconnected effects of lake size and water quality may be impacting other key components of fish habitat in our study area, including the light environment during summer, and water quality and quantity during the critical winter period.

4.2 | Reduced light may be limiting fish community health

Murkier water was strongly related to lower fish community health in our study lakes, including lower species richness, overall abundance, and the presence of northern pike and whitefish, two species that primarily use benthic habitats (Harvey, 2009; Richardson et al., 2001). In particular, we observed that higher DOC levels and lower Secchi depths had the strongest individual relationships with declining diversity and abundance metrics. Here, we note that Secchi depth may be interpreted as a composite index of both browning and eutrophication effects in our murky study lakes as it integrates interrelated components including algal productivity and water column DOC concentrations (Leech et al., 2018). Both DOC and nutrient concentrations are generally expected to have a unimodal relationship with lake productivity, where increases provide beneficial subsidies at low levels but becomes prohibitive of primary production and trophic energy transfer at high levels due to light inhibition (Creed et al., 2018). Murkier lakes (high nutrient and colour) have been associated with specific food web alterations ranging from more inedible plankton species to possible declines in fish growth, maximum size, functional diversity, and overall nutritional value (Creed et al., 2018; Hayden et al., 2019; Leech et al., 2018). Because lower Mackenzie River basin lakes have relatively high humic properties, and moderate–high nutrient levels, our results may provide important insight into potential ecosystem shifts occurring in murkier lakes. In particular, the steep drop-off in fish diversity and abundance when DOC exceeded *c.* 17–18 mg/L in our study lakes suggests that there could be an important light-limiting threshold for supporting higher trophic levels such as fish in lower Mackenzie River lakes. To our knowledge, a light-limiting threshold for subarctic fish diversity has not been specifically identified elsewhere, although gradual declines in fish abundance and biomass were noted over similar or even lower DOC ranges in Scandinavian boreal lakes (Finstad et al., 2014; Karlsson et al., 2015).

Individual fish species demonstrated differing relationships with water clarity variables that could be reflective of their respective habitat preferences and diet. As predicted, we observed that northern pike presence was less common in lakes with higher DOC values, mirroring other studies that have deciphered links between lowered water clarity, reduced pike feeding efficiency, and declining body condition (Casselman & Lewis, 1996; Harvey, 2009). In contrast, the expected shift toward stronger pelagic pathways with lowered light conditions may help explain why least cisco, a predominantly pelagic species, had the weakest response to water quality variables (Hayden et al., 2019; Leech et al., 2018). Based on this finding, we suggest that cisco may be experiencing trade-offs between increased pelagic food availability and lowered pike predation in larger lakes with low–moderate light conditions.

4.3 | Water quality degradation may be reducing winter survival in small, northern lakes

We found that larger, deeper, clearer lakes with lower DOC concentrations and with stronger hydrologic connections represented key habitats for fish across our study region, revealing potential insight into winter life history strategies and survival. Although lake size and hydrologic connectivity are universally important predictors for northern aquatic diversity (Haynes et al., 2014; Hershey et al., 2006; Laske et al., 2016; Ryder, 1965), they may be especially important for fish in the lower Mackenzie River basin where the landscape is dominated by small, shallow lakes that are covered by thick ice for much of the year (Kokelj et al., 2005; Lesack & Marsh, 2010). To survive in this landscape over winter, fish must seek lakes and rivers with sufficient water depths and oxygen levels, both of which may track downwards as winter progresses depending on local conditions such as ice formation and snow cover (Haynes et al., 2014; Hershey et al., 2006; Laske et al., 2016). Importantly, oxygen levels are strongly related to lake depth and trophic state, with depletion occurring faster in shallower and more eutrophic lakes (Mathias & Barica, 1980; Shuter et al., 2012). Further, previous studies have found that small northern lakes with elevated organic carbon experienced heightened oxygen depletion rates over winter, and were additionally linked to high levels of toxic methane production under ice (Clilverd et al., 2009; Cunada et al., 2018). Together, these potential mechanisms suggest that smaller lakes with poor water quality could pose a significant limitation for fish diversity and abundance in our study area, particularly if there is no hydrologic connection allowing seasonal habitat use.

