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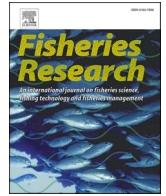
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## Genetic assessment of Inconnu (*Stenodus leucichthys*) in Great Slave Lake, Northwest Territories, Canada

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### ABSTRACT

Inconnu (*Stenodus leucichthys*) is a large freshwater migratory coregonid species that is commercially fished in some parts of its range. In Great Slave Lake, NT, Inconnu are one species that is caught in a mixed species gillnet fishery that is subject to restrictive management because four of the seven known stocks are declining or have been extirpated. The seven known Inconnu stocks have been identified based on the river systems that support or once supported a spawning population. To help identify key geographic areas for harvest control and other management approaches, we estimated the genetic diversity and population genetic structure of Inconnu in this area with 17 microsatellite loci. Temporal and spatial genetic structure was examined in four river systems, lower and upper Mackenzie River, Buffalo River, Slave River and Marian River/Lake and within Great Slave Lake. Analyses suggested that genetic diversity was greater in lower/upper Mackenzie River populations compared to populations in Great Slave Lake. Genetic structure was temporally stable at all locations except one, and spatial structure was found with significant isolation by distance detected among locations. Bayesian clustering analysis suggested five genetic groups of Inconnu, one in the lower and upper Mackenzie River and four within Great Slave Lake. The substructuring within Great Slave Lake included a genetic group representing fish collected in the lake itself. In addition, three genetic groups corresponded to river systems (Buffalo River, Marian River/Lake, Slave River), indicating that each river has genetically distinct Inconnu populations. These results suggest that the sustainability of Inconnu in and around Great Slave Lake depends upon maintaining stocks associated with river systems, especially those that are geographically disparate.

### 1. Introduction

Overexploitation and habitat degradation have led to declines in a number of Canadian fisheries. Overfishing by recreational and commercial fisheries has reduced stocks (e.g. Walleye) and caused fisheries to collapse (e.g. Lake Trout) (Eshenroder and Amatangelo, 2002; Post et al., 2002). In addition, watersheds near dams and mines have fewer fish (Thorpe et al., 1981; Wofford et al., 2005; Authman et al., 2015). In response, conservation efforts have focused on identifying and managing stocks to achieve sustainable fisheries. Generally, a stock is a group that can maintain and sustain themselves over time in a specified area (Booke, 1981; Kutkuhn, 1981; Waples and Gaggiotti, 2006). Stocks may be identified based on differences in geographic distribution (e.g. tagging and otolith microchemistry), morphology, and/or genetics (Begg and Waldman, 1999; Loewen et al., 2015). In particular,

population genetic analyses can be used to determine whether stocks are genetically discrete from other stocks. If the genetic variation of stocks is reduced, then the fitness of that stock may decline (Reed and Frankham, 2003). Further, effective conservation and management strategies rely on a thorough understanding of the biology of the species, its distribution, and the existing genetic diversity. Uninformed decision-making can contribute to population declines, or the possible extirpation of genetically distinct stocks, which can trigger changes in management strategies and could affect fishing practises (Smith et al., 1991; Ryman et al., 1995; Allendorf et al., 2008; Euclide et al., 2019).

Historical factors, such as glacial events, have contributed to shaping the genetic diversity and population genetic structure of fish stocks in North America (Bernatchez and Wilson, 1998). These events reduced dispersal and historical gene flow in populations, but their signature can still be detected in contemporary populations by testing for genetic

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bottlenecks. If present, genetic bottlenecks indicate a reduction in genetic diversity due to a small number of individuals or ‘founders’ originating from a much larger ancestral population establish new populations (Nei et al., 1975; Barton and Charlesworth, 1984). Compared to southern fish populations, northern fish populations experienced multiple glacial expansions and retreats (Avisé et al., 1984; Bernatchez and Wilson, 1998). It has been demonstrated that these

repeated glacial events have had a major influence on the historical gene flow, genetic structure and diversity of species with northern distributions (Bernatchez and Wilson, 1998; Hewitt, 2000). Contemporary factors such as geographic isolation can also affect the genetic diversity and genetic structure of fish populations. If isolation by distance (IBD) is influencing contemporary genetic structure of a fish species, then populations that are the furthest apart are expected to be the most

