Peel Watershed Fish Habitat Assessment

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Summary

By understanding the relationship between fish and their environment, we can better predict where to find them, at what time of year, and in what numbers. This information is the foundation of effective conservation and management of Yukon's freshwater fish.

The remoteness of most of Yukon's waterbodies poses a challenge to understanding the distribution and abundance of fish. Most waterbodies can only be reached by air and, for this reason, exhaustive censuses of fish distribution and abundance in these areas are impractical. By using landscape-scale statistical models to understand relationships between fish and their environment, we can predict and understand fish distribution at a site without site-specific field surveys.

In 2007, 2008, and 2010, Environment Yukon carried out a series of fish surveys in the remote upper Peel Watershed. Using these fish survey data, we developed statistical models that predict the distribution and abundance of Dolly Varden, slimy sculpin, and Arctic grayling. These models provide a basis for understanding the relationship between fish and fish habitat in the upper Peel Watershed.

The results of this research will inform land use planning, environmental assessment processes, fisheries management, and conservation decisions.

The methods presented in this report will also form a framework for future investigations into the relationship between Yukon fish and their environment.

Key Findings

- Field observations and model predictions showed nearly all 1st order streams did not contain fish, and nearly all 4th order streams did contain fish.
- Models based on stream volume were the best predictors of Dolly Varden and slimy sculpin presence, while models based on stream productivity were the best predictors of presence for Arctic grayling and all fish species combined.
- The probability of slimy sculpin presence was predicted to extend further upstream than any other individual species, followed by Dolly Varden and then Arctic grayling.
- Models predicting probability of Dolly Varden presence performed poorly.
- Models based on stream productivity were the best predictors of fish abundance for Dolly Varden, slimy sculpin, and Arctic grayling.

- Landscape-scale statistical modelling can be an effective way of using fish presence and abundance data gathered at sample sites to predict distribution and abundance across a larger study area.

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Introduction

Questions about distribution and abundance of species are at the heart of the science of ecology. The space a species inhabits, and the numbers of that species found there, are governed by their relationship with their environment. By understanding these relationships, we can learn more about the place of a species within its environment. We can then begin to predict the distribution and abundance of species without having to look specifically at the area in question. Instead, we can infer whether they will be there by understanding the environmental conditions that are present.

By understanding the relationship between Yukon fish and their environment, we can better predict where to find fish, at what time of year, and in what numbers. This information is the foundation of effective conservation and management of Yukon's freshwater fish. These fish are an important cultural, recreational, and subsistence resource, as well as a critical component of aquatic ecosystem function and biodiversity.

The relationship between fish and their environment is not a simple one. As mobile creatures inhabiting a dynamic environment, fish are able to follow and exploit favourable environmental conditions, and flee unfavourable ones. The remoteness of most of Yukon's waterbodies also poses special challenges for understanding the distribution and abundance of fish. Faced with these constraints, we can use landscape-scale statistical models to provide insight into the relationship between fish and their environment. Instead of attempting a complete census of fish within a watershed, we can gather information about fish distribution and abundance at a number of sample sites. We can then use these data to make predictions about fish distribution and abundance at sites that have not been sampled. With data from a suitable number of sample sites, we can build statistical models that accurately predict fish presence and abundance over entire watersheds. The information provided by these models is useful for land use and conservation planning, environmental assessment, and fisheries management.

Environment Yukon conducted three years of fish surveys in the remote upper Peel Watershed in 2007, 2008, and 2010 (Figure 1). Using these data, we developed statistical models that predicted the distribution and abundance of Dolly Varden (*Salvelinus malma*), slimy sculpin (*Cottus cognatus*), and Arctic grayling (*Thymallus arcticus*; Figure 2).

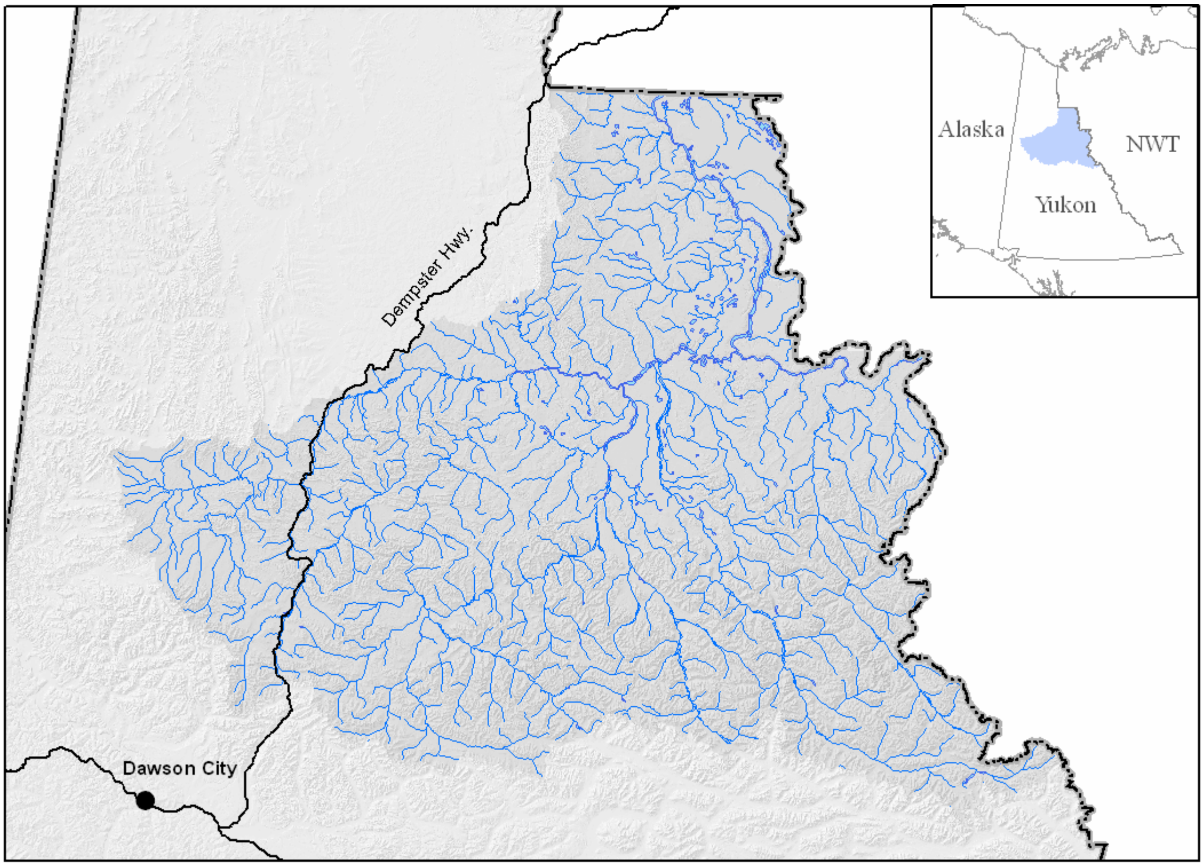

Figure 1. The Peel Watershed, including shaded relief, with location in Yukon (inset).

For each species, we developed a set of candidate models, based on hypothesized fish-habitat relationships. We evaluated these models for simplicity and accuracy, and chose the simplest and most accurate as the best model. We used these final models to link habitat variables to fish ecology. This understanding of fish ecology can provide a basis for environmental assessment, inform land use planning processes, and support effective fisheries management and conservation in the upper Peel Watershed. Models specific to Dolly Varden can also inform assessment and conservation of northern-form Dolly Varden, a population recommended in 2010 for classification as Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

Figure 2. Fish species of the upper Peel Watershed: Arctic grayling (top left), slimy sculpin (top right), and Dolly Varden (bottom).

1.1 Study Area

Vast and remote, the Peel Watershed is defined by the Peel River and its tributary waters, and characterized by its wilderness condition. No permanent settlements exist within the Yukon portion of the Peel Watershed. Only one permanent road, the Dempster Highway, intersects the western margins of the watershed. While seasonal camps and access routes exist within the Peel Watershed, most of the region has seen little or no significant human alteration.

