Title: Optimal sampling methods for modelling the occupancy of Arctic Grayling (*Thymallus arcticus*) in the Canadian Barrenlands

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Abstract

In occupancy models, imperfect detectability of animals is usually corrected for by using temporally-repeated surveys to estimate probability of detection. Substituting spatial replicates for temporal replicates could be an advantageous sampling strategy in remote Arctic regions, but may lead to serious violations of model assumptions. Using a case study of site occupancy of adfluvial young-of-year Arctic Grayling in Barrenland tundra streams, we assessed reliability and efficiency of alternative sampling strategies; i) randomly distributed vs sequential adjacent spatial replicates; ii) visual vs electrofishing surveys; and, iii) spatial vs temporal replicates. Sequential, adjacent spatial replicates produced spatially auto-correlated data. Autocorrelation was relieved using randomly distributed spatial replicates, but using these randomly distributed spatial replicates introduced significant error into estimates of the probability of occupancy in streams. Models designed for spatially-autocorrelated data could minimize this bias. Visual and electrofishing surveys produced comparable probabilities of detection. Spatially-replicated surveys performed better than temporal replicates. The easiest and relatively most cost-effective sampling methods performed as well as, or better than, the more established, expensive, and logistically difficult alternatives for occupancy estimation.

Key-words: Arctic, detection probability, correlated detections, electrofishing, occupancy model, multiscale model, salmonid, spatial replication, streamside visual surveys

Introduction

Freshwater ecosystems in the Arctic are experiencing rapid change in climate, and increasing pressure from ever-growing industrial development. The impacts of anthropogenic stressors on hydrology, water temperature, primary productivity, food web structure, and fish life history are expected to be far-reaching, but have been poorly quantified in these remote and under-studied ecosystems (Prowse et al. 2012, Reist et al. 2006a, Wrona et al. 2006). Comprehensive, standardized datasets are needed for larger-scale integration of data (Reist et al. 2006b), but studies to date on northern fishes have used a multitude of methods and data analysis tools that preclude synthesis on large spatial or temporal scales. Reliable monitoring programs can be costly in terms of both financial and personnel resources; thus, the development of a cost-effective data collection framework for sensitive northern fish populations is essential to their conservation.

In the Barrenlands region, adfluvial populations of Arctic Grayling (*Thymallus arcticus*, Pallas), like other migratory fishes, are sensitive to fragmentation or alterations of the habitats they utilize (Reist et al. 2006b). Young-of-year Arctic Grayling hatch and rear for several months in clear, cool, gravel or rock-bottomed streams (Scott and Crossman 1973) before migrating to overwintering sites in lakes (Jones and Tonn 2004). The Barrenlands landscape is a priority research area for many northern stakeholders including industries, regulators, and Indigenous groups working to mitigate effects of mine- and/or climate-related stream dewatering on populations of adfluvial Arctic Grayling. Despite this, habitat use by young-of-year, adfluvial Arctic Grayling in the Barrenlands has only been investigated in a handful of streams (e.g., Jones and Tonn 2004).

Occupancy, defined as the proportion of area, patches, or sample units that are occupied (i.e., species presence) by a given species, is a natural state variable that can be used in studies of species distribution and range. Occupancy models are a means of deriving information regarding the ecological niche of a species (e.g., Hutchinson 1957), as each species has a unique set of requirements that must be provided by habitats used. Identification of key habitat variables that species respond to can be used to develop habitat models that predict patch and landscape-level occupancy (e.g., see Verner *et al.* 1986; Scott *et al*. 2002). In remote northern environments, it may be particularly advantageous to apply an occupancy modeling framework (MacKenzie et al. 2002) to monitoring programs of landscapes that are too large and logistically difficult to survey extensively. Time and effort spent sampling a site can be reduced by focusing sampling efforts on collection of presence-absence data (instead of abundance data) in a manner that permits inference to the entire area of interest, allowing greater spatial and temporal coverage of a species' distribution across the landscape (Royle and Nichols 2003). Occupancy modeling also explicitly addresses issues of imperfect detection (i.e., false absence) (MacKenzie et al. 2002). Failing to account for false absences can introduce significant error into species distribution models (Gu and Swihart 2004).

The standard method for estimating detection probabilities in occupancy studies involves surveying a site multiple times over a defined 'season' (MacKenzie et al. 2002). Temporally-replicated surveys can be expensive and logistically difficult to implement in remote areas, and resources invested in visiting the same site multiple times within a given timeframe and budget limits spatial coverage of survey efforts. This may be especially problematic in surveys of Arctic fishes because repeat visits must be made within the relatively short ice-free season. Alternatively, the replicate surveys may take the form of randomly-selected spatial replicates within the sample site. Spatial replication is relatively less costly than multiple site visits, but occupancy of each replicate must be independent of the other replicates within the site (Hines et al. 2010), and there must be uniform availability of the species for detection in all spatial sub-units of an occupied site (Kendall and White 2009). These assumptions may be violated when, for example, fish exhibit non-random spatial distributions due to schooling behaviour or when they are subject to downstream displacement in stream ecosystems during high water flow events. As a result of the potential for violation of assumptions, some authors have cautioned against the use of spatial replicates instead of temporal replicates (Kendall and White 2009), yet the actual amount of bias induced by use of spatial replicates in an occupancy study has rarely been quantified using real data. Occupancy models that include a first-order Markovian occupancy process (Gillespie 1992), in which the probability of occupancy in a spatial replicate *j* depends on whether the species was present or absent from the previous spatial replicate *j-1*, have been developed (Hines *et al.* 2010) to handle issues where replicate spatial surveys suffer from a sequential form of spatial autocorrelation, such as may be present when replicates are constrained to linear landscape features like streams.