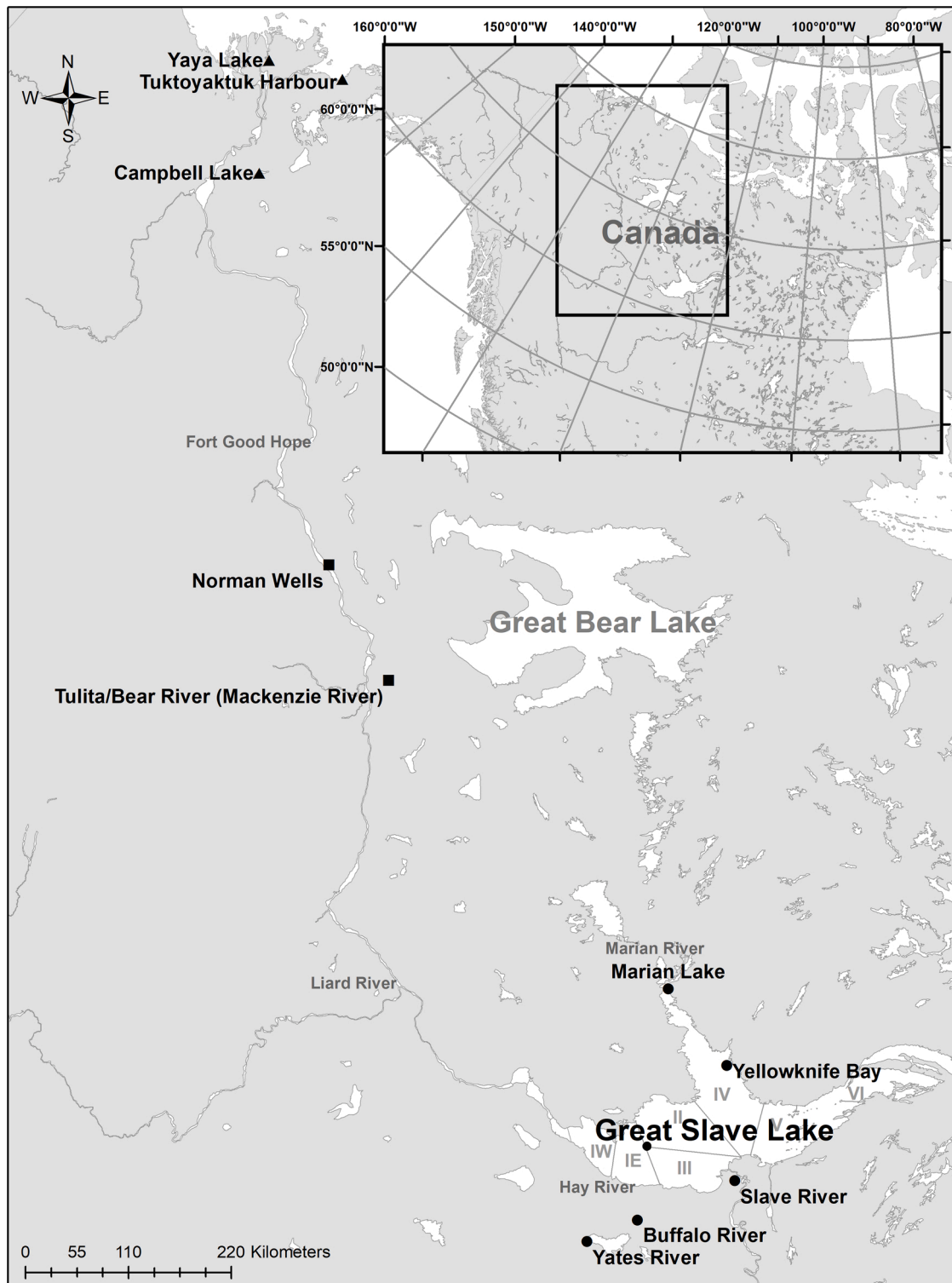


Fig. 1. Map of Inconnu (*Stenodus leucichthys*) sampling locations and seven management areas of Great Slave Lake in the Northwest Territories. The Mackenzie River system is split into three sections: lower Mackenzie (triangle); upper Mackenzie River (square) and Great Slave Lake (circle). Three management areas in Great Slave Lake were sampled, IW, IE and III.

genetically divergent with minimal gene flow among the populations (Wright, 1943; Primmer et al., 2006; Bradbury and Bentzen, 2007). Another contemporary factor that contributes to the genetic discreteness of fish populations is philopatry (Bradbury and Bentzen, 2007). For example, philopatry can increase genetic differentiation among fish populations especially at small spatial scales (Angers and Bernatchez, 1998; Primmer et al., 2006).

Inconnu are a large (adults can be > 1 m), piscivorous coregonid species with a northern distribution in Canada, that extends from the Mackenzie River Delta to Great Slave Lake in the Northwest Territories (Howland et al., 2000, 2009). Within Great Slave Lake, the presence of commercial, subsistence and recreational fisheries may have affected the genetic structure and diversity of Inconnu (Pinsky and Palumbi, 2014; Tallman and Howland, 2017). Several life history characteristics of Inconnu may make them more susceptible to overharvest by the commercial fishery. They are usually found in inshore areas of the main body of the lake, except in fall when they ascend rivers for spawning. Pre-spawning Inconnu will concentrate at the mouth of spawning rivers, which makes them especially susceptible to over-exploitation. They are fast growing, long-lived fish that mature late, and migrate from spawning river systems and lakes, into Great Slave Lake in the spring, making them vulnerable to fishing gear prior to maturity (Fuller, 1955; Reist and Bond, 1988; Howland, 2005; Day et al., 2013; Smith and Sutton, 2015). Historically, Inconnu were bycatch of the Lake Whitefish (*Coregonus clupeaformis*) commercial fishery, but higher market prices for Inconnu in the 1970's, and more recently in 2014, increased targeting (Day et al., 2013; VanGerwen-Toyne et al., 2013; DFO, 2014).

Currently, stocks of Inconnu are delineated by spawning runs and geographic distinctiveness. Historically, there were seven spawning runs recognized in Great Slave Lake: Yellowknife River, Taltson River, Buffalo River, Slave River, Marian River, Hay River and Little Buffalo River (Fuller, 1955; Howland et al., 2000; Day et al., 2013). However, it is not known whether these spawning runs are genetically different from each other, or if they supported more than a single genetic population. Higher market demand has increased fishing pressure leading to the decline in some stocks (Fuller, 1955; Day et al., 2013; VanGerwen-Toyne et al., 2013). Management actions by Fisheries and Oceans Canada (DFO), including seasonal and year-round management area closures, have been implemented for some stocks to reduce fishing pressure (VanGerwen-Toyne et al., 2013; DFO, 2014; Fig. 1). For instance, the Buffalo River stock was placed in the critical zone of the DFO precautionary approach (PA) model framework in 2010 in an attempt to reduce annual catches. In addition to this declining stock, there are several river systems that supported spawning populations that have been extirpated including Taltson River, Hay River, Little Buffalo River and Yellowknife River. Historically, these stocks had large spawning runs, but may have collapsed due to harvesting by communities situated near the rivers or habitat alterations related to dam and mine activity (Fuller, 1955; Day et al., 2013; VanGerwen-Toyne et al., 2013; Tallman and Howland, 2017). It is critical to understand the number, and geographical extent of the genetic stocks of Inconnu that use Great Slave Lake, so that fisheries management decisions can focus limited resources on protecting declining stocks and their habitat.

The genetic diversity of Inconnu could also be affected by philopatric behaviour that is driven by specific spawning requirements. Inconnu in Alaska preferred to spawn in areas with variable substrate size (i.e. very coarse to coarse pebble and gravel to fine sand and silt) and fast-flowing, shallow water (Alt, 1977; Howland, 2005; Stuby, 2012). Local knowledge suggests that Inconnu in Great Slave Lake spawn near rapids with an abundance of coarse substrate that provides cover and allows any drifting eggs to settle. Around Great Slave Lake, the geographic distance between river systems with a known spawning ground varies considerably (~40 km to ~300 km). Although these systems are connected by Great Slave Lake, if Inconnu exhibit philopatry, then site fidelity to natal spawning grounds may lead to higher genetic differentiation among spawning river systems.

In our study, samples from long-term stock assessment monitoring were used to test whether there were temporal or spatial influences on the genetic structure and diversity of Inconnu in Great Slave Lake. Deglaciation events in the Northwest Territories would have resulted in the colonization of Inconnu from the lower Mackenzie region into Great Slave Lake (McPhail and Lindsey, 1970; Howland, 2005; Stephenson et al., 2005). We hypothesized that if a founding event occurred post-glaciation, then Inconnu from Great Slave Lake would have less genetic diversity than the lower/upper Mackenzie River. Further, if Inconnu are philopatric to river spawning sites, then Inconnu from each river were predicted to constitute a discrete genetic population. In addition, we tested whether there were any changes in the genetic composition of particular sites by comparing the population genetics of samples collected in different years.

## 2. Methods

### 2.1. Origin of tissue samples

Samples were collected by DFO and local community members that were part of the commercial and subsistence fisheries in Great Slave Lake and its tributaries from 1988 to 2017 (Table 1). Great Slave Lake is the fifth largest lake in North America with a surface area of 28,568 km<sup>2</sup>, that spans different physiogeographic regions, with the northern region occurring in the Precambrian shield and the southern region occurring in the Mackenzie lowlands. The Mackenzie River extends ~1500 km from the Rocky Mountains to the Arctic lowlands and includes Great Slave Lake.

Samples were collected from 11 locations with multiple sites sampled within a location (Table 1; Fig. 1). In our study, Mackenzie River was divided into two areas: the lower Mackenzie and the upper Mackenzie. The lower Mackenzie encompasses the Mackenzie River from Fort Good Hope to the Mackenzie Delta (three locations: Yaya Lake, Campbell Lake, Tuktoyaktuk Harbour). The upper Mackenzie extended from Fort Good Hope to Great Slave Lake and included two locations: Tulita/mouth of Bear River (i.e. Tulita), Norman Wells). The other six locations occurred in Great Slave Lake (one location: Areas 1E, 1 W and III), in a river associated with Great Slave Lake (one location: Yates River), and in areas where four Inconnu stocks occur (four locations: Buffalo River, Marian River and Lake (i.e. Marian River/Lake), Yellowknife Bay and Slave River) (Fig. 1). Samples collected during the fall spawning run include Marian River/Lake (1995 and 2015), Slave River (1993–1995) and Buffalo River (2017).