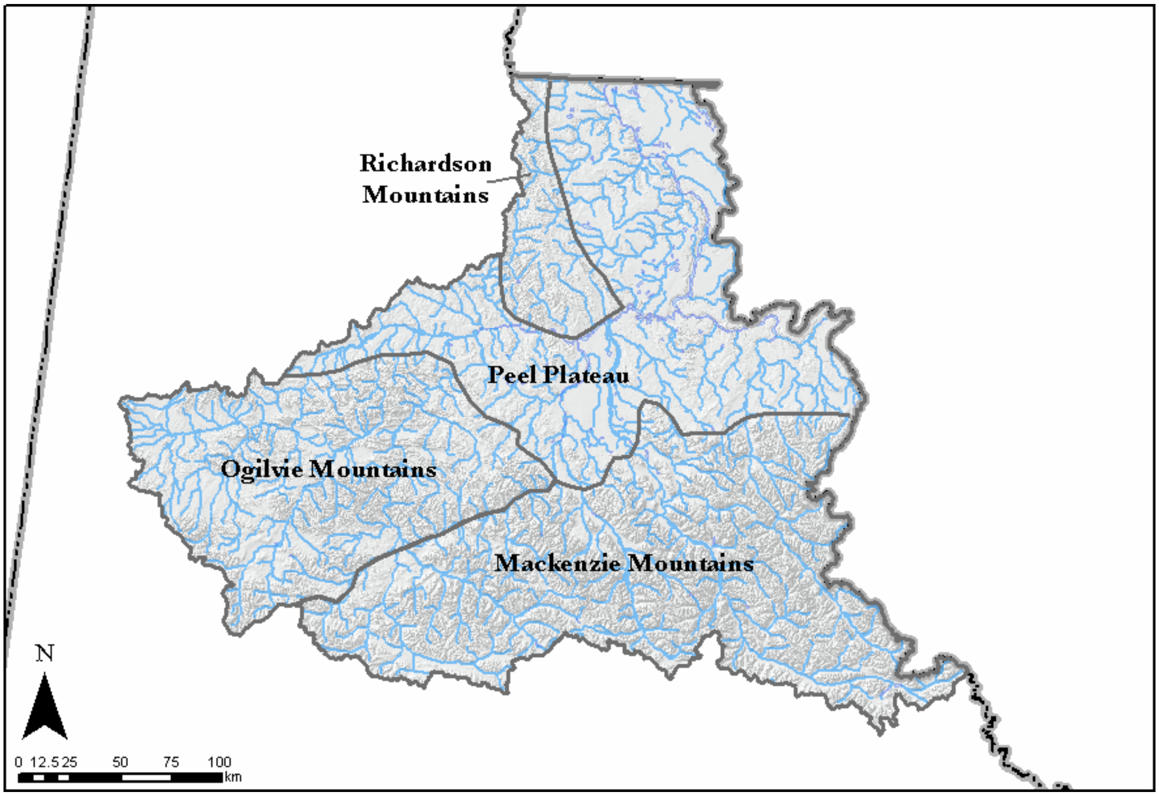

Figure 3. Ecoregions of the Peel Watershed.

1.1.1 Ecoregions of the Peel Watershed

The Peel Watershed consists of four distinct landscapes: the Ogilvie, Mackenzie, and Richardson mountains, and the Peel Plateau (Figure 2). The Ogilvie Mountains, source of the Ogilvie, Blackstone, and Hart rivers, are composed of sedimentary rock that remained unglaciated during the Pleistocene. Large areas of exposed rock are common (Figure 3). To the east of the Ogilvies lie the Mackenzie Mountains, a series of high, rugged ranges consisting of both sedimentary and igneous rocks. Past glacial activity has created broad valleys and sharply-sloped mountain peaks (Figure 3). Collectively, the Ogilvie and Mackenzie mountains form the upper Peel Watershed.

We limited our study area to the mountainous upper Peel Watershed within the Ogilvie and Mackenzie mountains. Our results are therefore only applicable to this region of the watershed.

1.1.2 Aquatic environment

The Peel Watershed's highly seasonal climate has a dramatic influence on the aquatic environment. Extremely cold winter temperatures drastically reduce river flows by completely freezing smaller streams. Fish are thus forced to seek winter refuge in larger streams and

Figure 4. Photos representative of topography and vegetation from the Ogilvie (*left*) and Mackenzie (*right*) mountain ranges, upper Peel Watershed.

rivers that have sufficient flow to remain unfrozen. In spring and summer, fish move outward from their overwintering sites to re-inhabit small seasonal streams. Aquatic habitats are also heavily influenced during open-water seasons by flooding and drying, particularly in mountainous areas. Many high-elevation streams in the Peel Watershed flow through expansive gravel, cobble, and boulder fields, and lack surrounding vegetation to buffer precipitation extremes. Many 1st order streams, and some 2nd order streams, are ephemeral, drying completely in summer. The extreme seasonality and low primary productivity of the Peel Watershed also limits the amount and availability of food resources to fish. The highly dynamic nature of the aquatic environment in the Peel Watershed constrains and determines the distribution and abundance of resident fish populations.

What is stream order?

Stream order is a classification hierarchy based on evaluation of a stream's sources. Streams that originate from the ground, without inflow from other streams, are classified as 1st order. Where two 1st order streams join, they create a 2nd order stream. Similarly, where two 2nd order streams join, the resulting stream is classified as 3rd order. Streams move up in order only when they join a stream of equal order; the resulting stream from a 2nd order stream flowing into a 3rd order stream remains 3rd order.

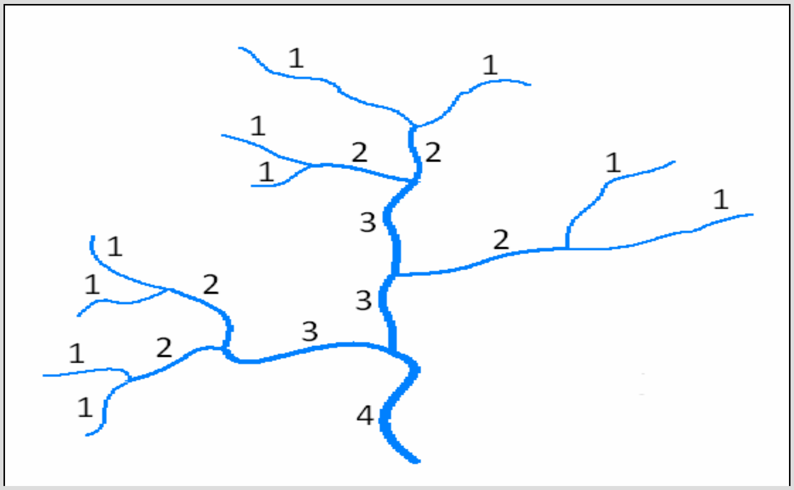

Figure 5. Clockwise from top right: a small, high-gradient, ephemeral Blackstone River tributary; a small, low-gradient Hart River tributary flowing through dwarf shrub tundra; a broad, heavily-braided section of a Blackstone River tributary, with remnant aufeis; spruce trees lining a small tributary of the Ogilvie River.

Methods

2.1 Fish sampling

2.1.1 Survey site selection

We chose our stream sampling sites with two goals in mind: a) obtaining a suitable representation of the diversity of stream habitats in the upper Peel Watershed, and b) sampling the largest number of streams possible by making efficient use of travel and personnel time. Sampling was confined to wadeable 1^{st}-4^{th} order streams, with all streams $\geq 5^{th}$ order considered to be fish-bearing. The bulk of our sampling sites were in 2^{nd} and 3^{rd} order streams, where we found the greatest variability in fish presence and abundance. We conducted our sampling in late summer (July 17-19 2007, Aug. 9-13 2008, Aug. 2-6 2010), when the upstream extent of fish distribution was expected to be at its maximum.

2.1.2 Site sampling protocol

We accessed sample sites by helicopter. We determined fish presence and abundance by electrofishing, using a Smith-Root LR-24 backpack electrofisher (Smith-Root Inc., Vancouver, WA). At each stream site, we thoroughly electrofished a stream reach of 100 to 300 m. The length of stream electrofished was proportional to stream width and amount of cover, with longer reaches fished in narrow streams with little cover, and shorter reaches fished in wider, more complex streams. We momentarily stunned fish with the electrofisher, collected them in a dip net, and transferred them to a container of water to recover. We weighed, measured, and identified all fish to species, and released them back into the stream once they were able to swim again. We also recorded counts and species identification of fish that were seen but not caught during electrofishing.

2.2 Statistical modelling

2.2.1 Stream network data

We based our remote sensing data and model predictions on newly-completed National Hydrographic Network (NHN) data, which are digital representations of lake and stream networks, for the upper Peel Watershed. NHN data are available from GeoBase (www.geobase.ca). NHN data are compiled by federal, provincial, and territorial governments from the best available data, and have been adopted as the national standard for hydrographic data by the Canadian Council on Geomatics.

2.2.2 Habitat variables

Using the framework provided by our survey locations and Peel Watershed NHN data, we examined a number of physical and ecological habitat variables for their effect on fish presence and abundance. We only considered variables hypothesized to have a direct effect on fish distribution and abundance. Because we required our results to be applied to the entire upper Peel Watershed, the variables we examined were limited to those for which data were available for the entire study area. The predictor variables we considered were:

Elevation: meters above sea level, as provided by 1:50,000 Canadian Digital Elevation Model (CDED) data (available at www.geobase.ca). Elevation relates to the temperature and productivity of a stream, as well as the difficulty for migrating fish in reaching it.

Mean slope: mean slope (in degrees) within a 500-m radius of each stream pixel, providing an estimate of terrain steepness surrounding each stream pixel. Terrain steepness, in part, determines the susceptibility of a stream to flash flooding. Mean slope was derived from 1:50k CDED data.

Upstream extent: cumulative length, in meters, of all stream segments upstream of the stream segment of interest. Upstream extent relates to the volume and variability of flow of water within a stream, and the susceptibility of a stream to flooding, drying, and freezing.

Distance to ≥5th order stream: distance, in meters, from each stream pixel to the closest ≥5th order stream. Streams of 5th order or greater were assumed to have sufficient water volume and flow to act as overwintering areas for fish. The distance to these presumed overwintering areas relates to the ability of migrating fish to recolonize smaller streams in summer.

Rock proportion: the proportion of exposed rock within a 500-m radius of each stream pixel. The amount of exposed rock surrounding a stream increases its propensity for flash flooding. Land cover data was derived from 25-m ecological land classification data, available from Environment Yukon.

Vegetation proportion: the proportion of vegetated area within a 500-m radius of each stream pixel. The amount of vegetated area surrounding a stream relates to stream productivity. Land cover data was derived from 25-m ecological land classification data, available from Environment Yukon.