The probability of detecting a species can also be influenced by the sampling method used (Nichols et al. 2008). Backpack electrofishing and visual counts from streambanks are two commonly used fish detection techniques. The relative efficiency of these two methods in producing abundance estimates is well-characterized (Bozek and Rahel 1991), however, their efficiency in collecting presence-absence data for occupancy studies has not been addressed. Both techniques can suffer from bias resulting from fish size and behaviour, and can only be used in relatively shallow, (<1 m) clear water (Ensign et al. 2002). Electrofishing techniques require less observer standardization, but the electrical current can harm fish (Dwyer and White 1997, Reynolds 1996). Streamside visual surveys are less likely to result in altered behaviour or harm to fish (Brewer and Ellersieck 2011), but the identification of cryptically-coloured fish from the stream bank requires a greater level of skill (Bozek and Rahel 1991). Electrofishing gear is typically heavy (10-15 kg), expensive, and can be difficult to use in remote, rugged terrain, whereas streamside visual surveys do not require the operator to enter the water (when streams are narrow enough) and do not require any specialized equipment (Bozek and Rahel 1991).

Occupancy models were developed using field observations of adfluvial young-of-year Arctic Grayling near a diamond mine development in the Northwest Territories, Canada (DeBeers' Gahcho Kué). The objectives of this study were to quantify bias in occupancy models that results from alternative sampling methods, and specifically compare: 1) models of data derived from surveys of sequential, adjacent spatial replicates to models of data derived from randomly-selected spatial replicates; 2) relative detection probabilities of two commonly used observational techniques for freshwater fishes (backpack electrofishing vs. streamside visual); 3) relative efficiency of using only spatial vs. only temporal replicates to estimate site occupancy; and, 4) using the best models, examine Arctic Grayling young of-year occupancy patterns in streams as they related to habitat characteristics and industrial activities.

Methods

Case study area

The Kennady Lake drainage system is located approximately 280 km north northeast of Yellowknife, Northwest Territories, Canada (63°26'15 N, 109°11'51 W) (Fig. 1) within the sub-Arctic Tundra Shield ecozone. Situated north of the treeline, it is part of a vast area commonly referred to as the Barrenlands region; a semi-arid sub-arctic landscape with low levels of precipitation (between 200-300 mm annually - over half of which falls as snow; (Environment Canada 1991)). The development of a new open-pit diamond mine (Gahcho Kué), required draining a section of Kennady Lake. Prior to development, Kennady Lake provided overwintering habitat for an adfluvial population of Arctic Grayling, as well as several other fish species. The adfluvial Arctic Grayling in this system likely will continue to use the undrained portion of Kennady Lake as overwintering habitat, in addition to several other downstream chain lakes. The study area encompassed Barrenland streams ranging 90-800 m in length, with each end connected to lakes, over approximately 100 km^2. The study area includes streams within the Kennady Lake drainage basin, the Kirk lake drainage basin and the Walmsley Lake drainage basin in the Northwest Territories of Canada.

Field survey methods

Prior to the start of the dewatering of Kennady Lake in 2014, baseline data of occupancy of Arctic Grayling young-of-year in streams were collected. Sixty-seven stream segments (segments=spatial replicates of streams that were each 30 m in length) in nine streams (KLM system; Fig. 1) downstream of Kennady Lake were surveyed four times each during the summer of 2014. In summer 2015, after lake dewatering had begun, 105 segments in 20 streams were surveyed up to three times in three areas: i) streams immediately downstream of Kennady Lake, now affected by dewatering (the original KLM systems, n=9 streams); ii) streams further downstream of Kennady Lake but less likely to have been affected by dewatering (the P system, n=5 streams); and, iii) streams in a reference watershed not affected by dewatering, downstream of Walmsley Lake (the W system; n=6 streams) (Fig. 1).

To quantify the bias introduced to spatially-replicated stream occupancy models by organisms exhibiting a lack of independence in their spatial distribution (project objective 1), sequential adjacent stream segments were surveyed in 2014. The entire length of each stream in the KLM system was surveyed in 30-m segments, of all streams (which served as the spatial replication within the stream) (see Fig. S1a in Supporting Information). Results were compared to those generated by surveying a random selection of segments in 2015; up to six stratified, randomly-selected 30-m segments were surveyed in each stream (Fig. S1b) instead of entire streams. It was necessary to collect these data sets in separate years for them to be considered independent, where *a posteriori* resampling of the data would be equivalent to non-parametric bootstrapping (Efron and Tibshirani 1994), which tends to return the same point estimate as the original data (Kendall and White 2009). To compare relative efficiency of using spatial vs. temporal replicates to estimate stream occupancy (objective 3), we collected both spatially-replicated and temporally-replicated survey data in each survey year (Fig. S1a and b).