4.4 | Limited evidence for direct temperature effects on fish community structure

Considering that the Mackenzie Delta region is experiencing some of the most rapid warming worldwide, the limited evidence for direct temperature effects on lower Mackenzie River basin lake fish was

unexpected. The two coldwater Coregonid species demonstrated relatively weak responses to warmer temperatures, whereas the effect was negligible for all other indicators. As warmer lakes were linked to higher concentrations of DOC, we suggest that fish fitness, abundance, and survival may have been compromised by rising DOC levels before concurrently rising temperatures reached sufficiently stressful levels in certain lakes. However, water temperatures at the end of July and beginning of August when we began sampling were between 15 and 20°C for many of our study lakes, some of which supported species that we predicted would have lower thermal preferences such as cisco (12.4°C) and lake whitefish (12.7°C; Hasnain et al. 2010). In contrast, the lack of a relationship for northern pike may be due to the wide thermal habitat tolerances observed for this species and its preference for warmer temperatures overall (19–23°C; Harvey 2009).

There are a few potential reasons that may help explain why summer thermal habitat appeared to have a minimal influence on fish community health in our study lakes. The first is that many of the warmest lakes in our dataset had connections to major habitats, allowing potential behavioural thermoregulation to avoid rising temperatures (Magnuson, Crowder, & Medvick, 1979). Both least cisco and whitefish display migratory periods during the summer, and it is possible that they were actively moving during our sampling period (Richardson et al., 2001). An additional consideration is that some of the warmest lakes contained only juvenile whitefish, which require warmer thermal habitat for growth in comparison to adults (15.5–19.5°C; Edsall, 1999). Another possibility is that our use of July air temperature as a proxy for mid-summer lake water temperature was insufficient for capturing potential lake thermal variability that could arise due to local geomorphic processes (O'Reilly et al., 2015). Finally, we acknowledge that our *snapshot* results do not preclude the possibility that fish communities in our study lakes may have already experienced impacts from warming over the past several decades. However, the temporal data required to test this possibility are unfortunately unavailable for most of our study lakes and likewise for many remote, high-latitude regions (Lento et al. 2019). Despite the limited evidence for direct temperature effects found here, we caution that further warming may still be able to impact coldwater fish species once temperature thresholds are surpassed in larger and more isolated tundra lakes of this region.

4.5 | Potential evidence for changing regional lake water quality

Although our water quality analyses faced some notable limitations, using the available data for this region we presented some potential evidence for changes in regional water quality over time. In particular, we observed increases in lake TP, DOC, and conductivity in association with environmental change variables including climate warming (DOC, TP) and road type (TP, conductivity). Notably, our fish sampling study lakes had some of the highest concentrations of TP and DOC that may be explained by various factors including the

more recent sampling, positioning along the road corridor, greater area:depth ratios that could enhance lake nutrient mixing (Gorham & Boyce, 1989), the low number of lakes with shoreline retrogressive thaw impacts, and the inclusion of lakes in the taiga plains ecoregion. While we recommend that future studies aim for a more balanced study design across lake sizes, ecoregions, and thaw/road impacts to verify these results, we note that our preliminary results do align with many other studies and observations from Indigenous knowledge holders that have reported evidence for declining water quality across the circumpolar north (Hayden et al., 2019, 2017; Knopp et al., 2020; Wauthy et al., 2018; Wrona et al., 2016).

The emergence of warming rate as a potentially important predictor for both DOC and TP is an interesting finding as it suggests that water quality changes may be associated with warming-related impacts on land cover and permafrost thaw. Notably, our fish sampling lakes had experienced some of the greatest warming rates in the regional dataset, including record-high winter temperatures in 2018 and 2019 which may have contributed to permafrost degradation and resultant changes in water quality (Nitze et al., 2020; Segal et al., 2016b). Both tundra and taiga regions have experienced substantial land cover change in north-western North America over the past several decades due to longer growing seasons and warming-related disturbances such as permafrost thaw and fire (Wang et al., 2020). For example, widespread shrub expansion has been documented across previously unvegetated tundra regions, which could be leading to increased dissolved organic matter and nutrient delivery to lakes (Myers-Smith et al. 2019; Wrona et al., 2016). In contrast, impacts in the more southern taiga have varied depending on local disturbances such as permafrost thaw, insect infestations, and fire (Myers-Smith et al. 2019; Wang et al., 2020). One particularly relevant change for lake water quality is the loss of forest cover to fen and bog expansion in the taiga region following permafrost degradation (Wang et al., 2020; Wrona et al., 2016). Warming-induced permafrost thaw in the taiga region may be additionally elevating lake nutrient and DOC levels as thermokarst shoreline processes can erode banks and destabilise riparian vegetation, increasing woody debris and soil transport into lakes (Burn & Kokelj, 2009).

