

Genetic structure and within-generation genome scan analysis of fisheries-induced evolution in a Lake Whitefish (*Coregonus clupeaformis*) population

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Abstract Size-selective harvest may lead to over-exploitation of commercial fisheries, but the population genetic and evolutionary consequences of such practices remain poorly understood. We investigated the role of within-generation selection in a historically over-exploited Lake Whitefish (*Coregonus clupeaformis*) population associated with fisheries-induced evolution in Lesser Slave Lake, Alberta, Canada. DNA from archived scales of Lake Whitefish collected between 1986 and 1999 were genotyped at 20 microsatellites and 51 gene-coding SNPs associated with growth and reproduction. We found that the Lake Whitefish in Lesser Slave Lake consisted of a single genetic stock, with microsatellites revealing more temporal than spatial variation in allele frequencies. A comparative genome scan among replicate cohorts from commercially harvested versus random survey samples identified one candidate SNP under divergent selection. This SNP localized within a gene encoding nucleoside diphosphate kinase A, a protein associated with differential growth. Collectively, the results highlight the utility of within-generation genome scans towards investigating the evolutionary consequences of harvest in the wild.

Keywords *Coregonus* · Lake Whitefish · SNP · Archived DNA · Historical DNA · Fisheries-induced evolution · Within-generation selection

Introduction

Understanding the genetic bases of adaptive phenotypic change is a fundamental question in evolutionary biology (Lewontin 1974; Orr and Coyne 1992; Stinchcombe and Hoekstra 2008). How populations respond to environmental change is increasingly relevant to their survival given the speed at which evolution can occur, especially with respect to human induced selection pressures (Hendry and Kinnison 1999; Palumbi 2001; Fenberg and Roy 2008; Smith and Bernatchez 2008; Allendorf and Hard 2009; Darimont et al. 2009; Sih et al. 2011). Selection studies in the wild and experimental evolution studies in the laboratory have confirmed that evolutionary change and adaptation can be rapid, occurring within a few generations (e.g., Reznick et al. 1997; Jørgensen et al. 2007; Conover and Baumann 2009; Audzijonyte et al. 2013) or even a single generation (e.g. Barrett et al. 2008; Christie et al. 2012). However, the rapid evolutionary outcomes stemming from anthropogenic selection are frequently detrimental to humans and often occur with unforeseen consequences, such as the evolution of pesticide resistance or resistance to antibiotics (Bayer et al. 2013; Carroll et al. 2014). Consequently, given the emerging goal of limiting human-induced evolutionary change, it is crucial to understand the links between genotype, phenotype and selection.

Commercially harvested fish are considered large-scale experiments in evolution (Rijnsdorp 1993) given the selective harvest of larger sized fish in most fisheries (Stokes and Law 2000; Law 2007; Kuparinen and Merilä 2007; Audzijonyte et al. 2013). Such harvest-induced evolution must meet two criteria to occur: (1) the fishing must be selective for phenotypic traits; and (2) those traits must be heritable (Enberg et al. 2012). Size-selective harvesting for larger fish has ubiquitously resulted in

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populations with lower average ages and sizes at maturation (Handford et al. 1977; Ricker 1981; Law 2000; Heino and Godø 2002; Swain et al. 2007; Hansen et al. 2009; Sharpe and Hendry 2009). Although previous experiments have attempted to tie selection pressure against larger fish directly to the phenotypic response of slower growth, debate continues over whether population changes are genetically or environmentally determined (Walsh et al. 2006; Enberg et al. 2012). For example, four generations of strong directional selection in an experiment on Atlantic silverside (*Menidia menidia*) resulted in significantly lower average weight-at-age and juvenile growth rates in the populations where the largest individuals were selected against (Conover and Munch 2002). Although heritability in growth rate has been shown, insights into fisheries-induced evolution in natural populations remain limited in the absence of including ecological, genetic or environmental factors (Hilborn 2006).