To quantify the detection efficiency of two common fish detection techniques (project objective 2), we used both techniques to independently detect fish in all surveys. Field surveys were conducted by moving upstream from the furthest downstream end of each stream. Polarized sunglasses were worn during surveys to reduce glare from the water surface. Streamside visual surveys were conducted from streambanks. Observations were conducted by two observers simultaneously from opposite banks of the stream. These surveys were combined to a single observation of presence or absence of Arctic Grayling young-of-year was recorded for each stream segment (i.e. each spatial replicate). Quantitative estimates of variables that may affect the probability of detection were recorded, including cloud cover and surface visibility (glare and turbulence; see Table S1). Starting again at the furthest downstream end of each stream, single-pass electrofishing surveys were conducted moving upstream using a Smith-Root LR-20B backpack electrofisher with a 6-inch anode ring (Voltage – 990 V; Duty Cycle – 50%; Frequency – 35, 0.20 A output). The backpack operator and netter moved upstream together using a zig-zag pattern to shock fish, sampling micro-habitats proportionally. Low specific conductivity of stream water (10-15 $\mu S\ cm^{-1}$) limited the effective range of the electrofisher to approximately 2 m. Presence or absence of Arctic Grayling young-of year was recorded for each 30-m stream segment.

Habitat variables hypothesized to affect occupancy or detection of Arctic Grayling young-of-year were collected from each stream. Covariates that were expected to affect detection of fish were assessed at the scale of the individual survey (see Table S1), whereas covariates expected to affect the occupancy of fish in streams were measured at each stream segment (except discharge and distance to overwintering habitat), and averaged to produce a single value representative of the entire stream.

Proportion of stream margins with floodplain wetlands (defined as the presence of shallow, standing surface water over hydric soils, adjacent to the main stream channel, (Tiner 1999)), proportion of stream margins with undercut banks (defined as a stable bank which overhangs a stream (Dohner et al. 1997), and percent cover of vegetation types (emergent, submerged and good overhanging vegetation (Nielson and Johnson 1983)) were estimated visually. Stream width (tape measure), depth, and velocity (Hach FH950 handheld flow meter mounted on a wading rod) were also quantified. Distance to overwintering habitat was assessed as the minimum number of lake crossings required for Arctic Grayling young-of-year to reach lakes with overwintering habitat (<4 m in depth which included Kennady Lake, Lake M4, Lake 410, Kirk Lake and Walmsley Lake). Discharge was assessed using the United States Geological Survey mid-section method (adapted from (Buchanan and Somers 1969) at a single fixed location for each stream. All covariates were standardized to z-scores prior to analysis and checked for excessive collinearity. Those found to be highly correlated (correlations ≥ 0.50) were not included together in a single model, but considered only in competing models to prevent overestimation of probability of occupancy or detection.

Statistical analysis

Following MacKenzie et al. (2002), models of probability of Arctic Grayling young-of-year occupancy in streams (herein the term "probability of occupancy" will always refer to occupancy of Arctic Grayling young-of-year in streams, unless otherwise specified) were assessed using the occupancy modeling estimation and information theoretic approach. To estimate the relative utility of using sequential spatial replicates vs randomly-selected spatial replicates (objective 1), and the relative utility of using visual surveys vs. electrofishing surveys (objective 2), we modelled the probability of occupancy of Arctic Grayling young-of-year with hierarchal models that utilized all data from spatially- and temporally-replicated surveys (data configurations shown in Fig. S1 a and b) for each observational technique (visual and electrofishing) and for each year (2014 and 2015). Four hierarchical data sets were created and used in modelling: 2014-visual hierarchical, 2014-electrofishing hierarchical, 2015-visual hierarchical and, 2015-electrofishing hierarchical. Each of these four data sets was modeled by testing the relative fit of three *a priori* candidate model structures and evaluated using the adjusted Akaike information criterion (AIC_c; using the number of stream segments as the sample size). The difference in AIC_c values was used to provide a relative weight-of-evidence for each candidate model structure (w_i) for each data set. All modeling was performed using the program PRESENCE v10.7 (Hines 2006).

The first candidate hierarchical spatial-temporal model structure was a simple "multi-season"-style model, [ψ(.), γ(.), ε(.), *p*(.)], (referred to as Candidate Model 1: Open Occupancy, see Supplemental Data S1 in Supporting Information for more details on each of the candidate models and explanations of variables). These models are typically used when surveys are repeated annually (or "seasons"), but in the present study we treated each survey period within each of 2014 and 2015 as a "season". Spatial replication within each season was used to assess probability of detection, and results were used to provide guidance on the most appropriate timing for surveys if only one spatially-replicated survey were to be conducted in each year. Two additional candidate models were used to approximate a possible lack of independence in occupancy of segments within streams, which would test whether spatial heterogeneity of fish in the streams existed, and was not explained by habitat covariates, and if the randomly-selected spatial replicates survey style alleviated spatial dependency. A multi-scale occupancy model, [ψ(.), θ(segment), *p*(.)], (referred to as Candidate Model 2: Clustered Spatial Correlation) was used to approximate nested spatial scales in the sampling design; stream segments (θ) were nested within streams (ψ), and streams were nested within survey period. A multi-season Markovian occupancy model structure, [ψ(.), θ_0(.), θ_1(.), γ(.), ε(.), *p*(.), θ_0*π(=0)], (referred to as Candidate Model 3: Sequential

Spatial Correlation with Open Occupancy) was used to test downstream spatial autocorrelation in the occupancy of replicate segments within streams. In this model, a first order Markovian spatial process is used; the probability of occupancy of Arctic Grayling young-of year in a stream is decomposed into three components - occupancy, ψ, and two availability variables given absence or presence in the adjacent stream segment, θ_0 or $\theta_{1,}$ respectively (Hines 2010).