2.2.3 Hypothesis-driven models

Using our selected habitat variables, we built models corresponding to six different hypotheses concerning fish distribution in the upper Peel Watershed. Our hypotheses considered different combinations of factors that could affect fish presence and abundance. Our models explored different aspects of our overarching hypothesis: that the dynamic nature and low productivity of the Peel Watershed's aquatic environment drives fish distribution and abundance. Hypothesis-driven models considered were:

Flooding: Frequent and severe floods can physically remove fish from small streams by flushing them into larger rivers. Such floods can also limit fish abundance by reducing food supplies and destroying habitat required for cover and spawning. The *Flooding* model incorporated variables for *Rock proportion*, *Mean slope*, and *Upstream extent*, which relate to the severity of flood risk, and *Distance to ≥5th order stream*, which relates to fishes' ability to recolonize after floods.

Freezing: In the sub-arctic Peel Watershed, streams with low water volumes and groundwater inputs can freeze solid in winter. To survive the winter, fish must travel to overwintering areas, where sufficient volumes of water remain unfrozen. In spring, fish must travel back from overwintering areas to recolonize streams that were frozen solid. The *Freezing* model incorporated *Elevation* as an indication of winter climate, *Upstream extent* as a proxy for water volume, and *Distance to ≥5th order stream*, which relates to fishes' ability to recolonize a stream after ice-out.

Drying: Small streams, particularly those surrounded by large areas of exposed rock, are prone to drying completely during dry summer periods. After a drying event, fish must travel back to the stream from refuge areas. The *Drying* model incorporated *Upstream extent*, as a proxy for water volume, and *Distance to ≥5th order stream*, which relates to fishes' ability to recolonize following drying events.

Stream volume: Fish presence and abundance can be influenced by stream volume, with larger streams holding more fish than smaller streams. The *Stream volume* model incorporated only *Upstream extent*, as a proxy for water volume.

Migration: In the upper Peel Watershed, freezing and drying of small streams happens often. To survive these events, fish must seek refuge in large streams and rivers, and must travel outward from these refuges to recolonize small streams. The more difficult the migration route, the fewer fish are expected to complete the journey. The *Migration* model incorporated variables for *Elevation* and *Distance to ≥5th order stream*, both of which relate to the difficulty encountered by fishes recolonizing a stream.

Productivity: Fish presence and abundance can be determined by the amount of food available within a stream. The *Productivity* model incorporated variables for *Vegetation proportion*, as a measure of terrestrial vegetation surrounding a stream, *Elevation*, as an indicator of climate, and *Upstream extent*, as a proxy for stream volume.

2.3 Model structure and evaluation

We used our fish survey data to build statistical models for each of our hypotheses. We modelled two different parameters for fish in the Peel Watershed: fish presence (distribution) and fish abundance. For each of these parameters we used different types of models: weighted logistic regression for fish presence, and negative binomial regression for fish abundance. We built presence and abundance models for each of the three fish species individually. In the case of fish presence, we also constructed models for all fish species combined. This process provided us with a set of candidate models predicting presence and abundance for each fish species. We used Akaike's Information Criterion to select the single best model for presence and for abundance for each species from within our set of candidate models (Burnham and Anderson 2002). We used area-under-curve values to evaluate the performance of our final fish presence models (Lin *et al.* 2003), and Wald tests to evaluate model fit for our final fish abundance models (Cameron and Trivedi 1998).

2.3.1 Predicting fish presence

We estimated probability of fish presence using weighted logistic regression models. Logistic regression uses one or more predictor variables to calculate a probability of an event. In this case, we used logistic regression to calculate the probability of fish presence in a stream. Because it was non-random, however, our sampling design did not incorporate 1st-4th order streams in proportion to their availability within the upper Peel Watershed (Table 1).

Table 1. Percentage of upper Peel Watershed and of total sample sites made up of 1st, 2nd, 3rd, and 4th order streams.

Stream order	Upper Peel Watershed	Sample Sites
1	55%	7%
2	20%	31%
3	10%	35%
4	5%	27%

To account for this, we gave data collected for each sampling site a weight dependent on how many sites of the same order were in our sample, and how many were within the study area, such that:

$$\text{Case weight} = \frac{\text{Proportion of } x^{\text{th}}\text{-order streams in study area}}{\text{Number of } x^{\text{th}}\text{-order stream sites sampled}}$$

We used weighted logistic regression to estimate probabilities of occurrence across our study area for:

- all fish species combined;
- Dolly Varden;
- slimy sculpin; and
- Arctic grayling.

2.3.2 Predicting fish abundance

We investigated the association between fish abundance and our predictor variables using negative binomial regression. Negative binomial regression uses one or more predictor variables to estimate the probability of a count of events being a specified value (e.g. the probability that seven Dolly Varden would be caught in 1000 seconds of electrofishing effort at a sample site). For our purposes, the greatest benefit to fitting negative binomial regressions to our data was to determine which variables had the most significant impact on fish abundance, and to examine the magnitude and direction of these relationships.

Because electrofishing effort, determined by seconds electrofished per site, differed among sites, we adjusted fish species counts to a standard effort corresponding to fish count/1000 seconds, such that:

$$\text{Adjusted fish species count} = \frac{\text{Fish species count}}{\text{Seconds electrofished} \cdot 1000 \text{ seconds}}$$

We used negative binomial regression to examine the relationship between habitat variables and the abundance of:

- Dolly Varden;
- slimy sculpin; and
- Arctic grayling.

2.3.3 Model selection: which model works best?

We used Akaike's Information Criterion (AIC) to select models which best described fish presence and abundance using the fewest number of predictor variables (Burnham and Anderson 2002). Model selection using AIC ranks competing statistical models by their predictive power and simplicity, with models that perform well using few variables ranked higher than models that perform poorly or are more complex. AIC model selection also indicates which candidate models performed nearly as well as the top-ranked model (where the difference in AIC value from the top-ranked model was ≤2.00), and which models performed poorly compared to the top-ranked model (where the difference in AIC values from the top-ranked model was >2.00).

2.3.4 Model performance: fish presence models

After selecting the top-ranked fish presence models using AIC, we assessed their performance by calculating area-under-curve (AUC) values for each model (Lin *et al.* 2003). AUC values are calculated by plotting a model's true positive rate (incidence of the model correctly identifying fish presence) against its false positive rate (incidence of the model incorrectly predicting fish presence) along a continuum of probability cutoff values, and examining the area under the resulting curve. Models that perform well have a large area under the curve (the incidence of true positives increases faster than the incidence of false positives along a classification cutoff continuum), whereas models that perform poorly have a smaller area under the curve (roughly equal incidence of true positives and false positives along a classification cutoff continuum; Table 2).

Table 2: Relative model performance corresponding to area-under-curve values (after Roomp *et al.* 2010).

AUC	Model performance
0.50 - 0.60	very poor
0.60 - 0.70	poor
0.70 - 0.80	fair
0.80 - 0.90	good
0.90 - 1.00	excellent

2.3.5 Model performance: fish abundance models

We evaluated model fit for abundance models using Wald tests, which tell us whether a model performs significantly better than a null model (Cameron and Trivedi 1998).

Results

We surveyed 98 stream sites over the course of the 2007, 2008, and 2010 seasons. We caught 232 Dolly Varden, 262 slimy sculpin, 73 Arctic grayling, and one round whitefish (*Prosopium cylindraceum*). Electrofishing effort averaged 421 seconds (SE = 10.6 seconds) per site.

3.1 Fish presence models

3.1.1 All fish species combined

The highest-ranked model predicting the probability of occurrence of all fish species combined within the upper Peel Watershed was the *Productivity* model, which incorporated variables for *Vegetation proportion*, *Elevation*, and *Upstream extent* (Tables 3, 4). The model had an AUC value of 0.80, which is considered “good” model performance. As anticipated, the predicted probability of fish presence showed positive relationships between *Vegetation proportion* and *Upstream extent* (Tables 3, 8). We found an unanticipated positive relationship between predicted probability of fish presence and *Elevation*, but *Elevation* was shown to be a non-significant addition to the model. Other models that performed nearly as well were the *Drying*, *Freezing* and *Flooding* hypothesis models (Table 4). The highest-ranked model showed very low probabilities of fish presence in 1st order streams and the upper reaches of many 2nd order streams (Figure 7). Most 3rd and 4th order streams, however, had very high predicted probabilities of fish presence.

3.1.2 Dolly Varden

The highest-ranking model predicting the probability of Dolly Varden presence was the *Stream volume* model, which incorporated only the *Upstream extent* variable (Tables 3, 5). The model had an AUC value of 0.65, which is considered “poor” model performance. The relationship between predicted probability of Dolly Varden presence and Upstream extent was positive, indicating that the probability of Dolly Varden being present increases with stream volume (Tables 3, 9). Other models that performed nearly as well were the *Drying* and *Productivity* hypothesis models (Table 5). The *Stream volume* model predicted probability of Dolly Varden presence near nil in 1st and 2nd order streams (Figure 8). The upper reaches of many 3rd order streams also had very low probabilities of Dolly Varden presence, whereas predicted probabilities in 4th order streams were very high.

Alpine lake outlets – a special case

In only one case did we record fish presence in a 1st order stream. This was a small, high-gradient stream flowing through boulders and cobble, the only outlet of a small alpine lake with no inflows. Unusually, this stream had our highest Dolly Varden count (24 Dolly Varden captured in 517 seconds of electrofishing, or 46 Dolly Varden / 1000 seconds electrofishing effort). Because we did not sample other 1st order lake outlets, and this case was such an extreme outlier, we did not include it in our presence or abundance modeling efforts. Lacking further evidence, we consider alpine lake outlets to be a special case, with the possibility that they support very high Dolly Varden abundance.