Inconnu were caught using gillnets (133 mm and 140 mm mesh size), which is a common method used in fisheries stock assessment and commercial fisheries (Day et al., 2013). Tissue samples consisting of finclips preserved in 95 % ethanol or frozen muscle tissue were used for genetic analysis.

### 2.2. Microsatellite genotyping and scoring

A total of 17 microsatellite loci, originally developed for other fish species, were tested in Inconnu using four multiplexes (Table A.1; A.2). Tissue samples were collected from 999 individuals (Table 1). DNA was extracted using the Qiagen DNeasy® blood and tissue kit protocol (Qiagen, Valencia, California) following manufacturer's instructions. DNA extractions were also performed on an additional 105 samples using the Chelex® 100 DNA extraction method (Walsh et al., 1991). A 1 mm<sup>2</sup> piece of tissue was soaked in water to remove ethanol and then placed in 200 µL of 5% Chelex® (Bio-Rad Laboratories, CA, USA) containing 0.2 mg /mL proteinase K. Samples were incubated at 56 °C for 2 h and then boiled at 100 °C for 8 min. Microsatellite alleles were amplified using four multiplex PCR reactions with three to five loci per mix and one locus was amplified on its own with a final volume of 10 µL per (Table A.1). Samples were run on a 3130xl Genetic Analyzer (Applied Biosystems, Inc., Foster City, California) using the GeneScan™

**Table 1**

Parameters describing genetic variation among 11 locations. Sample size ( $N$ ), allelic diversity ( $N_a$ ), expected heterozygosity ( $H_s$ ), allelic richness ( $A_r$ ), multi-locus  $F_{IS}$  and  $P$ -value for each sample location using 17 microsatellite markers. Values not in HWE are bolded (Bonferroni-corrected;  $P = 0.003$ ).

Area	Location	Site	Year	$N$	$N_a$	$H_s$	$A_r$	$F_{IS}$	$P$ -value	
Lower Mackenzie River	Yaya Lake		1992	43	2–37	0.616	3.86	0.020	0.315	
		Campbell Lake	1988	8	2–31	0.607	3.86	–0.041	0.058	
Upper Mackenzie River	Tuktoyaktuk Harbour		1992	27						
		Tulita/Bear River	2016	48	2–37	0.626	3.93	–0.009	0.636	
Upper Mackenzie River	Tulita/Bear River	Tulita	1996	14	2–22	0.603	3.68	0.040	0.152	
		Bear River	1996	12						
Great Slave Lake	Norman Wells		2016	30	2–31	0.634	3.92	0.018	0.441	
		Marian River/Lake	1994	18	1–28	0.487	3.13	0.000	0.987	
	Yellowknife Bay	Lake	Lake	1995	37					
			River	2015	20					
			Lake	2015	40					
			Lake	2010	9	1–12	0.557	3.41	0.019	0.687
	Slave River	Lake	Lake	2011	17	1–19	0.493	3.49	0.004	0.899
			Lake	2012	4	1–2	0.265	3.31	–0.944	<b>0.000</b>
			Lake	2015	34	2–24	0.534	1.53	0.042	0.085
			Lake	1993	26	2–35	0.526	3.37	–0.036	<b>0.000</b>
	Slave River	Cunningham	Cunningham	1994	42					
			Fort Smith	1995	3					
Salt River			1994	44						
Fort Resolution			1994	51						
Slave River	Taltson River	Taltson River	1994	35						
		Taltson River	2016	19						
		Taltson River	2017	1						
		Taltson River	2013	10	2–12	0.521	3.27	0.030	0.522	
Buffalo River Mouth	Taltson River	Taltson River	1993	47	2–37	0.498	3.34	0.001	0.941	
		Taltson River	1994	35						
		Taltson River	2011	160						
		Taltson River	2017	24						
Management Areas	Hay River/Area IE	Hay River/Area IE	1996	14	2–32	0.523	3.42	0.011	0.336	
		Area IW, IE, III	2012	70						
		Area IW	2016	15						
		Area IE	2017	42						

600Liz size standard (v. 2.0 Applied Biosystems Inc.). Alleles were scored and edited using GENEMAPPER (v. 3.7 Applied Biosystems Inc.)

### 2.3. Population genetic analyses

To determine whether there was temporal genetic structure within locations, we estimated pairwise population differentiation between years within a sampling location with  $F_{ST}$  (Weir and Cockerham, 1984). Six locations were sampled in more than one year resulting in 30 pairwise year by location combinations (Table A.3). To calculate  $F_{ST}$ , we did not assume Hardy Weinberg equilibrium (HWE) and specified 10,000 iterations in FSTAT v.2.9.3 (Goudet, 1995). To further assess temporal genetic structure, we determined whether sampling years clustered within a location by performing Bayesian clustering analysis in STRUCTURE v2.3.4 (Pritchard et al., 2000). This analysis assumes that populations are in HWE and linkage equilibrium. Ten replications were run for  $K$  values, 1–30, using the admixture model and correlated allele frequencies with a burn-in of 100,000 followed by 100,000 iterations of Markov Chain Monte Carlo (MCMC). A priori location information (LOCPRIOR) was not used. If no significant genetic differentiation or clustering was found in a location according to year, then temporal samples were pooled before additional genetic analyses were conducted.

For each location, levels of polymorphism, observed heterozygosity ( $H_o$ ) and expected heterozygosity ( $H_e$ ) were calculated per locus in GENEPOP v4.0 (Raymond and Rousset, 1995; Rousset, 2008). Within each location, we tested for deviations from HWE (per locus and multilocus) by estimating  $F_{IS}$  using SPAGEDI v1.5 (Hardy and Vekemans, 2002). Loci that did not meet HWE expectations were removed from the analyses. Linkage disequilibrium (LD) was tested with an exact test

based on the Markov chain method in GENEPOP v4.0 using 5000 dememorizations, 5000 batches and 5000 iterations per batch. Sequential Bonferroni correction was performed to correct for multiple tests (Rice, 1989). MICROCHECKER (van Oosterhout et al., 2004) was used to test each locus for excess homozygosity in all populations by using a Fisher's combined probability test calculated using the  $P$ -values of all homozygote classes. The  $P$ -values were calculated using a cumulative binomial distribution and ranking the frequency distribution of randomized genotypes (van Oosterhout et al. 2004). In MICROCHECKER, deviations from HWE indicate the presence of null alleles, scoring errors and short allele dominance.

To determine the influence of a post glacial founder event, we tested whether the lower and upper Mackenzie locations were more genetically diverse than Great Slave Lake locations. The average expected heterozygosity ( $H_s$ ) was calculated in SPAGEDI (Hardy and Vekemans, 2002) and compared with a Kruskal-Wallis test. Allelic richness ( $A_r$ ) was calculated using HP-Rare software v1.0 (Kalinowski, 2005) using rarefaction to account for unequal sample sizes, followed by a Kruskal-Wallis test. We estimated  $H_s$  and  $A_r$  for each of the 11 locations (lower and upper Mackenzie: Yaya Lake, Campbell Lake, Tuktoyaktuk Harbour, Mackenzie River at Tulita and Norman Wells; Great Slave Lake: Marian River/Lake, Yellowknife Bay (2010, 2011, 2012, 2015), Slave River, Buffalo River, Yates River, Great Slave Lake management areas (1E, 1 W and III)). We tested for recent genetic bottlenecks in each location using BOTTLENECK v1.2.02 (Piry et al., 1999). This program suggests a bottleneck when the number of alleles decreases more rapidly than the expected heterozygosity. We tested for bottlenecks assuming a step-wise mutation model (SMM) and the two-phase mutation model (TPM) (95 % single-step mutations and 12 % variance of multi-step mutations). We

tested for significance with the Wilcoxon's signed rank test with 1000 iterations (Luikart and Cornuet, 1998; Piry et al., 1999).