The relative rankings of the three candidate models described above were used to address objective 1. If spatial heterogeneity existed in the occupancy of fish in streams, then candidate model 2 (clustered occupancy) or 3 (sequentially clustered occupancy) should rank highest by AIC for the 2014-visual hierarchical and the 2014-electrofishing hierarchical data sets in which sequential spatial surveys were used (Hines et al. 2010). If spatial heterogeneity exists in the occupancy of fish in the study streams, and the use of randomly-selected spatial replicated surveys, as were used in 2015, ameliorated the effect of this spatial heterogeneity, then candidate model 1 (open occupancy-no clustering in occupancy) should rank as the highest model by AIC for the 2015-visual hierarchical and 2015-electrofishing hierarchical data sets, suggesting that randomly-selected spatial segments may be a useful survey design for Arctic stream fish.

Using the best of the three candidate hierarchical models as selected by AIC_c ranking, a benchmark hierarchical model was produced for each of the 4 data sets using a sequential model-building strategy to account for non-random (i.e., resulting from biological or measurement covariates) variation in probability of occupancy or detection. The probability of occupancy was modelled as a function of stream-level biological covariates, and the probability of detection was modelled as a function of segment-level measurement parameters. First, a detection (*p*) model was built using all subsets of covariates for the detection parameter (2014=2 detection covariates, 4 models; 2015=4 detection covariates, 16 models), while holding all other model parameters constant. Occupancy models were then constructed using all covariates singly (due to small sample sizes) on the large-scale occupancy parameter, ψ (2014=12 covariates, 48 models; 2015=8 covariates, 32 models), while holding *p* at the most parsimonious model. Multi-model inference was achieved by averaging β parameter estimates and estimated probability of occupancy of streams (ψ) of all models having ΔAIC_c estimates within 2 of the top-ranked model (Richards 2005). Unconditional standard errors were estimated using the delta method (Falke et al. 2012). The importance of covariates was estimated based on the relative difference of model-averaged β estimates from zero (0=no importance). Beta coefficients for these benchmark hierarchical models are presented in Table S2 in the Supporting Information.

Objective 2 of this study was assessed by comparing the mean (± 95% confidence intervals) probabilities of detection of Arctic Grayling young-of-year produced by the best 2014-visual hierarchical model vs. the best 2014-electrofishing hierarchical model, and by comparing probabilities of detection produced by the best 2015-visual hierarchical model vs. the best 2015-electrofishing hierarchical model. Because we cannot know the true probability of detecting Arctic Grayling young-of-year, we were only able to assess how similar the probabilities of detection for each observational method were to each other and how small the range of error was for each observational method. If the two observational methods produced similar probabilities of detection within the same year, then the prudent choice of the "best" observational method would be the one that is relatively less expensive in terms of effort and money, and produces the smallest amount of error in the estimates pf probability of detection and occupancy.

We addressed objective 3 by comparing relative amount of bias in probability of occupancy produced from models applied to a simulated temporal-replicate-only data set (Fig. S1 c) vs a representative spatial-replicate-only data set (Fig. S1 d). Data from the 2015 survey campaign were used. Here, bias refers to differences in probability of occupancy relative to estimates produced by the assumed best (benchmark) hierarchical spatial-temporal model. To simulate a temporally-replicated data set, presence/absence data from each spatial replicate within a stream were condensed to a single presence/absence data point that represented the entire stream for each of the three sampling periods in 2015. This data set thus consisted of presence/absence data for 20 streams visited up to three times in 2015. To represent a spatially-replicated data set, data from the second sampling period of 2015 were used. This data set consisted of presence/absence data for 20 streams, with up to six segments surveyed without temporal replication. Four datasets were thus produced from the 2015 survey data, 2015-visual-temporal only data (configuration c in Fig. S1), 2015-visual-spatial only data (configuration d in Fig. S1), 2015-electrofishing-spatial only data (configuration c) and, 2015-electrofishing-temporal only data (configuration d). Small sample size (n=9 streams) precluded conducting the same analysis on data collected in 2014. Each of these data sets was modeled by evaluating the relative fit of two *a priori* candidate model structures using AIC_c, which were single season versions of the candidate models described in the previous model set. The two candidate models included a simple single-season model, [ψ(.), p(.)], and a single-season with correlated detections model, [ψ(.), θ_0(.), θ_1(.), p(.), $\theta_0 * \pi(=0)$], and the sequential model-building strategy outlined earlier in the methods was used. Probabilities of occupancy produced by the best model of each of the 2015-visual-temporal only data (configuration c, Fig. S1) and 2015-visual-spatial only data (configuration d, Fig. S1) were compared to the probabilities of occupancy produced by the benchmark hierarchical model of the 2015-visual hierarchical data (configuration b, Fig. S1). This was accomplished by calculating the root mean square deviance (RMSD) ± 95% confidence intervals. Again, we assumed that the benchmark hierarchical occupancy models produced the truest estimates of site occupancy. Similarly, probabilities of occupancy of streams produced by the best model of each of the 2015-electrofishing-temporal only data (configuration c, Fig. S1) and the 2015-electrofishing-spatial only data (configuration d, Fig. S1) were compared to the probabilities of occupancy produced from the benchmark hierarchical model of the 2015-electrofishing hierarchical data set (configuration b, Fig. S1).