3.1.3 Slimy sculpin

The highest-ranking model predicting the probability of slimy sculpin presence was also the *Stream volume* model, incorporating only the *Upstream extent* variable (Tables 3, 6). The model had an AUC value of 0.80, which is considered "good" model performance. The relationship between predicted slimy sculpin presence and Upstream extent was positive, indicating that the probability of slimy sculpin presence increases with stream volume (Tables 3, 10). The other model that performed nearly as well was the *Productivity* hypothesis model (Table 6). The *Stream volume* model predicted very low probability of slimy sculpin presence in most 1st and 2nd order streams, and high probability of presence in 3rd and 4th order streams (Figure 9).

3.1.4 Arctic grayling

The highest-ranked model predicting the probability of Arctic grayling presence was the *Productivity* model, which incorporated variables for *Vegetation proportion*, *Elevation*, and *Upstream extent* (Tables 3, 7). The model had an AUC value of 0.75, which is considered "fair" model performance. Predicted probability of Arctic grayling presence had a positive relationship with *Vegetation proportion* and *Upstream extent*, and a negative relationship with *Elevation* (Tables 3, 11). The other model that performed nearly as well was the *Freezing* hypothesis model (Table 7). Predicted probability of Arctic grayling presence was near nil in 1st and 2nd order streams and very low in most 3rd order streams, but approached one in most 4th order streams (Figure 10).

3.1.5 Presence model maps

We used the highest-ranked fish presence models for all fish species combined, Dolly Varden, slimy sculpin, and Arctic grayling to predict their presence across the entire upper Peel Watershed. As an example, we have presented predictions of fish presence in the vicinity of Michelle Creek (Figs. 6-10).

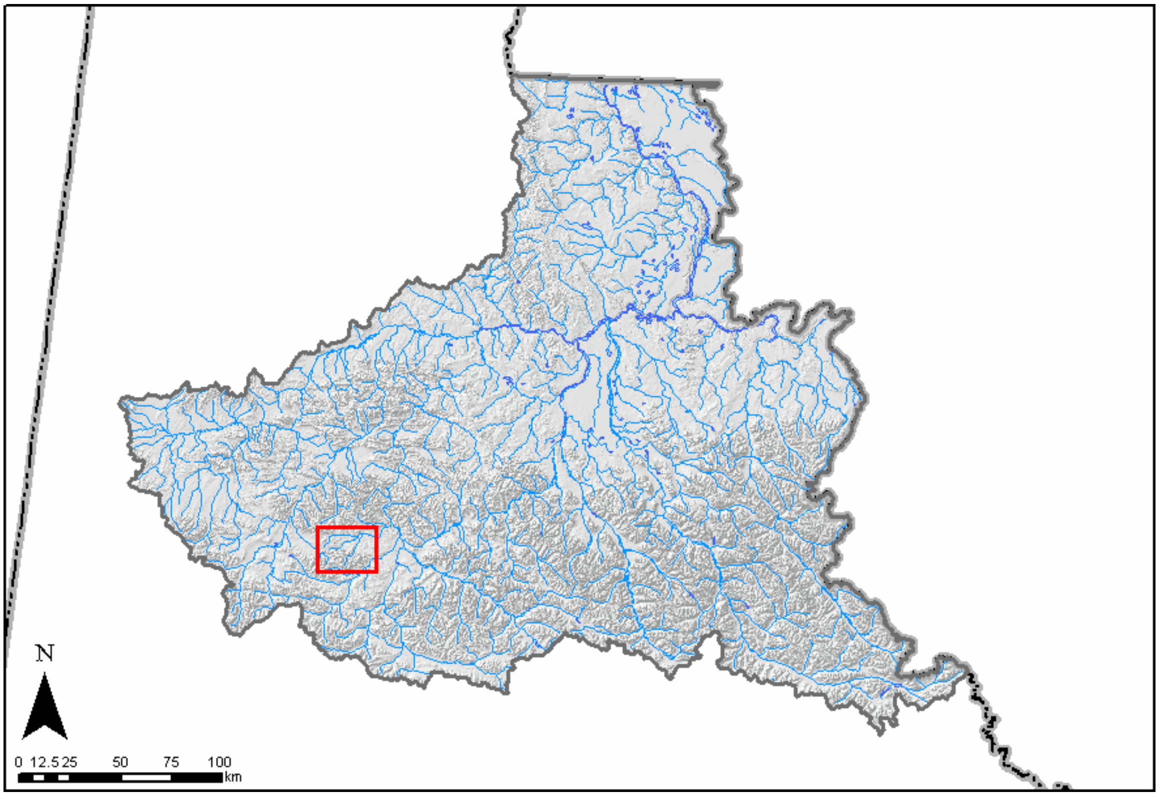

Figure 6. Peel Watershed within Yukon, showing the Michelle Creek area of detail (red outline).

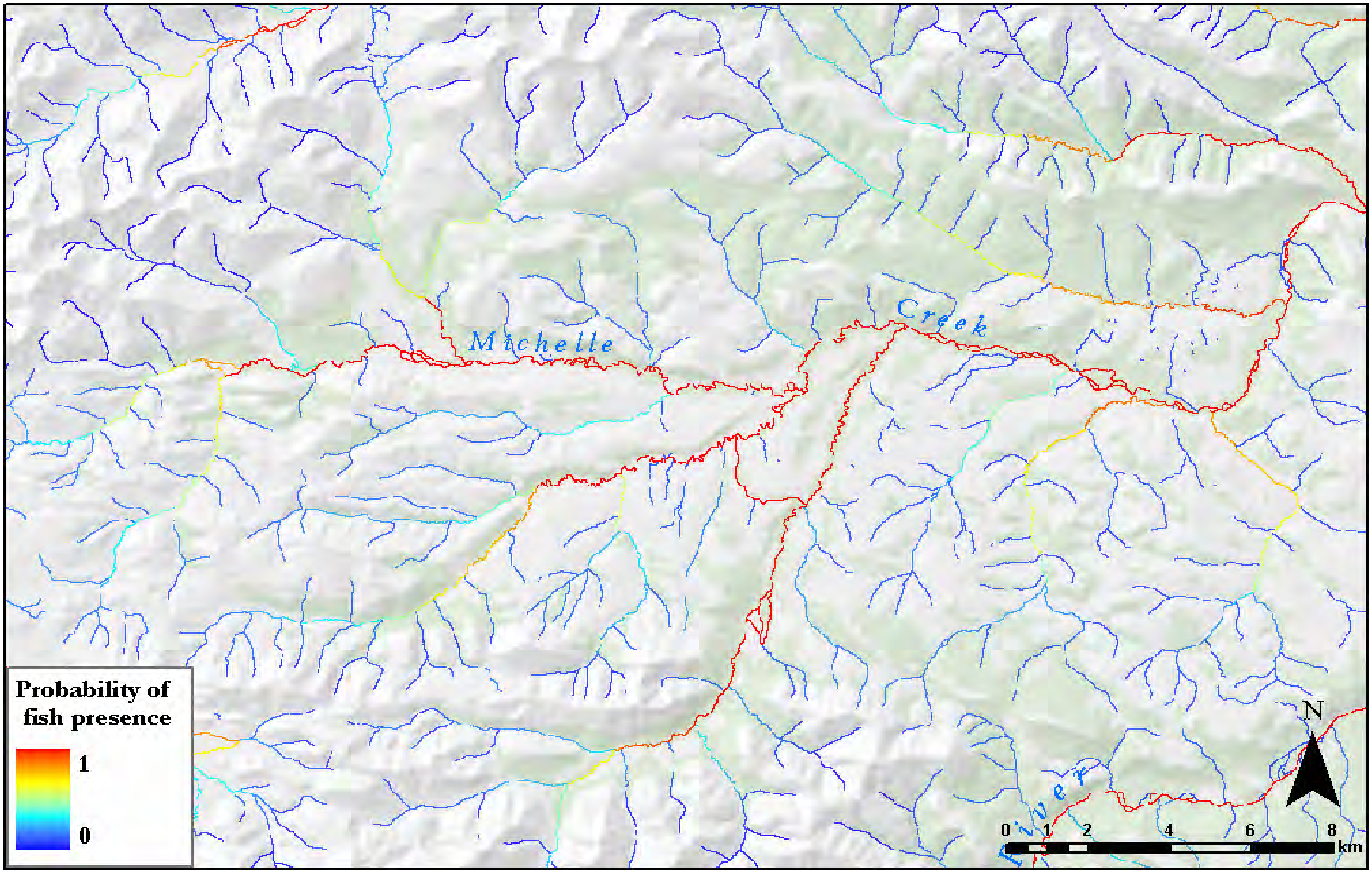

Figure 7. Probability of presence of all fish species combined in the vicinity of Michelle Creek (see Figure 3), as predicted by the Productivity model. Green shading denotes forested areas.