Integrated approaches that connect genotype, phenotype and fitness are being increasingly applied to natural populations subject to selection (e.g., Dalziel et al. 2009; Jakobsdóttir et al. 2011; Pukk et al. 2013) and are relevant to address fisheries-induced evolution. Yet, to our knowledge only one study has assessed whether size-selective harvesting generates detectable changes at gene loci over short time scales and this was a controlled experiment in guppies (van Wijk et al. 2013). Despite the advent of recent methods that take environmental conditions into account (e.g., Gaggiotti et al. 2009; Kuparinen et al. 2012), disentangling demographic and evolutionary effects continues to be a primary issue in ruling out the role of environmental factors in modulating phenotypic changes due to overharvest (Kuparinen et al. 2009). A potential solution to this problem involves testing whether fisheries impose a selective bias on growth. Namely, whether the design of commercial gill nets catches individuals of greater size and higher condition factor, i.e., the fastest growing fish at a certain age, while allowing smaller fish to survive (Hamley 1975; Handford et al. 1977; Carol and Garcia-Berthou 2007). To test the size-selective bias of gill net sizes commonly used in fisheries, a comparison is required. Multi-mesh test netting surveys (MMTN) uses multiple sizes of gill nets, are widely used to survey fish stocks by governmental agencies and allows for a less biased, more representative sampling of the population with respect to size (Clay 1981) that is suitable for fisheries management (Acosta 1997).

Lake Whitefish (*Coregonus clupeaformis*) are a post-glacial salmonid found in cold, freshwater lacustrine environments across the Northern hemisphere (Reshetnikov 1988; Mee et al. 2015). In several lakes across Canada, the life history of the Lake Whitefish include

sympatric species pairs that have rapidly evolved in association with limnetic and benthic environments in the last 15,000 BP (Landry et al. 2007; Bernatchez et al. 2010; Mee et al. 2015). Remarkably, the limnetic (dwarf) ecotype resembles the phenotype of many fishes that have undergone fisheries-induced evolution and is smaller at maturity, has a higher basal metabolic rate, a younger age at maturation and lower fecundity (Fenderson 1964; Rogers et al. 2002; Rogers and Bernatchez 2007; Bernatchez et al. 2010). Recently, 89 SNPs functionally annotated to genes involved in energy metabolic functions that also showed large allele frequency differences between dwarf and normal Lake Whitefish ecotypes in nature, were characterized. These included genes underlying metabolism and condition factor associated with smaller fish that reproduce earlier (Renaut et al. 2010, 2011).

In Lesser Slave Lake, Alberta, Canada, a commercial fishery for several species (including Lake Whitefish) has been operating since the turn of the 20th century. Median sizes of harvested Lake Whitefish have decreased significantly since measurements on them began (McCombie and Fry 1960; Handford et al. 1977). Handford et al. (1977) represented the first published inference of contemporary evolution driven by selective harvesting, with the agent of selection thought to be gill nets targeting larger, slower growing, and early maturing fish (Palumbi 2001). The Lesser Slave Lake fishery experienced a stock collapse resulting in the closure of the fishery from 1965 until 1972. The minimum mesh size increased in the late 1990s from 127 to 140 mm and the fishing quotas have increased steadily since the mid-1990s (Alberta Environment and Sustainable Resource Development Fisheries and Wildlife Management Information Systems 1996–2015).

Our first objective was to test the genetic population structure of Lake Whitefish in Lesser Slave Lake, Alberta, Canada using 20 neutral microsatellite genetic markers. We used archived fish scales collected from fisheries management censuses to account for different lake regions (see next section for details). Second, based on the availability of these temporal archived samples to reflect a random removal of fish with respect to size and age (following MMTN survey techniques), we investigated temporal stability in genetic diversity and effective population sizes with microsatellites. Third, given that the removal of specific phenotypes (e.g., in this case bigger fish) is predicted to implicate a non-random removal of genetic variants in association with these phenotypes (Schwartz et al. 2007; Enberg et al. 2012), we performed an outlier analysis using functional SNPs from Renaut et al. (2011) to compare genetic divergence (F_{ST} values) between multi-mesh and gill net caught individuals.