Contrary to other studies observing declining nutrients with higher latitudes (Gregory-Eaves et al., 2000; Medeiros et al., 2012; Ruhland et al., 2003), we observed high total phosphorus values in many of our fish sampling lakes in the tundra uplands that may be partly attributed to new road development. We further noted that conductivity values in road-adjacent tundra lakes were significantly elevated (mean difference = 32 µS/cm; t test: t_{50} = −2.4, p = 0.02) compared to tundra reference lakes sampled by Korosi et al. during a similar time period, which has been an important indicator of road disturbance elsewhere (Gunter, 2017; Zhu et al., 2019). However, we caution that our inferences here are limited as most lakes along the new road corridor were not sampled prior to construction, and it is possible that other unmeasured variables or sampling differences could be responsible for enriched road-adjacent lakes. While there is some previous work looking at the effects of infrastructure and road

use over permafrost terrain on ecosystems, few have looked directly at impacts on lakes (Raynolds et al., 2014; Walker & Everett, 1987; Zhu et al., 2019). A noted exception is one other study included in our regional analysis, which concluded that total phosphorus values did not significantly vary according to road proximity; however, they examined effects along the Dempster Highway, which has been in operation for 40+ years (Zhu et al., 2019). Although there is still much uncertainty surrounding the cascading ecological effects of development over permafrost, other studies have documented substantial impacts on the surrounding landscape including increased flooding and thermokarst (Gill et al., 2014; Raynolds et al., 2014). Based on these observed impacts elsewhere, we speculate that nutrient-rich gravel fill excavated from permafrost and used to build the new highway could have leached into nearby waterbodies during spring flooding events (Raynolds et al., 2014; van der Sluijs et al., 2018; Zhu et al., 2019). Another possibility is that despite best management practices, the road construction itself could have disturbed nearby permafrost, creating a positive feedback mechanism that may have resulted in increased solute delivery to nearby lakes (Gill et al., 2014; van der Sluijs et al., 2018).

4.6 | Opportunities for biodiversity stewardship

Traditional food activities (hunting, fishing, gathering) are fundamental to the well-being of thousands of Indigenous citizens residing in the Gwich'in Settlement Area and the Inuvialuit Settlement Region (Hovel et al., 2020; Kavik-Stantec Inc., 2012). Our study results have direct implications for local Gwich'in Peoples and the Inuvialuit as regional lakes provide both seasonal and year-round habitat for culturally important species such as broad whitefish, lake whitefish, lake trout, inconnu, northern pike, and cisco. The community-based fishing plan developed for lakes along the Inuvik-to-Tuktoyaktuk Highway provides a proactive conservation-focused template for protecting newly accessible fisheries resources, including individualised restrictions to community members and sport fishers (Inuvik and Tuktoyaktuk Hunters and Trappers Committees 2017). Results from this study could directly tie into these ongoing and future conservation planning efforts, including the identification of large and well-connected lakes that may serve as key biodiversity refuges amid continued environmental change. As these same lakes are likely to garner the most fishing attention, extra preventative measures could be considered to protect them, and their hydrologic connections, from rising regional human pressures (Meredith et al. 2019; Tyson et al., 2016).

To our knowledge, ours is the first study to identify that lake browning and nutrient enrichment could be adversely affecting aquatic diversity in the lower Mackenzie River basin. We conclude that fishes relying on the numerous small lakes that dominate the lower Mackenzie landscape could be disproportionately vulnerable to water quality degradation, which was unexpected given the relatively low human influence in the region. We note that our findings align with observations made by Indigenous knowledge holders across the circumpolar north that have included permafrost thaw,

declining water quality, and changes in fish biodiversity (Knopp et al., 2020). Based on our study results, we advise that future research should aim to understand how projected environmental change may accelerate water quality degradation and potentially contribute to declining biodiversity in permafrost regions, including: (1) focusing on the potential link between seasonal water quality and under ice-oxygen during the rapidly changing winter period; (2) examining how new infrastructure on permafrost may be impacting surrounding aquatic environments; and (3) incorporating a broader range of permafrost thaw impacts on freshwater habitat into future studies. Finally, as northern climate change and human development pressures are expected to escalate further in the coming decades, building on existing standardised monitoring data while also prioritising opportunities for impactful community-based collaborations will be key for addressing this complex conservation challenge (Hovel et al., 2020; Knopp et al., 2020; Wong et al., 2020).

CONFLICT OF INTEREST

The authors report no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon request.

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SUPPORTING INFORMATION

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