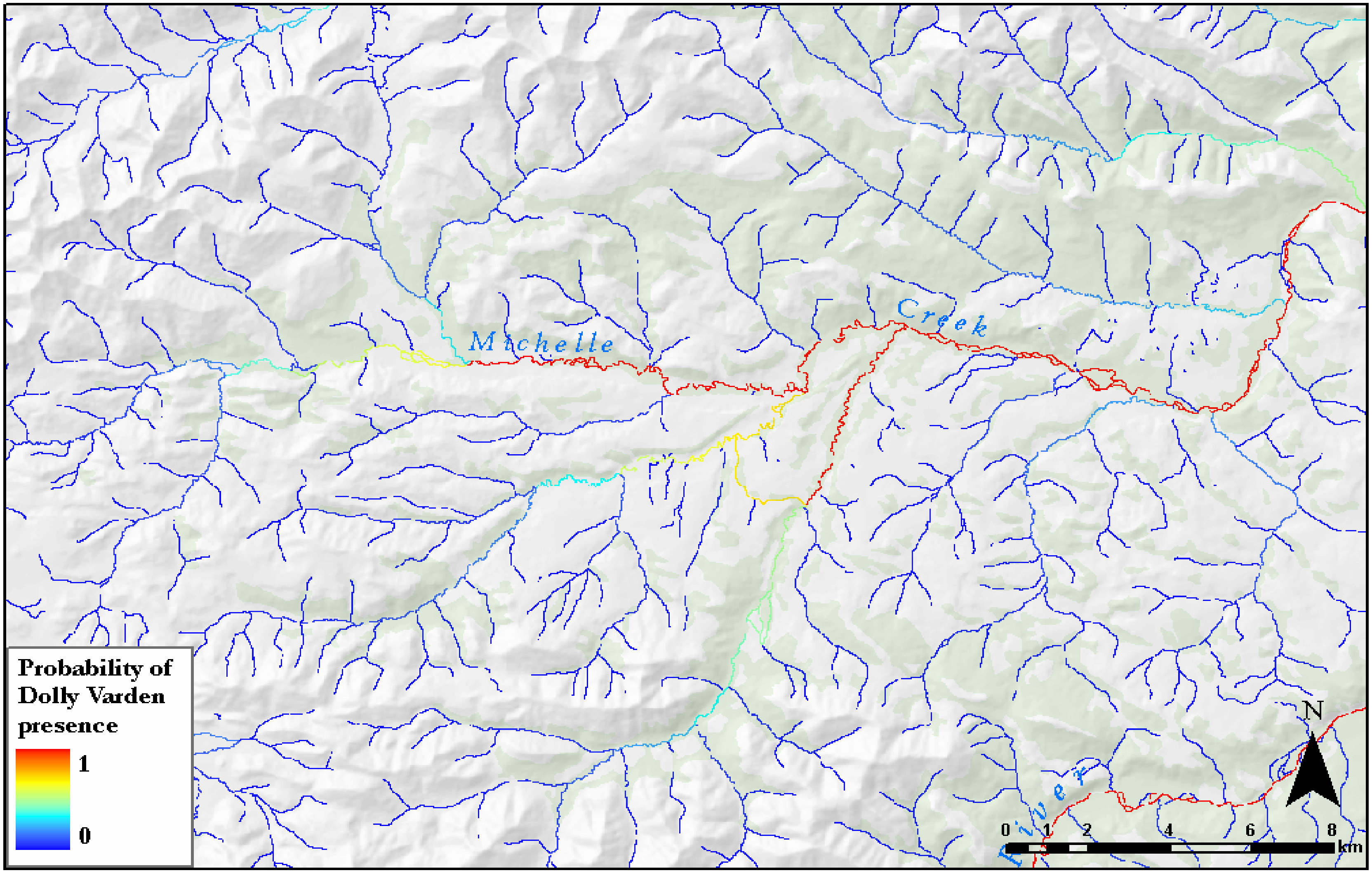

Figure 8. Probability of presence of Dolly Varden in the vicinity of Michelle Creek (see Figure 3), as predicted by the Stream volume model. Green shading denotes forested areas.

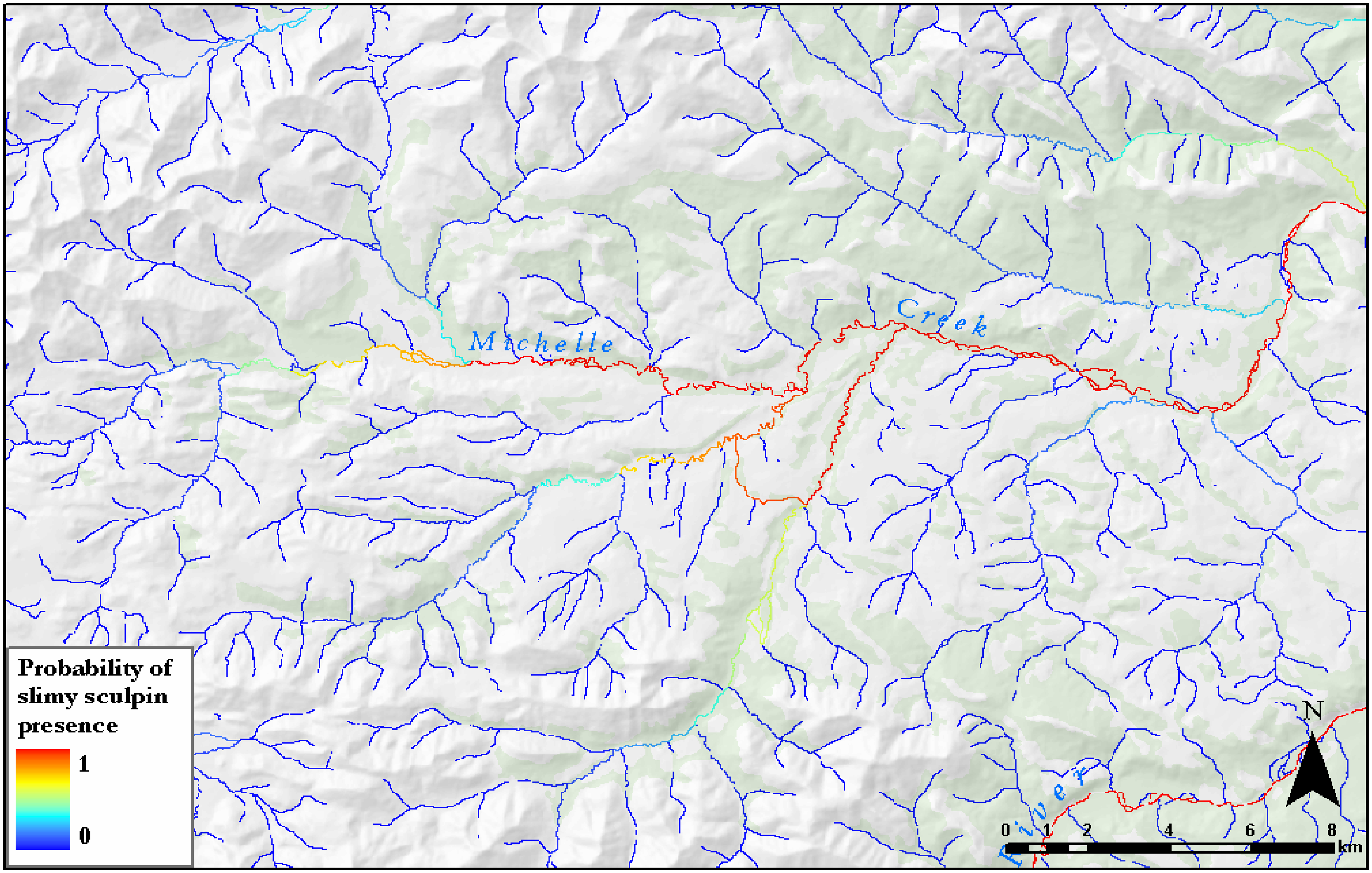

Figure 9. Probability of presence of slimy sculpin in the vicinity of Michelle Creek (see Figure 3), as predicted by the Stream volume model. Green shading denotes forested areas.