Materials and methods

Study area and sampling collection

Lesser Slave Lake is located in the North-central region of Alberta, Canada (55°26'26"N, 115°29'19"W), with a surface area of 1168 km². Two sources of Lake Whitefish samples were collected. First, scale samples were collected by Alberta Environment and Sustainable Resource Development (AESRD) for population census estimates in 1986 and 1999 using MMTN surveys (ranging from 38 to 140 mm gill nets) that catch fish in a less selective manner with respect to size and age. Second, tissue samples were collected by commercial fishermen using 127 mm size-selective gill nets in years spanning from 1992 to 1996. For each sample, weight and lengths were recorded and scales from each individual were packaged into separate envelopes and stored in a dry environment. Samples from individuals caught using MMTN surveys in 1986 (n = 192, 10 locations) and 1999 (n = 192, 23 locations) encompassed the geographic range of the lake and were used for genetic population structure and temporal stability analyses (Fig. 1). Samples from individuals caught by MMTN surveys (n = 137, 32 locations) and by commercial gill net fishery (n = 139) were chosen from three distinct cohorts for the genome scan selection analysis (Table 1).

Sample preparation and genotyping

Total DNA was extracted from scale samples using a DNA spin-column binding method (Qiagen DNeasy Blood and Tissue Extraction Kit, Qiagen, Venlo, Netherlands) modified to increase DNA yield. Genomic DNA was run in 1 % w/v low-melting-point agarose with SYBR[®]-safe DNA Gel Stain (Invitrogen, Carlsbad, CA, USA) to observe potential DNA degradation in the archived samples.

Table 1 Number of samples (N) for each of three cohorts (A, B, and C) caught using multi-mesh test netting surveys (MMTN) and commercial gill net fishery for selection analyses

Cohort	Year class	MMTN		Gill nets	
		Age	N	Ages	N
A	1985	1	46 (37)	8 and 9	46 (46)
B	1984	2	45 (42)	9 and 10	47 (46)
C	1983	3	46 (41)	10 and 11	46 (45)

Year class represents the cohort and the age given is the age at which the individual was caught. Numbers in brackets are the samples that passed genotyping quality checks and were used in subsequent analyses

PCR was performed on 384 individuals from 1986 and 1999 using microsatellite primers previously characterized for Lake Whitefish (Rogers et al. 2004). Forward primers were labelled with the fluorescent tags FAM, NED, VIC, and PET represented by the superscripts, ^{F,N}, ^V, and ^P, respectively. The 20 microsatellite loci primers used were BWF2^F, Cocl4^V, Cocl6^V, Cocl8^V, Cocl10^P, Cocl18^F, Cocl22^V, Cocl32^P, Cocl41^F, Cocl45^N, Cocl49^N, Cocl52^V, Cocl61^P, Cocl68^F, Cocl74^N, Cocl216^P, C2-157^F, C2-5B^P, C3-152^F, and C4-17^F. The data for an additional six loci were excluded due to poor amplification (Cocl5^F, Cocl19^P, Cocl80^N) or low levels of polymorphism (Cocl224^P, Cocl11^N, PPY-300^P). A 10 µl PCR reaction was performed in an ABI C1000 thermocycler (Applied Biosystems, Carlsbad, CA, USA) and included 0.25 mM of dNTPs, 0.1 µM of forward and 0.1 µM of reverse primers, 10× NEB Taq DNA polymerase buffer, 1 U of NEB Taq DNA polymerase, 0.2 mg/ml of BSA, 5.35 µl of ddH₂O, and ca. 10 ng of DNA template. The thermocycler program included an initial denaturing step at 95 °C for 5 min, followed by 30 cycles of 95 °C for 1 min, 55–59 °C for