To determine if geographic distance affected Inconnu genetic structure, we tested for isolation by distance among locations. Geographic distances between locations were measured following contemporary waterways (i.e. river systems) and estimated with least cost path analysis on a one million scale map downloaded from the Open Government Portal (Government of Canada, 2017) using the Spatial Analyst toolbox and cost distance tool in ArcGIS v10.4.1 (ESRI, 2015). Pairwise population differentiation ( $F_{ST}$ ) was estimated for all locations using FSTAT v.2.9.3 (Goudet, 1995; Weir and Cockerham, 1984). RECODEDATA v.0.1 (Meirmans, 2006) was used to calculate the maximum possible divergence among populations ( $F_{ST-max}$ ) followed by standardizing the  $F_{ST}$  value by dividing the raw  $F_{ST}$  by  $F_{ST-max}$ . Geographic distances were combined with pairwise  $F_{ST}$  values to test for isolation by distance with the Mantel test using GENALEX 6.5 (Peakall and Smouse, 2006, 2012).

To further test for genetic structure among locations, we used a Bayesian clustering approach as performed by the program STRUCTURE v2.3.4 (Pritchard et al., 2000) to define the number of genetic groups present in the dataset. We ran ten replications for each  $K$  value 1–17. The parameters were set to the same specifications as above. The most likely number of clusters was determined using the maximum log probability of the data (Pritchard et al., 2000) and the ad hoc test  $\Delta K$  (Evanno et al., 2005).

Once the most likely number of clusters was determined, a hierarchical approach using additional STRUCTURE runs (with the same parameters above) was implemented to determine whether further genetic substructure was present within each identified cluster. Maximum log likelihood was used to determine the most likely number of clusters. The ad hoc test  $\Delta K$  was not used because it cannot be applied to populations with  $K = 1$  (Evanno et al., 2005). For each fish, we estimated the probability that an individual belongs to a particular population with the  $Q$ -heuristic from STRUCTURE. Individuals with  $Q > 0.80$  were considered a member of that genetic cluster, fish with  $Q < 0.80$  were considered to be of admixed ancestry between different genetic groups (Garroway et al., 2010).

We also assessed population structure with principal components analysis (PCA) to determine if the results differed when the analysis did not assume HWE and linkage equilibrium (Jombart, 2008). We used the ADEGENET package to import the genetic data and then analyzed population structure with the package ade4 using R statistical software (Jombart, 2008; R Core Team, 2018). PCA summarizes variability among individuals and within groups using a matrix of allele frequencies, but does not predict variation between populations as well as STRUCTURE (Jombart, 2008). After performing PCA on the entire dataset, an individual from Yates River was deemed an outlier and removed.

### 3. Results

#### 3.1. Origin of tissue samples

This study included a total of 999 samples from Inconnu collected from 11 locations over the course of nearly 30 years. Of the seven locations that had samples collected over multiple years (Campbell Lake, Mackenzie River at Tulita, Marian River/Lake, Slave River, Buffalo River, Yellowknife Bay and Great Slave Lake), only Yellowknife Bay showed genetic variation across years. Therefore, in subsequent analyses, samples across years were combined except for Yellowknife Bay. (Table 2; Table A.3). A total of 14 populations were recognized: four with one temporal sample, six with pooled sampling by year, and one location with each sampling year treated as a separate population (Table 2).

**Table 2** Genetic differentiation of Inconnu among 14 populations in the Northwest Territories. Pairwise  $F_{ST}$  (bottom) and standardized  $F_{ST}$  (top) using 15 loci at 11 locations (sampling years were combined for all location except for Yellowknife Bay) in the Northwest Territories. Bolded values are significant after Bonferroni correction ( $P < 0.00055$ ).

	Yaya Lake	Campbell Lake	Tukttoyaktuk Harbour	Norman Wells	Mackenzie River <sup>a</sup>	Marian R./L.	Yellowknife Bay 2010	Yellowknife Bay 2011	Yellowknife Bay 2012	Yellowknife Bay 2015	Slave River	Yates River	Buffalo River	GSL <sup>b</sup>
Yaya Lake	-	0.004	-0.005	-0.015	0.135	0.325	0.196	0.311	0.689	0.212	0.254	0.340	0.284	0.239
Campbell Lake	0.001	-	-0.012	-0.008	0.169	0.303	0.174	0.279	0.740	0.174	0.210	0.305	0.255	0.198
Tukttoyaktuk Harbour	-0.001	-0.002	-	-0.010	0.038	0.139	0.072	0.114	0.306	0.078	0.100	0.119	0.119	0.091
Norman Wells	-0.002	-0.001	-0.004	-	0.013	0.135	0.065	0.106	0.322	0.070	0.098	0.109	0.112	0.088
Mackenzie River <sup>a</sup>	0.019	0.023	0.014	0.005	-	0.195	0.117	0.165	0.349	0.119	0.146	0.120	0.156	0.135
Marian River/Lake	0.067	0.063	0.062	0.061	0.090	-	0.040	-0.009	0.271	0.066	0.095	0.085	0.039	0.059
Yellowknife Bay 2010	0.031	0.028	0.028	0.026	0.047	0.020	-	0.027	0.271	-0.015	-0.002	0.038	0.023	-0.011
Yellowknife Bay 2011	0.055	0.050	0.047	0.044	0.071	-0.005	0.013	-	0.291	0.044	0.073	0.072	0.032	0.042
Yellowknife Bay 2012	0.145	0.159	0.137	0.147	0.163	0.149	0.147	0.162	-	0.302	0.290	0.273	0.239	0.248
Yellowknife Bay 2015	0.036	0.030	0.032	0.029	0.050	0.033	-0.007	0.021	0.159	-	0.000	0.064	0.032	0.000
Slave River	0.048	0.040	0.043	0.042	0.064	0.046	-0.001	0.035	0.151	0.000	-	0.065	0.052	0.010
Yates River	0.055	0.050	0.047	0.043	0.049	0.042	0.017	0.035	0.151	0.030	0.030	-	0.043	0.037
Buffalo River	0.057	0.052	0.053	0.050	0.071	0.020	0.011	0.016	0.127	0.015	0.025	0.021	-	0.016
GSL <sup>b</sup>	0.044	0.037	0.039	0.038	0.059	0.029	-0.005	0.020	0.129	0.000	0.005	0.017	0.008	-

<sup>a</sup> Mackenzie River @ Tulita/mouth of Bear River.

<sup>b</sup> Great Slave Lake management areas IW, IE, III.