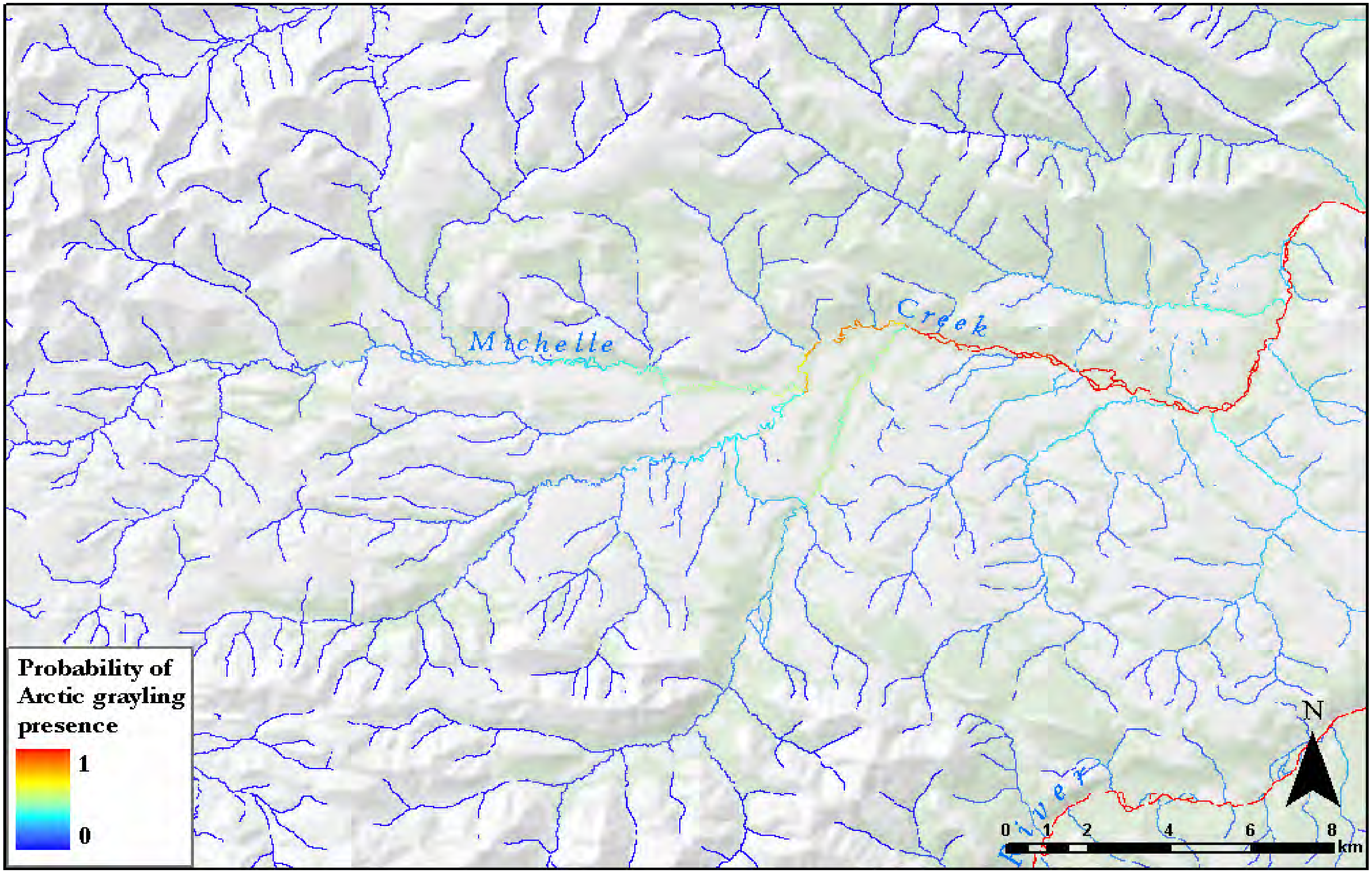

Figure 10. Probability of presence of Arctic grayling in the vicinity of Michelle Creek (see Figure 3), as predicted by the Productivity model. Green shading denotes forested areas.

Table 3. Best models predicting presence and abundance of fish species in the upper Peel Watershed, as chosen using AIC. The effect of each predictor variable on the response variable is indicated as positive [+] or negative [-] and the significance of the variable within the model is given.

Response variable	Species	Best model	Variables					
			Elevation	Mean slope	Upstream extent	Distance to ≥5th order stream	Rock proportion	Vegetation proportion
Presence	All	Productivity	+		+ ***			+
	Dolly Varden	Stream Volume			+ **			
	Slimy sculpin	Stream Volume			+ ***			
	Arctic grayling	Productivity	-		+			+
Abundance	Dolly Varden	Productivity	+ **		+ *			-
	Slimy sculpin	Productivity	-		+ ***			+ ***
	Arctic grayling	Productivity	- **		-			+

Wald significance; 0.05< * <0.10, 0.01< ** <0.05, *** <0.01

3.2 Fish abundance models

3.2.1 Dolly Varden

The highest-ranked model predicting Dolly Varden abundance was the *Productivity* model, which incorporated variables for *Vegetation proportion*, *Elevation*, and *Upstream extent* (Tables 3, 12). While increased Dolly Varden abundance was found to correspond with decreases in *Vegetation proportion*, the relationship was non-significant (Tables 3, 15). The positive relationship between Dolly Varden abundance and *Elevation*, however, was shown to be significant. The model performed significantly better than for a null model (Table 15). Other models that performed nearly as well were the *Stream size*, *Drying*, *Migration*, and *Freezing* hypothesis models (Table 12).

3.2.2 Slimy sculpin

The highest-ranked model predicting slimy sculpin abundance was also the *Productivity* model (Tables 3, 13). In the case of slimy sculpin, the relationship between abundance and the predictor variables was as hypothesized: negative for *Elevation*, and positive for *Vegetation proportion* and *Upstream extent* (Tables 3, 16). *Vegetation proportion* had a particularly strong relationship with slimy sculpin abundance, with small changes in Vegetation proportion modelled to have large effects on abundance. The model performed significantly better than for a null model (Table 16). The *Elevation* coefficient was not a significant addition to the model (Tables 3, 16). Other models that performed nearly as well were the *Flooding*, *Freezing*, and *Stream size* hypothesis models (Table 13).

3.2.3 Arctic grayling

The highest-ranked model predicting Arctic grayling abundance was also the *Productivity* model (Tables 3, 14). While *Upstream extent* appears to have an unexpected negative relationship with grayling abundance, the relationship was non-significant (Tables 3, 17). Model performance was significantly better than for a null model (Table 17). Other models that performed nearly as well were the *Migration*, *Stream size*, *Flooding*, and *Freezing* hypothesis models (Table 14).

Discussion

4.1 Fish presence and abundance models

4.1.1 All fish species combined

The *Productivity* model was the top-ranked model predicting presence of all fish species combined. Not surprisingly, the predicted presence of all fish species combined was more extensive than the predicted presences of individual fish species (Figure 7). Even this model, however, showed very low probabilities of fish presence in 1st order streams and the upper reaches of many 2nd order streams. Most 3rd order streams, however, had probabilities of presence ≥0.50, and 4th order streams had probabilities close to one. The low predicted probability of fish presence in 1st and 2nd order streams is not surprising. Many of these are high-elevation, high-gradient, low-volume streams, some of which have surface water for only a short time each spring, and are poor fish habitat.

While the *Productivity* model was ranked as the top fish presence model for Arctic grayling only (Tables 3, 7), both Dolly Varden and slimy sculpin AIC model evaluations ranked the *Productivity* model as second (behind Stream volume models; Tables 5, 6). Indeed, the difference in model performance between *Productivity* and *Stream volume* models for Dolly Varden and slimy sculpin was insignificant when judged by difference in AIC values (ΔAIC; Tables 5,6). It is not surprising, then, that the *Productivity* model was the highest-ranked model for predicting presence of all fish species combined (Tables 3, 4).

4.1.2 Dolly Varden

The predicted upstream extent of Dolly Varden presence (Figure 8) was considerably lower than that predicted for all fish species combined (Figure 7) and for slimy sculpin (Figure 9). In addition to probabilities near nil in 1st and 2nd order streams, the upper reaches of many 3rd order streams had very low probabilities of Dolly Varden presence. This result is somewhat at odds with the generally understood distribution of Dolly Varden relative to other fish; Dolly Varden appear able to navigate high-gradient streams very effectively, and are more often observed in smaller, higher, less-productive streams than other species (Bryant *et al.* 2004, Wissmar *et al.* 2010). The “poor” predictive nature of the Dolly Varden presence model (AUC = 0.65) may be to blame for the lack of agreement between our model and what others have observed, as none of our candidate models were sufficient to effectively model true Dolly Varden distribution.

Models relating Dolly Varden abundance to habitat variables may have been more accurate than those modelling presence. The best-ranked abundance model for Dolly Varden demonstrated a significant, positive relationship between Dolly Varden abundance and *Elevation*, contrary to our hypothesis of increasing abundance at lower elevations (Tables 3, 15). Dolly Varden's noted ability to inhabit high-gradient streams (Bryant *et al.* 2004, Wissmar *et al.* 2010) may mean they are able to exploit stream reaches where other fish species are scarce or absent, leading to high abundances in these low-productivity streams. Conversely, increased competition from fish such as Arctic grayling may reduce Dolly Varden abundance at lower elevations.

4.1.3 Slimy sculpin

Of the three fish species examined, slimy sculpin were the most likely to be found in upstream areas (Figure 9). Only the presence model for all fish species combined demonstrated higher upstream presence probabilities (Figure 7). These predictions mirror field observations; save for high-gradient, low-volume 1st and 2nd order streams, slimy sculpin were commonly found in the upper Peel Watershed field surveys. The upstream extent of slimy sculpin presence is remarkable, considering that many of these small streams are thought to freeze completely through the winter, and must be recolonized by sculpin moving upstream from winter refugia in larger streams and rivers. While fish such as Dolly Varden can be expected to make long-distance migrations relatively rapidly, the morphology of stream-living sculpins is assumed to limit them to much slower rates of long-distance movement (Hill and Grossman 1987, Schmetterling and Adams 2004), though occasional long-distance movements of 511 m upstream in 207 days (mottled sculpins; Breen *et al.* 2009) and 1711 m downstream in 75 days (Potomac sculpin; Hudy and Shiflet 2009) have been observed. Indeed, the observed and predicted upstream extent of slimy sculpin may indicate that they are able to use smaller, higher-elevation, lower-quality winter refugia than fish such as Dolly Varden, allowing them to effectively recolonize small mountain streams in summer.

The top-ranked model predicting slimy sculpin abundance was largely driven by Vegetation proportion, predicting large increases in sculpin abundance with modest increases in the amount of vegetation surrounding a stream (Table 16). While sculpin presence was common in the upper Peel Watershed, sculpin abundance was highly variable, with many sites having few sculpin, and some sites having many sculpin. The influence of surrounding vegetation, as a source of terrestrial food, a correlate of aquatic productivity, and a buffer against extremes in flow, appears the most important variable in predicting slimy sculpin abundance.

4.1.4 Arctic grayling

Of the three fish species we examined, Arctic grayling were least likely to be found in upstream areas (Figure 10). Only the larger, lower reaches of 3rd order streams were predicted to have probabilities of presence ≥0.50, with probabilities in upstream sections declining rapidly to nil. The probabilities of finding grayling in 4th order streams, as with other species, were very close to one. This reflected observed patterns of grayling presence; most grayling were found in larger, lower-elevation streams with large amounts of surrounding vegetation, often overhanging the stream. The top-ranked model of Arctic grayling abundance also corresponds to the hypothesis that riparian vegetation and elevation determine grayling abundance (Table 13), though the *Upstream extent* term is a non-significant addition to the abundance model (Tables 3, 17).