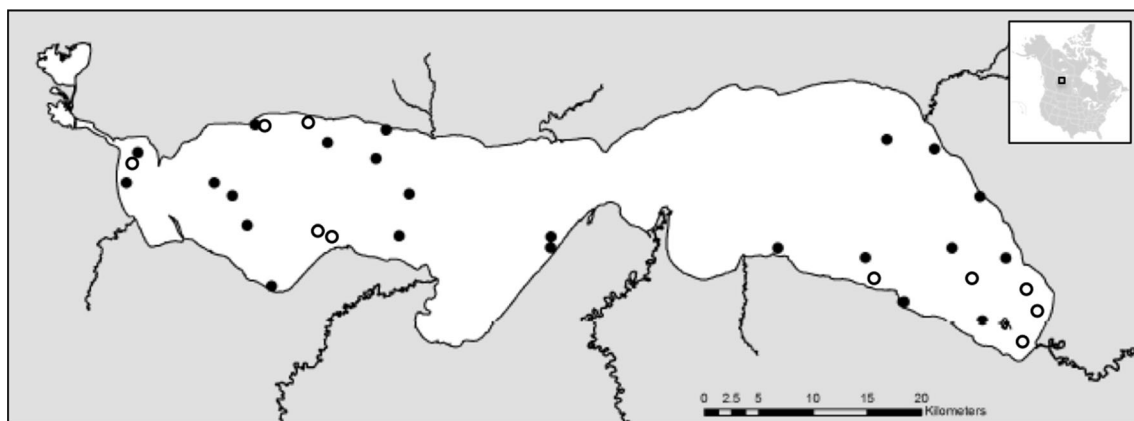


Fig. 1 Sampling locations of Lake Whitefish caught in Lesser Slave Lake in 1986 (open circles) and 1999 (closed circles) for population genetic analyses

30 s and then 72 °C for 45 s. Finally, an elongation step of 72 °C for 10 min allowed for additional polymerization time. Annealing temperatures are primer specific (Rogers et al. 2004). An equal mixture of FAM-, NED-, VIC-, and PET-labelled PCR products were pooled and 1 µl was mixed with 50 µl of GeneScan 500 LIZ size standard (Applied Biosystems) and 1000 µl of Hi-Di™ Formamide (Applied Biosystems) before the products were denatured at 95 °C for 5 min. The denatured PCR products were then separated by automated electrophoresis on an ABI 3500XL sequencer so that the alleles could be visualized and scored against an internal size standard using Genemapper™ 4.0 software (Applied Biosystems). The genotypes for these 384 samples were subsequently used in genetic population structure and temporal stability analyses.

For selection analysis, DNA samples from 284 (276 samples and 8 controls) Lake Whitefish were genotyped at the Genome Quebec Innovation Center (McGill University, Montreal, Canada) on two Sequenom (San Diego, CA, USA) Affymetrix (San Clara, CA, USA) GeneChip SNP panels containing 40 SNPs each using matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF). SNP panels were designed by Sequenom, Inc. at Genome Quebec Innovation Centre using genotyping assays reported in Renaut et al. (2011). This included positive controls for SNP genotyping assays from Lake Whitefish DNA originally used in the SNP development study.

Genetic and genotypic variation using microsatellites

Standard genetic diversity indices for both microsatellites and SNPs were calculated using GENEPOP 4.0 (Raymond and Rousset 1995) and estimates of allelic richness for each locus (corrected for sample size) were calculated in FSTAT 2.9.3 (Goudet 1995). Tests for allelic dropout with microsatellite loci, null alleles and allelic scoring errors at each locus were assessed by constructing randomized genotypes for observed alleles for each locus within samples such that observed genotypes could be compared with the randomized genotype distributions in MICRO-CHECKER 2.2.3 (Van Oosterhaut et al. 2004). Significant deviations from Hardy–Weinberg (HW) proportions were then compared with the occurrence of null alleles, short allele dominance, and/or potential scoring errors.

Genotypic frequencies and exact tests of Hardy–Weinberg Equilibrium were calculated for each locus, or pair of loci for linkage disequilibrium tests, using a modified version of Fisher's exact test of Hardy–Weinberg proportions with 10,000 dememorization steps and 5000 Markov chain iterations in each of 100 batches (Guo and Thompson 1992) using GENEPOP 4.0 (Raymond and Rousset 1995).