### 3.2. Population genetic analyses

Among these 14 populations, the number of alleles per each of the 17 loci ranged from 1 to 37 (Table 2). Multi-locus  $F_{IS}$  indicated that 2012 Yellowknife Bay and Slave River were out of HWE (Bonferroni-corrected,  $P < 0.003$ ; Table 2). Further, analysis performed on each locus per population revealed that *Sfo8* and *Clatet13* were not in HWE in several of the populations (Bonferroni corrected,  $P < 0.003$ ). According to MICROCHECKER, *Sfo8* was not in HWE in 10 populations due to excess heterozygosity and *Clatet13* had an excess of homozygosity due to the presence of null alleles in all populations. *Sfo8* and *Clatet13* were removed from all other analyses because no other loci were out of HWE in more than one population. Analyses performed with the remaining 15 loci found 76 out of 1470 pairs of loci among the 14 populations were in linkage disequilibrium ( $P < 0.05$ ). After sequential-Bonferroni correction, only 17 pairs of loci among the 14 populations were in linkage disequilibrium ( $P < 0.000476$ ). Four of these pairs were found in the Mackenzie River at Tulita location, but otherwise no pairs had significant LD in more than two locations. Based on these results, subsequent analyses were performed on 14 populations with 15 loci.

Expected heterozygosity and allelic richness were significantly greater in the lower and upper Mackenzie populations (Yaya and Campbell Lake, Tuktoyaktuk Harbour, Mackenzie River (at Norman Wells and Tulita)) compared to Great Slave Lake locations (Marian River/Lake, Yellowknife Bay, Slave River, Buffalo River and Yates River) ( $H_S: H = 9.0, P = 0.0027$ ;  $A: H = 9.02, P = 0.0027$ ). Two populations had signatures of genetic bottlenecks. The SMM and TPM models both resulted in significant departures for Yellowknife Bay in 2012 (SMM and TPM:  $P = 0.0006$ ) and Yates River (SMM:  $P = 0.0413$ ; TPM:  $P = 0.0302$ ). However, both populations had low sample sizes, (Yellowknife Bay,  $N = 4$ ; Yates River,  $N = 10$ ), which could have contributed to these results.

In addition to finding that most populations were temporally stable, there was evidence of spatial genetic structure. Significant isolation by distance was observed among locations ( $R_{xy} = 0.693$ ;  $P = 0.008$ ; Fig. 2). The influence of geography was also reflected in the most likely number of genetic clusters inferred from the STRUCTURE analysis. The ad hoc test ( $\Delta K$ ) suggested that  $K = 3$  represented the most likely number of genetic populations. As expected, the Mackenzie River populations were assigned to a different genetic group than the Great Slave Lake populations. Individuals from Marian River/Lake (location furthest North in GSL) assigned to the second genetic cluster and Inconnu from Slave River (location in the southeast GSL) comprised a third genetic group. Inconnu caught at the mouth of the Buffalo River, Yates River and Great Slave Lake management areas (IE, IW and III) were identified to belong to both GSL genetic clusters. Unexpectedly, Inconnu from one location (GSL junction of Hay River) grouped with the Mackenzie River genetic cluster. A principal components analysis also showed three distinct

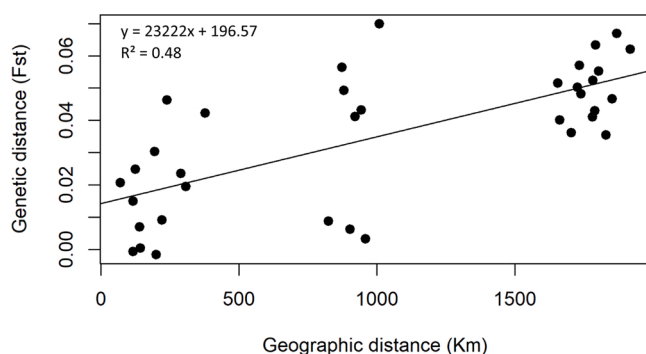


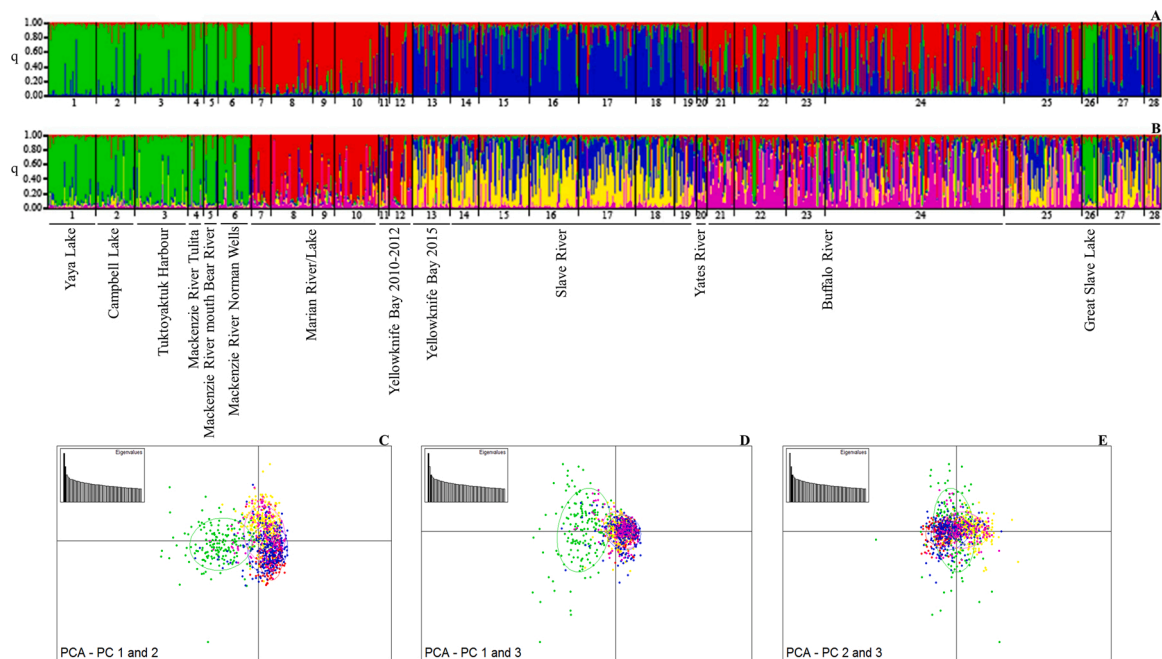
Fig. 2. Pairwise isolation by distance using genetic distance ( $F_{ST}$ ) and geographic distance (km) between 10 locations in which Inconnu were sampled: Yaya Lake, Campbell Lake, Tuktoyaktuk Harbour, Mackenzie River at Tulita, Norman Wells, Marian River/Lake, Yellowknife Bay, Slave River, Yates River and Buffalo River ( $P = 0.008$ ).

clusters. The first axis of the principal components (PC1) separated the upper and lower Mackenzie River fish from Great Slave Lake river systems (Marian River/Lake, Yellowknife Bay, Slave River and Buffalo River) (eigenvalues = 5.0, axis 1 explained 2.4 % of variation). PC2 indicated that fish from Marian River/Lake and Slave River were each a distinct genetic cluster (Fig. 3; eigenvalues = 3.51, axis 2 explained 1.7 % of variation). The third principal component (Fig. 3; eigenvalues = 2.72, axis 3 explained 1.3 % of variation) did not further differentiate the clusters. Similar to the Bayesian clustering, the PCA did not clearly show a distinct cluster for Buffalo River and Yates River because individuals from these locations clustered with fish from Slave River and Marian River/Lake (Fig. 3). Great Slave Lake was comprised of fish assigned to all three genetic clusters (Fig. 3).