The "fair" predictive ability of the Arctic grayling presence model (AUC = 0.75) was not unexpected, given the limited amount of data used to construct the model. Of the 98 sites we surveyed for fish presence and abundance, only 10 held Arctic grayling. While the habitat variables we selected may not be adequate to build models with greater predictive power, we suspect that surveying more streams in which grayling are present would greatly improve model performance.

4.2 Ecological implications

Our fish presence models and field observations present evidence for an unanticipated overwintering strategy in slimy sculpin in the upper Peel Watershed. Our models uncovered two patterns that were unexpected: a surprisingly high number of low-order streams had populations of slimy sculpin, and a surprisingly low number of these same streams had Dolly Varden.

While the unexpected predictions of the Dolly Varden presence model may be attributed to its "poor" predictive performance, the modelled distribution of slimy sculpin appears to be an accurate one, borne out by field observations. Considered a relatively sedentary species, slimy sculpin have been used as sentinels of local environments, as they are presumed to live, feed, and reproduce within a limited area and therefore be affected by very local environmental conditions (Gray *et al.* 2004, Rasmussen *et al.* 2009). Indeed, in Yukon, slimy sculpin are described as one of few stream-dwelling fish species that do not make seasonal migrations, and their presence is considered evidence that a stream offers suitable overwintering habitat (von Finster 2003). In contrast to slimy sculpin, Dolly Varden are capable of long-distance annual movements and can navigate high-gradient streams (Bryant *et al.* 2004, Wissmar *et al.* 2010).

Our findings, then, provide two competing hypotheses: either suitable slimy sculpin overwintering habitat exists in many low-order upper Peel Watershed streams, or slimy sculpin make annual migrations from downstream winter refugia to upstream sites. Such migrations would be on the order of kilometres. If slimy sculpin are making these migrations, then our observations and model results suggest that these migrations must be nearly equivalent to those of Dolly Varden, and greater than those of Arctic grayling. Conversely, if slimy sculpin find suitable overwintering sites in low-order streams, then either these refugia are mostly unsuitable for Dolly Varden and Arctic grayling, or Dolly Varden and Arctic grayling disperse nearly as slowly as slimy sculpin. Given their morphological constraints on migration, as compared to fish such as Dolly Varden, the most probable option is that slimy sculpin are able to overwinter in small stream refugia that are unsuitable for other fishes. This could have implications for industrial activities, such as ice bridge construction, that might otherwise assume fish to be absent from small streams in winter. Investigations into fish distribution in winter or early spring would allow for clarification of slimy sculpin overwintering and migration strategies.

4.3 Model assumptions and limitations

4.3.1 Data limitations

Other factors, as well as limited sample size for Arctic grayling, should be considered when interpreting the results of our models. Because we wished to extend our predictions across the entire upper Peel Watershed, we were limited to using predictor habitat variables that were available as watershed-wide GIS data layers, such as elevation, slope, and land cover. Many habitat variables that are potentially important drivers of fish distribution and abundance were not included, simply because we did not have access to the appropriate data. Likely the most significant omissions were location data for barriers to fish movement and aufeis fields. Barriers to fish movement, such as waterfalls or very high gradient reaches, prevent fish from colonizing otherwise-suitable upstream areas. The digital elevation model (DEM) data that we used were too coarse to allow us to reliably locate stream barriers. Aufeis fields—large masses of accumulated ice formed in stream beds by winter overflow (Figure 5)—are indicative of significant groundwater input and the presence of liquid water during winter, and are often important overwintering sites for fish. Without location data for aufeis fields, our models may underestimate fish presence and abundance in their vicinity. We also lacked sufficient information on groundwater inputs and the location of seasonally dry watercourses, two other data sources that could have contributed to our models.

Another limitation springing from our data was the misclassification of braided river channels within the NHN data. The relationship between stream segments within a braided river channel is difficult to define using common stream classification schemes, such as stream order. Because of this, stream segments in braided river channels were not labelled correctly in the NHN data, and we were not able to calculate variables such as *Upstream extent* and *Distance to ≥5th order stream* for these segments. As a consequence, we were not able to make valid predictions about fish distribution and abundance in these braided stream segments. In areas of braided river channel, only model predictions for the main stream channel should be considered valid.

4.3.2 Model application

When we extended our predictions across the entire upper Peel Watershed, we made the assumption that our habitat variables affected fish distribution and abundance in the same way across the whole of the study area. We limited model applicability to the Ogilvie and Mackenzie mountains, with their similar geographical and ecological properties, and distributed our sample sites throughout the study area, in an effort to construct robust, applicable models. The performance of our models, however, may vary across our study area, with the best performance expected in areas with the highest density of sample sites.

Because data on fish distribution and abundance were gathered in late summer, when upstream fish distribution is expected to be at its maximum, our models are applicable to this time period only. We expect that fish distributions in autumn, winter, and spring are much more restricted than summer distributions. By modelling the fish distribution at its expected maximum extent, we can better inform development decisions about effects on all possible fish habitat.

4.4 Recommendations for future spatial modelling

The data collected by our fish sampling methods – numbers of fish caught in a measured amount of electrofishing effort from sites spread across our study area – were well-suited to the logistic and negative binomial regression methods we used to model fish distribution and abundance. In 2007 and 2008, sample sites were also evaluated following the Canadian Aquatic Biomonitoring Network (CABIN) protocol for wadeable streams, which collects data on flow volume, substrate type, in-stream and riparian vegetation, water chemistry, channel morphology, and benthic invertebrates. While these data are informative, they are not useable for the spatial modelling of fish distribution and abundance, as these data do not exist for every stream in our study area. The collection of CABIN data was time-consuming; we were roughly twice as efficient at collecting fish data during 2010 surveys, when the CABIN protocol was not used. The utility and predictive ability of distribution and abundance models is strongly influenced by sample size. In future surveys where the main goal is spatial modelling of fish distribution and abundance, only the most pertinent field data should be collected, to maximize the number of sample sites surveyed.

As high-resolution satellite imagery becomes more readily available, we should consider the use of mid- to late-summer imagery for detecting aufeis fields. In high latitude watersheds, where many small streams freeze completely in winter, the presence and location of suitable overwintering areas for fish has a strong influence on fish distribution and abundance. With suitable satellite imagery available to detect aufeis fields, our current measure of distance to overwintering habitat (distance to ≥5th order stream) could be replaced by a much more precise measure.

Survey plans should be developed with the ecology and habitat requirements of target fish species in mind. While slimy sculpin and Dolly Varden habitat was thoroughly sampled by visiting 1st-4th order streams, sampling efforts were not effective at capturing many sites where Arctic grayling were present. In future surveys, where initial surveys find that target species are scarce within the planned survey areas, we should adapt survey plans to adequately sample that species.

4.5 Conclusions

We used fish presence and abundance data from 98 sample sites to predict fish presence and abundance across the entire upper Peel Watershed, using landscape-scale statistical models. Our models demonstrated species-specific patterns of distribution and abundance, and provided insight on the effects of environmental variables on fish ecology. These modelled relationships can provide the basis for informed decision-making about land use planning, environmental assessment, freshwater fisheries management, and fish conservation.

Developing spatial models of fish distribution and abundance is an effective way of understanding fish populations and their relationship with habitat in large and/or remote areas. These methods are particularly useful in Yukon, where many waterbodies can only be reached by air. In some cases, our models performed poorly. As the quality and availability of large-scale ecogeographic spatial data improves, we expect to improve our ability to precisely and accurately depict fish ecology using spatial models. With the ability to make landscape-scale predictions using data gathered at a set of sample sites, spatial models offer effective tools for management and conservation while requiring modest field effort and expense.

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Appendix

6.1 Presence models – AIC model selection

Table 4. Ranking of candidate weighted logistic regression models predicting probability of presence of fish of all fish species combined in 1st-4th order streams in the upper Peel Watershed. Models are shown with included covariates, number of parameters (*k*), AIC score (AIC), and AIC difference from the best-supported model (ΔAIC).

Model Hypothesis	Model Structure	*k*	AIC	ΔAIC
Productivity	Vegetation proportion + Elevation + Upstream extent	3	64.55	0
Drying	Upstream extent + Distance to ≥5th order stream	2	64.89	0.34
Freezing	Rock proportion + Elevation + Upstream extent + Distance to ≥5th order stream	4	65.62	1.08
Flooding	Rock proportion + Mean slope + Distance to ≥5th order stream + Upstream extent	4	66.26	1.71
Stream size	Upstream extent	1	67.47	2.92
Migration	Distance to ≥5th order stream + Elevation	2	85.37	20.82

Table 5: Ranking of candidate weighted logistic regression models predicting probability of presence of Dolly Varden in 1st-4th order streams in the upper Peel Watershed. Models are shown with included covariates, number of parameters (*k*), AIC score (AIC), and AIC difference from the best-supported model (ΔAIC).

Model Hypothesis	Model Structure	k	AIC	ΔAIC
Stream size	Upstream extent	1	63.88	0
Drying	Upstream extent + Distance to ≥5th order stream	2	64.61	0.73
Productivity	Vegetation proportion + Elevation + Upstream extent	3	64.77	0.89
Flooding	Rock proportion + Mean slope + Distance to ≥5th order stream + Upstream extent	4	66.81	2.92
Freezing	Rock proportion + Elevation + Upstream extent + Distance to ≥5th order stream	4	66.81	2.93
Migration	Distance to ≥5th order stream + Elevation	2	69.83	5.95

Table 6. Ranking of candidate weighted logistic regression models predicting probability of presence of slimy sculpin in 1st-4th order streams in the upper Peel Watershed. Models are shown with included covariates, number of parameters (*k*), AIC score (AIC), and AIC difference from the best-supported model (ΔAIC).