AIC assumes that the candidate model set contains at least one model that fits the data adequately; AIC is used to select the best model, but this is no assurance that the selected model is a good model, and substantial lack of fit can lead to inaccurate inferences (Anderson et al. 1994). Given the relative novelty and complexity of the models used in this study, robust methods available for testing the goodness-of-fit of the models have not yet been developed (pers. communication, D. MacKenzie). A qualitative testing procedure was used to indirectly assess the goodness of fit of the *a priori* candidate (or global) model for the hierarchical benchmark model selection for each of the 4 hierarchical data sets (Cooch 2012). If the fit of the benchmark global models (which contain all possible parameters) is adequate, all subsets of these models are assumed to also fit the data because they originate from the global model (Burnham and Anderson 2002). The quasi-likelihood estimation parameter (QAICc, (Wedderburn 1974) is typically calculated as a correction for overdispersion based on the parametric bootstrapped goodness-of-fit chi-squared statistic ($\hat{c}$). We arbitrarily set the $\hat{c}$ to values of 1 (perfect fit) to 3 (overdispersed), in increments of 0.25, to see how this affected the relative ranking of candidate models. By adjusting $\hat{c}$ to higher values, suggestive of a lack of fit of the models, the model selection becomes more conservative, which tends to favour models with less parameters. If overdispersion exists within the model set, the relative weightings and order of the candidate models change with small changes in $\hat{c}$, indicating a lack of fit of the *a priori* model structures, and indicating that the data may be too sparse for robust modelling. We found that the rankings of the *a priori* candidate sets did not change with changes in $\hat{c}$, lending some measure of confidence that the top-ranked models were a reasonable fit for the data (Cooch 2012).

Results and discussion

Occupancy modelling using sequential, adjacent spatial replicates vs. randomly-selected spatial replicates

The most supported model of the 2014 visual and electrofishing hierarchical data sets was Candidate Model 3: Sequential Spatial Correlation with Open Occupancy, indicating that sequential spatially replicated surveys of adjacent stream segments produced spatially auto-correlated data sets (Table 1). The presence of Arctic Grayling young-of-year in each stream segment was likely influenced by the presence of young-of-year in the upstream segment. In 2015, the selection of random segments resulted in segments being separated by an average distance 20 m (or approximately 0.7 segments, where one segment=30 m). Spatial auto-correlation was apparently relieved by the random spatial replicate selection process implemented in 2015, as the AIC analysis of the 2015 hierarchical data sets (both visual and electofishing) indicated that the best supported model was Candidate Model 1: Open Occupancy. Thus, when adjacent spatial replicates were surveyed, the presence of fish in these replicates was not independent of the presence of fish in the upstream segment. However, when we instead surveyed only a subset of randomly-selected, non-adjacent spatial replicates the spatial dependence of the presence of fish in spatially replicated surveys was ameliorated. These findings suggest that either the area occupied by an interacting group of Arctic Grayling young-of-year, or the relative size of suitable summer rearing habitat patches used by groups of Arctic Grayling young-of-year in a stream, could be larger than 30 m (the size of the segments used as replicates), but smaller than 50 m (the average distance between replicates in 2015 plus the size of the replicate). The home range of adfluvial populations of adult European Grayling (*Thymallus thymallus,* a sister species of the Arctic Grayling) in streams has been observed to be approximately 75-100 m, although daily movements ranged between 15-18 m (Nykänen et al. 2004). The home range of adfluvial populations of Arctic

Grayling appears to be less well characterized, but the typical size of cohesive groups of interacting Arctic Grayling young-of year in an Alaskan stream ranged between 4-52 m (Hughes and Reynolds 1994).

Probability of detecting fish with visual vs. electrofishing observational methods

In both 2014 and 2015, probabilities of detecting fish using streamside visual surveys were nearly identical to those using electrofishing surveys (Fig. 2A and 2B). Probability of detection with electrofishing surveys was 3.3 % higher in 2014 and 3.4 % lower in 2015 than with visual surveys ($p=0.0004$, $n=4$ temporal replicates and $p=0.0003$, $n=3$ temporal replicates, respectively, paired t-tests). While these results are statistically significant, we believe that a 3-4% difference in detection probability is trivial, and that either survey method would produce similar quality of data. Overall, detection probability was higher but more variable in 2014, averaging 54 ± 5%, compared to 40 ± 2% in 2015.

In the surveys performed prior to the start of the dewatering of Kennady Lake (2014 surveys), there was improved probability of detection at water velocities above 10 cm/s, and the effect of water velocity on detection was nearly identical between the two sampling methods (Fig. 2C). This may reflect the somewhat poor swimming ability of fry at higher water velocities. Small Arctic Grayling young-of-year are poor swimmers and have previously been observed to prefer water velocities between 0-10 cm s^{-1} (Jones and Tonn 2004). At water velocities above this preferred range, Arctic Grayling young-of-year may have been easier to detect because they were less able to swim quickly to a refugium in the higher water velocities.