In contrast, the highest maximum log likelihood value in the Bayesian analyses was at  $K = 5$  (lower/upper Mackenzie River (cluster 1), Marian River/Lake and Yellowknife Bay 2010–2012 (cluster 2), Slave River and Yellowknife Bay 2015 (cluster 3) Buffalo River (cluster 4) and Great Slave Lake (cluster 5)) (Fig. 3). A hierarchical Bayesian clustering approach was employed on each of the five clusters with  $K > 1$  only occurring in the lower/upper Mackenzie River genetic cluster ( $K = 2$ , separating the lower from the upper Mackenzie River individuals) using the highest maximum likelihood estimate.

Spatial structuring was not observed within the samples collected from the Great Slave Lake areas (IW, IE, III); however, the Bayesian cluster analysis indicated admixture. Fish collected within Great Slave Lake were highly admixed except samples from Great Slave Lake collected at the junction of Hay River ( $N = 26$ ) which were assigned to the genetic group comprised of Mackenzie River individuals (see  $K = 3, 5$ ; Fig. 3). At  $K = 4$ , fish from the southern extent of Great Slave Lake (Yates River and Buffalo River) split from samples collected from the northern extent (Marian River/Lake) of GSL. Although  $K = 5$  had the highest maximum log likelihood value, it suggests that Yellowknife Bay 2015 and Slave River are comprised of individuals of admixed origin (cluster 3: blue and yellow; Fig. 3).

Q-values from the Bayesian analysis provided further insights into the degree of admixture among the five genetic clusters. Within the lower/upper Mackenzie River (cluster 1), the majority of individuals (85 %) were assigned to their cluster of origin (i.e.  $Q > 0.80$ ), while 2% were assigned to two other clusters and 13 % were of mixed ancestry. Within Marian River/Lake and Yellowknife Bay 2010–2012 (cluster 2), the majority of individuals sampled (55 %) were assigned to their cluster of origin, less than 1% were assigned to the two other populations, and 44 % were of mixed ancestry. Within Slave River and Yellowknife Bay 2015 (cluster 3; yellow and blue), most individuals were of a 50:50 admixed origin (Fig. 3B). Therefore, individuals assigned to the yellow and blue group were treated as one genetic group, Slave River and Yellowknife Bay 2015. For each individual in this group, the Q-values for cluster 3 were summed, and if the sum was  $Q > 0.80$  for an individual, that individual was genetically assigned to the Slave River and Yellowknife Bay 2015 cluster. Using this method, the majority of individuals were assigned to the combined genetic cluster (73 %), suggesting that most fish in this Slave River and Yellowknife Bay 2015 share a similar genetic background. In addition, 3% of individuals from the combined genetic group were assigned to three other clusters, while the remaining individuals were of mixed ancestry (24 %). Within Buffalo River, 24 % of individuals were assigned to the Buffalo River genetic cluster, while 20 % were assigned to the three other genetic clusters and the remaining individuals were of mixed ancestry (56 %). Samples collected in the Great Slave Lake management areas (cluster 5) were assigned to the Slave River genetic cluster (42 %), the Buffalo River genetic cluster (13 %), and the Marian River/Lake and lower/upper Mackenzie River genetic cluster (10 %). The remaining individuals were considered mixed (42 %). Individuals with mixed ancestry may originate from genetic populations that were not sampled in our study.



**Fig. 3.** Bayesian clustering analysis of 11 sampling locations in Northwest. A:  $K = 3$ ; B:  $K = 5$ . Each number represents a separate location and year. Within Marian River/Lake the years include: 7)1994; 8)1995; 9)2015 (river); 10)2015 (lake). Within Slave River the years and locations include: 14) Slave River 1993; 15) Slave River 1994/1995; 16) Slave River @ Cunningham 1994; 17) Slave River @ Fort Smith 1994; 18) Slave River @ Salt River 1994; 19) Slave River @ Fort Resolution 2016. Buffalo River samples include: 21) Buffalo River mouth 1993; 22) Buffalo River Mouth 1994; 23) Buffalo River Mouth 2011; 24) Buffalo River mouth 2017. Great Slave Lake years and areas include: 25) GSL Area 1E/1 W/III 2012; 26) GSL Junction of Hay River summer 27) GSL Area 1E 2017; 28) GSL Area 1 W 2016. Principal components analysis plot of eigenvectors (C) 1 and 2; (D) 1 and 3; (E) 2 and 3 showing the four genetic clusters in Northwest Territories Clusters include Lower/Upper Mackenzie River populations (green), Marian River/Lake and Lake/Yellowknife Bay 2010-2012 (red), Slave River/Yellowknife Bay 2015 (yellow) Buffalo River /Yates River (blue) and Great Slave Lake (pink). Eigenvalues are: PC1 = 4.82, PC2 = 3.52, PC3 = 3.30. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

#### 4. Discussion

Our study suggests that Inconnu stocks in Great Slave Lake are less genetically diverse than Inconnu in the Mackenzie River system. Inconnu from the lakes, rivers and bays around Great Slave Lake had significantly lower expected heterozygosity and allelic richness compared to Inconnu from the lakes and river sites in the lower Mackenzie area and upper Mackenzie River. There are a few potential explanations for these results, which are not necessarily mutually exclusive. Less genetic diversity in Great Slave Lake populations could be a consequence of post-Pleistocene glaciation events (Hewitt, 1996, 2000). Indeed, our results with microsatellite loci are similar to what has been shown in previous studies using mitochondrial loci. Based on differences in haplotype diversity, Howland (2005) suggested that Inconnu originated from the Mackenzie Delta and then later colonized Great Slave Lake ~10,000 ya. Founder events within Great Slave Lake could have caused a decrease in heterozygosity and loss of alleles. If a small number of individuals from the Mackenzie River successfully dispersed and established populations in and around Great Slave Lake, genetic drift could then explain lower genetic diversity in the colonized population (Templeton, 1980; Hewitt, 2000).

Alternatively, higher genetic diversity in the lower/upper Mackenzie region may also indicate that this region has different ecotypes of Inconnu than in Great Slave Lake. In particular, greater genetic diversity could indicate the presence of anadromous individuals because anadromous and marine populations of fish tend to have greater genetic diversity compared to freshwater populations (Ward et al., 1994; DeWoody and Avise, 2000; Tonteri et al., 2007). Higher levels of genetic diversity in anadromous populations may be due to gene flow among populations over a long time span. When Inconnu migrate from the marine environment, into freshwater river systems to spawn, individuals may stray from natal spawning grounds into other river systems,

introducing novel alleles into that population (Tonteri et al., 2007). Radiotelemetry studies and strontium analysis indicate that sites within the lower/upper Mackenzie River system vary according to the proportion of anadromous and freshwater ecotypes (Howland et al., 2001; Howland et al., 2009). However, we could not test whether ecotypes influenced genetic diversity as the distribution and mixing of the ecotypes is not well characterized in the Mackenzie River system and for most of our samples the ecotype was not known. In future studies, analyzing a set of individuals that have been assessed for ecotype and population genetics would allow for testing whether genetic substructuring is mostly explained by ecotype or genetic differences in stocks. In addition, samples from known spawning stocks in tributaries of this regional river system such as the Arctic Red River and Peel River should be sampled as some of our locations in the lower/upper Mackenzie River system could have a mix of Inconnu from several different populations. A third explanation for comparatively lower diversity in Great Slave Lake is overfishing. For instance, it is clear that the Buffalo River stock has suffered a population decline due to over-harvest as the stock index is in the critical zone of the DFO PA framework (Day et al., 2013). Further, other populations in and around Great Slave Lake are vulnerable to commercial, recreational and subsistence fisheries. Overfishing could affect the contemporary population genetics of Inconnu, which microsatellite loci reflect (Pinsky and Palumbi, 2014).