Model Hypothesis	Model Structure	*k*	AIC	ΔAIC
Stream size	Upstream extent	1	38.16	0
Productivity	Vegetation proportion + Elevation + Upstream extent	3	39.17	1.01
Drying	Upstream extent + Distance to ≥5th order stream	2	40.23	2.07
Flooding	Rock proportion + Mean slope + Distance to ≥5th order stream + Upstream extent	4	40.96	2.8
Freezing	Rock proportion + Elevation + Upstream extent + Distance to ≥5th order stream	4	41.98	3.82
Migration	Distance to ≥5th order stream + Elevation	2	44.59	6.43

Table 7. Ranking of candidate weighted logistic regression models predicting probability of presence of Arctic grayling in 1st-4th order streams in the upper Peel Watershed. Models are shown with included covariates, number of parameters (*k*), AIC score (AIC), and AIC difference from the best-supported model (ΔAIC).

Model Hypothesis	Model Structure	*k*	AIC	ΔAIC
Productivity	Vegetation proportion + Elevation + Upstream extent	3	19.1	0
Freezing	Rock proportion + Elevation + Upstream extent + Distance to ≥5th order stream	4	20.88	1.79
Migration	Distance to ≥5th order stream + Elevation	2	21.27	2.18
Stream size	Upstream extent	1	22.02	2.92
Drying	Upstream extent + Distance to ≥5th order stream	2	22.96	3.86
Flooding	Rock proportion + Mean slope + Distance to ≥5th order stream + Upstream extent	4	24.61	5.52

6.2 Presence models – covariate values

Table 8. Model coefficients (β), SE, Wald statistics (*z*; *df* = 1 in all cases), and Wald significance (α) for the best-supported weighted logistic regression model (Productivity model) predicting probability of presence of all fish species combined in the upper Peel Watershed.

Predictor variables	β	SE	*z*	α
Constant	-5.83	2.44	-2.39	0.02
Vegetation proportion	2.4	1.54	1.56	0.12
Elevation	$1.45x10^{-3}$	$1.55x10^{-3}$	0.93	0.35
Upstream extent	$9.62x10^{-5}$	$3.02x10^{-5}$	3.18	0

Table 9. Model coefficients (β), SE, Wald statistics (*z*; *df* = 1 in all cases), and Wald significance (α) for the best-supported weighted logistic regression model (Stream volume model) predicting probability of Dolly Varden presence in the upper Peel Watershed.

Predictor variables	Estimate	SE	*z*	P
Constant	-2.15	$3.79x10^{-1}$	-5.67	<0.01
Upstream extent	$2.33x10^{-5}$	$1.03x10^{-5}$	2.27	0.02

Table 10. Model coefficients (β), SE, Wald statistics (*z*; *df* = 1 in all cases), and Wald significance (α) for the best-supported weighted logistic regression model (Stream volume model) predicting probability of slimy sculpin presence in the upper Peel Watershed.

Predictor variables	Estimate	SE	*z*	P
Constant	-3.17	$5.61x10^{-1}$	-5.65	<0.01
Upstream extent	$3.94x10^{-5}$	$1.38x10^{-5}$	2.865	<0.01

Table 11. Model coefficients (β), SE, Wald statistics (*z*; *df* = 1 in all cases), and Wald significance (α) for the best-supported weighted logistic regression model (Productivity model) predicting probability of Arctic grayling in the upper Peel Watershed.

Predictor variables	Estimate	SE	*z*	P
Constant	-5.56	5.19	-1.07	0.28
Vegetation proportion	7.35	5.72	1.28	0.2
Elevation	-4.39×10^{-3}	2.82×10^{-3}	-1.56	0.12
Upstream extent	8.29×10^{-6}	1.18×10^{-5}	0.7	0.48

6.3 Abundance models – AIC model selection

Table 12. Ranking of candidate negative binomial regression models of abundance of Dolly Varden in 1st-4th order streams in the upper Peel Watershed. Models are shown with included covariates, number of parameters (*k*), AIC score (AIC), and AIC difference from the best-supported model (ΔAIC).

Model Hypothesis	Model Structure	*k*	AIC	ΔAIC
Productivity	Vegetation proportion + Elevation + Upstream extent	3	442.25	0
Stream size	Upstream extent	1	443.04	0.79
Drying	Upstream extent + Distance to ≥5th order stream	2	443.11	0.86
Migration	Distance to ≥5th order stream + Elevation	2	443.37	1.12
Freezing	Rock proportion + Elevation + Upstream extent + Distance to ≥5th order stream	4	444.01	1.76
Flooding	Rock proportion + Mean slope + Distance to ≥5th order stream + Upstream extent	4	445.12	2.87

Table 13. Ranking of candidate negative binomial regression models of abundance of slimy sculpin in 1st-4th order streams in the upper Peel Watershed. Models are shown with included covariates, number of parameters (*k*), AIC score (AIC), and AIC difference from the best-supported model (ΔAIC).

Model Hypothesis	Model Structure	k	AIC	ΔAIC
Productivity	Vegetation proportion + Elevation + Upstream extent	3	376.83	0
Flooding	Rock proportion + Mean slope + Distance to ≥5th order stream + Upstream extent	4	377.69	0.86
Freezing	Rock proportion + Elevation + Upstream extent + Distance to ≥5th order stream	4	378.7	1.87
Stream size	Upstream extent	1	378.73	1.9
Drying	Upstream extent + Distance to ≥5th order stream	2	380.07	3.24
Migration	Distance to ≥5th order stream + Elevation	2	382.44*	5.61*

* the AIC score for the Migration hypothesis model failed to converge on a stable value

Table 14. Ranking of candidate negative binomial regression models of abundance of Arctic grayling in 1st-4th order streams in the upper Peel Watershed. Models are shown with included covariates, number of parameters (*k*), AIC score (AIC), and AIC difference from the best-supported model (ΔAIC).

Model Hypothesis	Model Structure	k	AIC	ΔAIC
Productivity	Vegetation proportion + Elevation + Upstream extent	3	192.24	0
Migration	Distance to ≥5th order stream + Elevation	2	192.28	0.04
Stream size	Upstream extent	1	193.33	1.09
Flooding	Rock proportion + Mean slope + Distance to ≥5th order stream + Upstream extent	4	193.59	1.35
Freezing	Rock proportion + Elevation + Upstream extent + Distance to ≥5th order stream	4	194.08	1.84
Drying	Upstream extent + Distance to ≥5th order stream	2	194.99	2.75

6.4 Abundance models – covariate values

Table 15. Model coefficients (β), SE, test statistics (*z*), and significance (P) for the best-supported negative binomial regression model (Productivity model) predicting abundance of Dolly Varden in the upper Peel Watershed. Also given is the percentage effect of unit change of β on Dolly Varden abundance, given other predictor variables are held constant, ($100\cdot[e^{\beta} - 1]$).

Predictor variables	**β**	**SE**	***z***	**P**	**e^{β}**	**$100\cdot(e^{\beta} - 1)$**
Constant	-9.25×10^{-1}	1.35	-0.69	0.49		
Vegetation proportion	-7.11×10^{-1}	9.50×10^{-1}	-0.75	0.45	0.49	-50.87
Elevation	2.77×10^{-3}	1.09×10^{-3}	2.55	0.01	1	0.28
Upstream extent	9.27×10^{-6}	4.92×10^{-6}	1.88	0.06	1	9.27×10^{-4}

$\theta = 0.20$, $SE_{\theta} = 3.98\times10^{-2}$
Wald statistic = 7.91, *df* = 96, P = 0.05

Table 16. Model coefficients (β), SE, test statistics (*z*), and significance (P) for the best-supported negative binomial regression model (Productivity model) predicting abundance of slimy sculpin in the upper Peel Watershed. Also given is the percentage effect of unit change of β on slimy sculpin abundance, given other predictor variables are held constant, ($100\cdot[e^{\beta} - 1]$).

Predictor variables	**β**	**SE**	***z***	**P**	**e^{β}**	**$100\cdot(e^{\beta} - 1)$**
Constant	-2.58	1.81	-1.43	0.15		
Vegetation proportion	4.05	1.37	2.96	<0.01	57.4	5639.8
Elevation	-1.20×10^{-4}	1.42×10^{-3}	-0.09	0.93	1	-0.01
Upstream extent	2.23×10^{-5}	6.27×10^{-6}	3.56	<0.01	1	2.23×10^{-3}

$\theta = 0.12$, $SE_{\theta} = 2.56\times10^{-2}$
Wald statistic = 24.22, *df* = 96, P <0.01

Table 17. Model coefficients (β), SE, test statistics (z), and significance (P) for the best-supported negative binomial regression model (Productivity model) predicting abundance of Arctic grayling in the upper Peel Watershed. Also given is the percentage effect of unit change of β on Arctic grayling abundance, given other predictor variables are held constant, ($100 \cdot [e^{\beta} - 1]$).

Predictor variables	**β**	**SE**	***z***	**P**	**e^{β}**	**$100 \cdot (e^{\beta} - 1)$**
Constant	2.94	2.5	1.18	0.24		
Vegetation proportion	2.67	1.92	1.39	0.16	14.44	1344
Elevation	-5.39×10^{-3}	2.13×10^{-3}	-2.53	0.01	0.99	-0.54
Upstream extent	-1.14×10^{-6}	8.87×10^{-6}	-0.13	0.9	1	-1.14×10^{-4}

$\theta = 6.11 \times 10^{-2}$, $SE_{\theta} = 1.94 \times 10^{-2}$

Wald statistic = 8.46, $df = 96$, P = 0.01