There was no apparent effect of water velocity on probability of detecting fish after the start of dewatering in 2015. Average water velocity in stream segments was higher in 2015 (33 cm s^{-1}) than in 2014 (8 cm s^{-1}), and was above the apparent threshold of 10 cm s^{-1} for maximum probability of detection in 2014 (Fig. 2C). The depth of stream segments was the only variable that appeared to affect probability of fish detection in 2015 (Fig. 2D). Observers likely had greater difficulty in detecting fish in deeper waters; the magnitude of this effect was greater for streamside visual surveys than for electrofishing surveys. Stream segment depths in the KLM system were on average 10 cm deeper in 2015 (26-54 cm) than in 2014 (18-44 cm), where 10 cm total was observed as the optimum water depth for Arctic Grayling young-of-year in another Barrenlands stream system (Jones and Tonn 2004). There was likely much less habitat of suitable depth available in 2015, which may explain why depth affected probability of detection in 2015 but not in 2014. The increase in water depth of the KLM streams in 2015 was likely partially a result of mine operations; water from Kennady Lake was pumped across a berm into a lake that drains into stream K5 (Fig. 1). Natural hydrological variability could also have affected stream depth. Water depths in the KLM system in 2015 were within the range of water depths observed in the P and W systems (see Table S1), and summer precipitation was higher in 2015 (at 79.2 cm) than in 2014 (at 58.4 cm) (Environment Canada 2016). Summer precipitation can strongly influence runoff and flooding into streams in the Barrenlands region (Marsh et al. 2008).

Streamside visual survey methods produced lower estimates (11 ± 4% lower) of the probability of occupancy than electrofishing methods. Although estimates of the probability of occupancy generated by models of streamside visual surveys were more variable than those generated by electrofishing surveys, the estimates of the probability of occupancy from streamside visual surveys were overall more similar to the naïve observations of fish presence in streams (Fig. 3A and B), and better able to distinguish sites where Arctic Grayling young-of-year appeared to be absent. Currently, electrofishing is regarded as the most effective monitoring technique of fish assemblages (Poos et al. 2007), however, the present study suggests that this convention may not hold when the monitoring goal is landscape-scale presence-absence of fish, as opposed to estimates of abundance. While subtle differences in the two observational methods were apparent, we think that ultimately, the visual and electrofishing surveys produced similar enough estimates of probabilities of both detection and occupancy that they could be considered as equivalent methods in terms of quality of data produced. However, the streamside survey method offers several logistical advantages. Streamside surveys are much less likely to disrupt or injure to fish, the cost of purchase and transport of gear is minimal, observers are not required to maneuver with heavy gear in the stream, and two observers can conduct independent streamside surveys, effectively doubling the data produced per unit of survey effort. In contrast, electrofishing surveys require two observers (an operator and a netter) to conduct a single survey.

Relative bias in occupancy models when using spatially replicated surveys vs. temporally replicated surveys

Estimates of probability of occupancy and detection produced from models of only spatially-replicated data better represented the benchmark hierarchical models (having open occupancy) than models using only the temporally-replicated data. Detection probabilities were comparable between the hierarchical and spatially-replicated data sets (p of ~0.50), whereas the temporally-replicated data sets appeared to have much higher detection probabilities than the benchmark hierarchical models (Fig. 4A). The overestimation of detection probabilities in the temporally-replicated models likely resulted from combining the data from all spatial replicates into a hypothetical single survey; the probability of detection for the temporally-replicated model applies at the scale of the stream whereas the probability of detection for the spatially-replicated and benchmark hierarchical models apply at the scale of the spatial replicate; the30-m segment. As such, we do not suggest that differences in probability of detection between spatially and temporally replicated models should be interpreted as one method producing better probabilities of detection over the other.

Both the single period of spatially-replicated surveys and the condensed temporally-replicated surveys produced positively biased and more variable probabilities of occupancy of streams than the benchmark hierarchical model. On average, models of the spatially-replicated streamside visual surveys overestimated the proportion of streams occupied by 28.7 ± 5% compared to the hierarchical spatially/temporally-replicated model (Fig. 4B). Spatially-replicated electrofishing surveys overestimated probabilities of occupancy by 32.1 ± 9.4% compared to hierarchical spatially/temporally-replicated electrofishing surveys (Fig. 4B). Temporally-replicated streamside visual and electrofishing surveys resulted in greater overestimations of the probability of occupancy (49.6 ± 5.9% and 43.3 ± 12.7%, respectively; Fig. 4B). Due to unequal sample sizes (spatial: n=6, and temporal: n=3) these results do not necessarily disagree with previous occupancy studies, which report that spatial replication may not be a robust substitute for temporal replicates (Kendall and White 2009). Models of the spatially-replicated streamside visual survey data set were re-run using only 3 replicates, and the overestimation of the probability that streams are occupied that was produced by the equalized replication of spatial surveys increased from 28.7% to 40.3%; however, this is still a better estimate of the probability of occupancy than the temporally-replicated streamside visual surveys (at 49.6% overestimated probability of occupancy relative to the benchmark model).