Inconnu populations in the Mackenzie River system were the most genetically different from populations in Great Slave Lake. The majority (84.6 %) of fish from this river system were grouped into one genetic cluster by Bayesian and PCA analyses. At each of the five sampling locations in the lower/upper Mackenzie River (Yaya Lake, Campbell Lake, Tuktoyaktuk Harbour, Tulita and Norman Wells), no significant LD was observed, and all populations were in HWE. Most pairwise comparisons between sites resulted in low but significant to non-significant  $F_{ST}$  values suggesting high gene flow among fish in the lower/upper Mackenzie

River. However, more locations should be sampled to better understand the dispersal and gene flow within this river system. A lack of fine-scale population differentiation among Inconnu in large watersheds has also been observed in Alaskan Inconnu from the Yukon, Selawik, Kobuk and Kuskokwim watersheds (Olsen et al., 2017). However, the presence of two genetic populations in the Mackenzie River system may suggest that there are additional genetic populations using this river system that were not included in this study. Additional sampling could further clarify genetic structure in the lower/upper Mackenzie River.

The genetic differences between Inconnu in the Mackenzie River system and Great Slave Lake may also be due to some degree of geographic isolation. IBD analysis indicated that geography has significantly influenced the contemporary genetic structure of Inconnu in the Northwest Territories, with the greatest genetic differentiation occurring between locations ~1500 km apart (i.e. between the lower/upper Mackenzie and Great Slave Lake). These results agree with radio telemetry and other tagging studies, which show that individuals from the Mackenzie Delta and Great Slave Lake rarely co-occur (Howland et al., 2000, 2009). However, our genetic results suggest that individuals from the lower/upper Mackenzie River occur in Great Slave Lake. This result is supported by direct observations in which Inconnu tagged in the Liard River (a river connected to Mackenzie River) were recaptured in or near Great Slave Lake (Stephenson et al., 2005). In Fig. 3, the group of green individuals in the Great Slave Lake group ( $K = 3$  and  $K = 5$ ) collected at the mouth of Hay River in 1996 were assigned to the lower/upper Mackenzie cluster. This location is relatively close to the headwaters of the Mackenzie River (~75 km) which could explain the genetic similarity to fish from the lower/upper Mackenzie. These individuals were assigned to the lower/upper Mackenzie population with high certainty (78.5 % of individuals). Hay River is another stock that used to have a large spawning run but was recently extirpated. It is unknown whether the Hay River stock was historically genetically different from fish in the lower/upper Mackenzie. The contemporary genetic similarities could be due to the combined absence of the original Hay River stock and the recent use of this area by fish from the Mackenzie River system. Further evidence of IBD was observed between populations in Great Slave Lake, with significant genetic differentiation occurring between the southern sampling locations (Slave River, Buffalo River and Yates River) and the northern location, Marian River/Lake.

Genetic differences among three stocks sampled in Great Slave Lake (Slave River, Marian River/Lake and Buffalo River), supports the hypothesis that genetic structure is driven by philopatric behaviour of Inconnu. Each of these stocks corresponds to a major river system supporting a spawning run: Slave River, Marian River/Lake, and Buffalo River. Genetic differentiation between three stocks varied from low to moderate ( $F_{ST} = -0.005$ – $0.162$ ). The locations that differed the most were also the most geographically distant suggesting that in addition to philopatry, there may be a role of spatial isolation in the genetic structure of Inconnu even though they are highly migratory.

The Slave River population was significantly genetically different from all sampled locations except Inconnu from the Yellowknife Bay 2010 and 2015 site. Most fish sampled from Slave River were a combination of two populations. In our sampling, there was no genetic cluster that was comprised of individuals that were primarily assigned to either of these genetic groups (i.e. absence of any predominantly blue or yellow clusters). This suggests that more sampling is needed to find additional source populations. In the hierarchical analysis, the presence of a single population ( $K = 1$ ) across all sampling years (1993–2016) suggests that the population has been admixed for generations, which may indicate that this stock has strong site fidelity to natal spawning grounds. There was no LD within Slave River which suggests that the influence of gene flow and genetic drift is low within this population. Similar to Yellowknife Bay, Slave River had a significantly negative multilocus  $F_{IS}$  value with all but two individual loci (*One104* and *Cocl-Lav6*) having a negative  $F_{IS}$  value which may be explained by outbreeding depression. Outbreeding depression can occur when

individuals are the product of mating between two isolated populations, which can reduce fitness in future generations (Frankham et al., 2011). However, additional sampling is needed to determine whether the results found for Slave River are explained by unsampled genetic populations. Alternatively, the presence of two genetic clusters in Slave River could reflect that the Bayesian clustering analysis was having trouble assigning individuals to a population due to the influence of IBD (Frantz et al., 2009). STRUCTURE has the tendency to overestimate the number of populations when there is IBD (Frantz et al., 2009). Therefore, Inconnu in the Slave River may only represent a single population. Distinguishing between outbreeding depression, unsampled populations or the influence of IBD is important for managers to consider, as the Slave River population could be a source of migrants for other stocks, especially declining ones such as Yellowknife Bay.

Another genetic population in the Bayesian clustering analysis was comprised of fish from Marian River/Lake. This population was significantly genetically different from other populations (Table 2) and the majority of individuals (55 %) were assigned to this cluster ( $Q > 0.80$ ) (Fig. 3), while 1% were assigned to the other clusters. However, 44 % of individuals had mixed ancestry indicating that gene flow is occurring with fish from other river systems (i.e. Slave River and Buffalo River). Marian River/Lake was in HWE and linkage equilibrium signifying that the population is genetically stable and likely randomly mating with minimal influences of genetic drift and mutation.

Yellowknife Bay did not identify as a distinct stock and instead appeared to be comprised largely of individuals that were most genetically similar to fish from Slave River and Marian River/Lake stocks. Evidence of Slave River ancestry in Yellowknife Bay fish suggests that the migratory behaviour of Inconnu may reduce genetic differentiation between some stocks particularly in cases where there have been substantial population declines. This result is supported by tagging studies that showed Inconnu tagged in Slave River were recaptured in Yellowknife Bay (VanGerwen-Toyne et al., 2013). Migration from Slave River and Marian River/Lake was evident in the Bayesian clustering analysis and the PCA where Yellowknife Bay fish were separated into at least two populations. Yellowknife Bay 2015 showed a greater range in allelic diversity compared to 2010, 2011 and 2012, which may suggest the genetic diversity of Inconnu is increasing in this area. Sample size among the four years varies, with 2015 having a greater number of individuals, which may be an additional reason for an increase in genetic diversity in 2015. Among the four years (2010–2012, 2015) of sampling within Yellowknife Bay, all years were within HWE with no LD except in 2012, which could be explained by a low sample size ( $N = 4$ ). Although the clustering analyses suggested that Inconnu from other areas colonized the empty niche, monitoring assessments in Yellowknife River indicate that Inconnu have not yet re-established because there is no evidence of migration or spawning in this system (DFO, 2018). Several factors could have caused the extirpation of the Inconnu population in Yellowknife River, including mining activity leading to the subsequent accumulation of metals and a reduction in population size (Yellowknives, Dene, 2005; Authman et al., 2015; Sandlos and Keeling, 2012). In addition, a growing community supported by opportunities from mining may have led to an increase in harvest of Inconnu in the river system resulting in the extirpation of the Inconnu population in Yellowknife River (Tallman and Howland, 2017).