Bias (compared to the benchmark hierarchical models) in the estimates of probability of occupancy was greater for streams in the system affected by the draining of the upstream lake (KLM system) compared to the control (P and W) streams (Fig. 4B). Spatially-replicated streamside visual surveys produced the most consistent (although still somewhat overestimated) estimates of probability of occupancy of streams in the KLM system and the control streams. All other combinations of survey method and replications failed to detect the probable decline in stream occupancy in the KLM system resulting from alteration of water flow in the area downstream of Kennady Lake in 2015 (see presence data in Fig 3). In any monitoring scenario, detecting even small declines in affected populations of animals is of paramount importance. Given the relatively higher quality data produced at lower financial and human costs, when the hierarchical spatial/temporal survey style is not economically feasible, the recommended survey method for detecting changes in the occupancy of streams by Arctic Grayling young-of-year is streamside visual surveys.

Lake dewatering effects on downstream populations of Arctic Grayling

Results from the hierarchical model showed that during the summer of 2014, prior to the dewatering of the upstream Kennady Lake, the probability that streams in the KLM system were occupied by Arctic Grayling young-of-year was on average 78 - 89% (Fig. 3A) (each data range in this section gives the estimate from the streamside visual method followed by the estimate from the electrofishing method from the hierarchical model). There was a 28 -38% chance that a stream would become unoccupied by fish between survey periods. There was a fairly narrow range of abiotic and biotic conditions in the KLM streams during the 2014 surveys (see Table S1); conditions were relatively uniform across streams and were well within the ranges reported by Jones & Tonn (2004) as being suitable for use by young-of-year Arctic Grayling in Barrenland streams. Water velocity in streams early in the season (Fig. 5A) had the strongest influence on the probability of occupancy, with decreasing probability of occupancy as water velocities increased from 0.05 to 0.2 m/s. This is nearly identical to the findings of a previous study conducted on Arctic Grayling young-of-year (Jones and Tonn 2004). Overall, the ranges of ideal depths and velocities in streams in the KLM system in 2014 provided a great deal of suitable Arctic Grayling young-of-year rearing habitat.

After the start of the dewatering of Kennady Lake in 2015, the probability of streams being occupied by Arctic Grayling young-of-year in the affected streams (KLM system) was lower. The probability that streams were occupied was only 31-39% (compared to 78-89% prior to dewatering). There was negligible probability of occupancy in several streams of the KLM system, including K5 (the first stream immediately downstream of Kennady Lake), and only very small portions of streams M3, M2 and M1 were likely to have been occupied (Fig. 3B). The probability of occupancy in the downstream control P system and the unconnected control W system was higher than in the affected KLM system; averaging 48-82% and 40-73% respectively, despite these streams having otherwise similar habitat characteristics to the KLM system (see Table S1). Only one control stream, P8 had no observations of Arctic Grayling young-of-year. Stream P8 was also the deepest (60 cm) and had the fastest average water velocity (1.02 m/s) of all the streams sampled in 2015. Within the affected KLM system, stream L1B had the highest probability of occupancy (94%, Fig. 3B) and was also both the shallowest stream in July (average of 24 cm), and had the lowest amount of connected wetlands (16%).

Greater water depths early in the open-water season (early July) likely reduced the probability that Arctic Grayling young-of-year would occupy a stream throughout the summer of 2015 (Figs 5B and 5C). Unlike the conditions prior to dewatering in 2014, after dewatering activities had begun there was a slightly positive relationship between increasing water velocity and Arctic Grayling young-of-year probability of occupancy (Fig. 5C). Water velocities in 2015 were a great deal higher in the affected KLM system than the previous year (see Table S1), although within the range of water velocities observed in the two control (P and W) systems. Jones and Tonn (2004) reported that there was clearly a weaker preference for optimal water velocities (0.1 m s^{-1}) over optimal water depths (10-20 cm) for larger Arctic Grayling young-of-year in Barrenlands streams. With shallow habitats in short supply, Arctic Grayling young-of-year may have been forced to tolerate less optimal water flows in the shallowest areas of the streams in favour of avoiding predators, such as Northern Pike, inhabiting deeper water.

Although water flow in the affected streams in the KLM system in 2015 was within the range observed in control streams, the area of wetlands surrounding the streams and amount of submerged vegetation (vegetation may have become submerged as water moved out laterally from the flooded streams) was higher in the affected KLM system than in the control streams. Where stream water was deeper, there was a greater prevalence of floodplain wetlands along the sides of the stream channel (R^2=0.50, Fig. 5B), coincident with a declining probability that young-of-year Arctic Grayling were present in the stream. The area of wetlands surrounding the streams in the KLM system was much higher after lake dewatering began in 2015 (16-50%) than prior to dewatering in 2014 (0-34%). Given the relatively flat landscape, the excess discharge of water into the system as a result of the dewatering of Kennady Lake likely moved out laterally from streambanks of the affected KLM streams, to fill wetlands instead of significantly increasing the depth of these streams. Based on the findings of this study, the persistence of this Barrenlands population of Arctic Grayling should be ensured if appropriate, site-specific targets of minimum, maximum and ideal water depths and velocities are established and closely monitored in streams immediately downstream of dewatering activities.

Implications for monitoring

The design of a cost-effective monitoring plan is crucial to the protection of animals in areas affected by anthropogenic activities. An occupancy-modelling framework was used to provide guidance on several common issues in the prediction of habitat use by a sentinel and valued species of fish, including imperfect detection, appropriate sampling methods and the best allocation of efforts spatially and temporally during very short seasons in difficult and remote terrain. Currently, we know of no other studies that have addressed issues of sequential spatial correlation in occupancy modelling of stream fish populations, given the inevitability that the standard method of observing fish while walking along the stream will produce spatially auto-correlated, and thus biased, estimates of site occupancy (Hines et al. 2010).

Streamside visual surveys performed similarly to electrofishing surveys for Arctic Grayling young-of-year in these shallow streams. Given the minimal potential for injury to imperilled fish populations, we recommend the use of the less invasive streamside visual survey method over electrofishing for occupancy models of fish in non-turbid streams. The comparison of spatially-replicated with temporally-replicated occupancy study designs showed that the spatially-replicated model produced probabilities of occupancy that were the least biased compared to the (best) hierarchical model. Most importantly, the spatially-replicated data set was capable of detecting the decline in the probability of occupancy in the streams affected by mining operations, whereas the temporally-replicated surveys could not. When there is a great need to survey large expanses of rough, remote terrain, there is often a trade-off in allocation of effort. Facing a decision between spatially-replicated or temporally-replicated surveys, we found that spatial replication can provide suitably sensitive, time and cost-effective standardized data sets for modelling the probability of stream occupancy of Arctic fishes.

Surveys of adjacent stream segments produced spatially correlated data, as expected. This issue was alleviated by surveying randomly-selected stream segments within a hierarchical spatially- and temporally-replicated occupancy model. The assumption that a site is closed to changes in the probability of occupancy in spatially-replicated surveys requires that the species' home range is similar to the size of the site, such that the species is available for detection in all of the spatial replicates within an occupied site (Kendall and White 2009). Positive bias in occupancy probabilities is commonly observed in spatial surveys where sites are sampled exhaustively and/or without replacement (Kendall 1999, Kendall and White 2009), leading to the overestimation of occupancy probabilities. This can increase the chances that a real decline in a population will go undetected. Currently, we know of no other studies that have addressed issues of sequential spatial correlation in occupancy modelling of stream fish populations, given the near certainty that the standard method of observing fish while walking along the stream will produce spatially auto-correlated, and thus biased, estimates of site occupancy (Hines et al. 2010). Iterations of occupancy models have been designed to account for violation of the assumption of independent observations (spatial-autocorrelation), and to account for violation of the assumption of closure in time (staggered entry models), but there is no model that allows for the violation of the assumption of closure in space. We suggest that it may be better to avoid violating the spatial closure assumption by relaxing the effect of violating the assumption of independence of spatial replicates. A downstream sequential survey style, but with replicate surveys taking place immediately downstream of the first observation, might help to better meet the assumption that fish are available in all segments, when present in the stream. Correlation in the presence of Arctic Grayling young-of-year in sequential segments likely arises from the poor swimming ability of a group of newly hatched fry that are easily displaced downstream during early larval stages (Deleray and Kaya 1992).

The observed absence of young-of-year Arctic Grayling in some spatial replicates of otherwise occupied streams suggests that they may use smaller suitable patches within a stream, as opposed to occupying the entire length of a stream. If true, mitigating the effects of anthropogenic alterations of water flow on whole streams may be less important than ensuring that a smaller portion of the stream be maintained as suitable rearing habitat for Arctic Grayling young-of-year and that other portions of the stream simply remain passable for fish migration.

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Data accessibility

Data used in this study will be accessible from the University of Waterloo's institutional repository searchable from: https://uwspace.uwaterloo.ca/handle/10012/9937 (data will be deposited at time of article acceptance with a direct address provided here).

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Figure Captions

Fig. 1. Location of study area.

Fig. 2. Comparison of the detection probabilities ± 95% CI estimated from two common fish sampling methods in A) 2014 and B) 2015. Detection probabilities were affected by C) water velocity (m/s) in 2014, and D) water depth (m) in 2015.

Fig. 3. Probability of occupancy ± SE vs. observed presence of Arctic Grayling young-of-year in streams in A) 2014 and B) 2015 based on survey method.

Fig. 4. Relative bias in probabilities ± 95% CI of A) detection and B) occupancy produced by simulated occupancy surveys of only spatial or only temporal replicates compared to the combined hierarchical model including both spatial and temporal replication.

Fig. 5. Proportion of streams occupied modelled as a function of influential habitat variables based on data from A) 2014 streamside visual surveys, B) 2015 streamside visual surveys, and C) 2015 electrofishing surveys. No habitat variables were found to significantly influence the probability of occupancy of streams in 2014 electrofishing surveys.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Supplemental Data S1. Description and rationale for use of *a priori* candidate hierarchical occupancy models.

Table S1. Ranges of sampled habitat variables.

Table S2. Beta coefficients for benchmark hierarchical models.

Fig. S1. Conceptual representation of the data configurations used of the analysis of presence-absence.

Table 1. Benchmark model selection results of *a priori* candidate models of the 2014-visual hierarchical, 2015-electrofishing hierarchical, 2015-visual hierarchical and, 2015-electrofishing hierarchical data sets of presence-absence of Arctic Grayling young-of-year in Barrenland streams. ΔAICc (corrected for small sample size) of each model from the minimum model was used to calculate AICc weight (w_i) and rank of each model, and to select the most parsimonious model from the three candidate structures. K is the number of model parameters, and -2log(L) is the negative of twice the logarithm of the likelihood

function evaluated at the maximum likelihood estimates. * indicates models that failed to converge mathematically and were removed from consideration