A third genetic population within Great Slave Lake is the Buffalo River, which had a large spawning run that supported a highly active commercial fishery until it declined in the 1970s (VanGerwen-Toyne et al., 2013). Experimental catch-per-unit-effort (CPUE) data for all sex and maturity stages combined from spring samples taken at the mouth of Buffalo River, suggested that the abundance of Inconnu in this area has decreased by approximately 85 % from the mid-1970s to 2008 (M. Y. Janjua, Fisheries and Oceans Canada, unpublished). The abundance of the Buffalo River stock was estimated to have declined from its unexploited state in the late 1940s, with changes in age structure suggesting high mortality due to fishing (Tallman and Howland, 2017). Given its

historical importance to the Inconnu fishery in Great Slave Lake and its current management status, it is important to conduct further research to better understand the proportion of fish from Buffalo River that are contributing to the commercial fishery on Great Slave Lake. The genetic uniqueness of the fish from the Buffalo River system is less clear compared to the other two river system stocks. Bayesian clustering analysis at  $K = 3$  shows that individuals within this location were assigned primarily to Marian River/Lake and Slave River populations. At  $K = 5$ , Buffalo River had many individuals (75.7 %) that were not highly assigned to that cluster suggesting that it is comprised primarily of individuals from other stocks or unsampled populations. Mixed ancestry of most individuals could be due to gene flow and migrants from the surrounding river systems. However, sample collection could also explain some of the mixed ancestry of these fish. These samples were collected at the mouth of Buffalo River during the spring when Inconnu aggregate at the mouth of the river to feed, and thus could be comprised of individuals from multiple stocks. To determine if fish from Buffalo River are genetically unique compared to other locations, samples that correspond to natal sources, preferably eggs or spawning individuals, should be collected from within the river system at the spawning locations.

As expected, samples collected in Great Slave Lake itself had individuals with genotypes corresponding to ancestry from all of the river systems: Mackenzie River, Slave River, Marian River/Lake and Buffalo River. A mix of genotypes from different river systems was expected in Great Slave Lake as Inconnu spawn in the river systems during the fall, and in the spring and aggregate in Great Slave Lake to feed. According to Bayesian analysis, the highest proportion of fish in Great Slave Lake management areas IW, IE and III originated from the Slave River population (44.7 %) suggesting that Slave River is an important source of fish for these areas in Great Slave Lake. The significance of Slave River in Great Slave Lake management areas is supported by a tagging study in which Inconnu tagged in Slave River were caught in all three areas of Great Slave Lake (VanGerwen-Toyne et al., 2013). Likewise, genetic differentiation between Slave River and these Great Slave Lake management areas was very low indicating gene flow between fish in these locations. Due to the proximity of Buffalo River to the management areas, we would have expected a greater proportion of individuals assigned to Buffalo River. However, individuals highly assigned to Buffalo River only comprised 12.8 % of the total Great Slave Lake samples, while 42.4 % were mixed ancestry and the remainder were from different river systems. The recent decline in the Buffalo River stock could explain why there was a low percentage of Buffalo River individuals at the mouth of Buffalo River. In response, fish from Slave River may have expanded their range into three sampled areas (IW, IE, III) of Great Slave Lake and thereby increased the proportion of Slave River individuals being caught. A second explanation is that fish from Buffalo River have admixed with other populations and this mixed population is represented in the commercial fishery. Further understanding of Inconnu distribution within river systems, and identifying genetic baseline or unsampled populations, in addition to a mixed stock fisheries analysis would provide a more accurate representation of the proportion stocks contribute to the commercial fishery.

In some cases, where stocks were extirpated, such as Yellowknife River, fish that are genetically similar from nearby river systems are now found in the adjacent Yellowknife Bay area. Hay River and Little Buffalo are river systems that previously had spawning populations, however, very little is known about why the populations disappeared and whether Inconnu are returning or not. The Taltson River stock may have been extirpated after a dam was built on the river, but local knowledge suggests that Inconnu may be returning to this system making its contribution to the fishery in Great Slave Lake unclear. Sampling at additional sites, especially rivers, is needed to determine if there are more genetically distinct populations in Great Slave Lake and their contribution to the Great Slave Lake fishery.

## 5. Conclusion

This research has implications for the management of Inconnu in Great Slave Lake. Determining population structure can inform managers about whether designated stocks are genetically unique and the geographic distributions of particular stocks. In this study, genetic analyses found that Inconnu populations largely corresponded to expected stock structure and that geography has a significant role in the genetic structure. Each stock exhibits different population dynamics (i.e. bottlenecks, admixture) that need to be considered when managing Inconnu in Great Slave Lake. We found evidence of five discrete genetic groups ( $K = 5$  from Bayesian cluster analyses). However, these groups corresponded to four fishery stocks within the Northwest Territories; lower/upper Mackenzie, Slave River, Buffalo River and Marian River. Although genetic structure was observed, there was low to moderate genetic differentiation between the stocks indicating that the high migratory nature of Inconnu leads to gene flow between most locations (Table 3). Philopatry to river systems (Buffalo, Slave and Marian Rivers) and IBD have influenced the contemporary genetic structure of three stocks that use Great Slave Lake. Temporal structure was found within Yellowknife Bay indicating the possible expansion of surrounding stocks (Marian River/Lake and Slave River) into that area. In contrast to the substructure found within Great Slave Lake, there was no substructure based upon sample location observed within the upper and lower Mackenzie River suggesting high gene flow. However, further sampling at spawning locations within the upper and lower Mackenzie River is needed to further understand the genetic diversity in the area. Therefore, the management of Inconnu should continue to be according to the river systems in order to maintain the genetic structure and diversity of Inconnu in Great Slave Lake. However, future work should consider focusing efforts on sampling within river systems and not the mouth of river systems. Collecting samples from spawning grounds within river systems, and unsampled river systems around Great Slave Lake will increase our understanding of the unit stock structure of Inconnu contributing essential information for mixed stock fishery analysis.

## CRediT authorship contribution statement

**Lauren N. Wiens:** Conceptualization, Investigation, Formal analysis, Writing - original draft, Writing - review & editing, Funding acquisition. **Robert Bajno:** Methodology, Resources, Writing - review & editing. **Muhammad Yamin Janjua:** Funding acquisition, Writing - review & editing. **Jillian T. Detwiler:** Supervision, Conceptualization, Writing - original draft, Writing - review & editing. **Ross F. Tallman:** Project administration, Conceptualization, Funding acquisition, Writing - review & editing.

## Declaration of Competing Interest

The authors reported no declarations of interest.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2020.105784>.

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