Bonferroni *p* value corrections (Holm 1979) and false discovery rate method (Benjamini and Yekutieli 2001) were implemented with the MULTTEST (Pollard et al. 2005) package in R (R Core Team 2013) to adjust for Type I errors stemming from multiple comparisons.

Genetic population structure

The probability of $K = 1–14$ genetic clusters (corresponding to sampling sites), with 20 replicates of each putative K cluster, was performed in STRUCTURE 2.3.3 (Pritchard et al. 2000) using 100,000 burn-in iterations and 700,000 MCMC iterations assuming admixture and correlated allele frequencies with the microsatellite data. Replicate runs of populations (K) with the highest $\ln(P)$ were used to infer the most likely number of populations in both the 1986 and 1999 sampling periods. Genetic differentiation (θ_{st}) was calculated in FSTAT 2.9.3 (Goudet 1995).

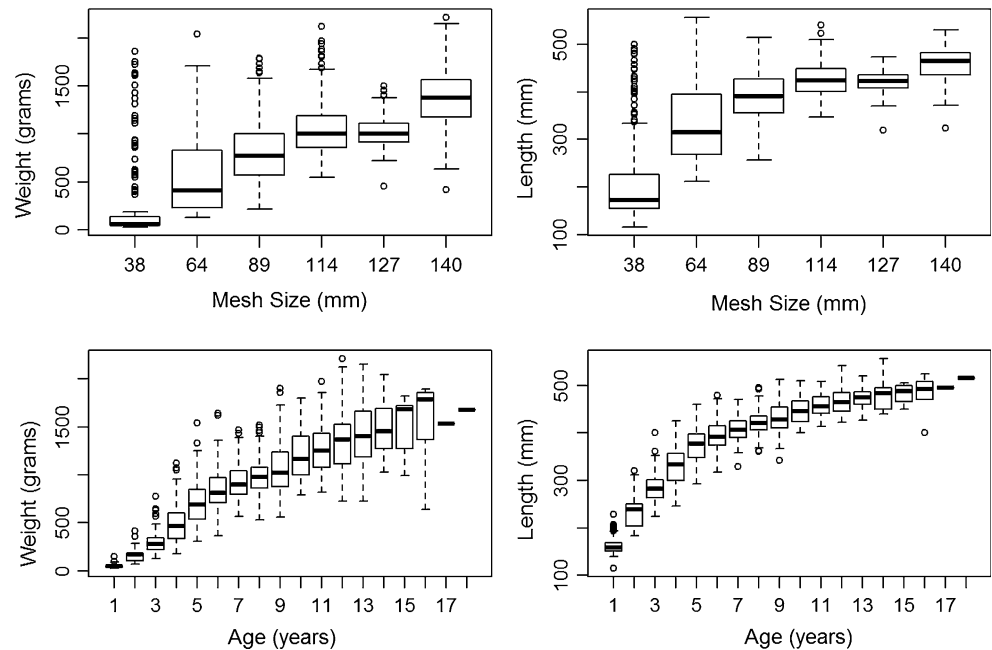
Bottlenecks

The Lesser Slave Lake fishery experienced a stock collapse in 1965, resulting in the closure of the fishery until 1972 (Handford et al. 1977). To test for possible historical bottlenecks, a Wilcoxon sign test, implemented in the software BOTTLENECK 1.2.02 and using microsatellite loci data was performed (Cornuet and Luikart 1996; Piry et al. 1999). This allowed comparisons for whether observed heterozygosity frequencies were significantly higher than those expected under three different microsatellite mutation models; the Infinite Allele Model (IAM) (Kimura and Crow 1964), the Step-wise Mutation Model (SMM) (Kimura and Ohta 1978) and the Two Phase Model (Di Rienzo et al. 1994). The TPM variance was set at 30.00, the proportion of TPM which were SMM was set at 70 % and the simulation was run for 10,000 replications.

Effective population sizes estimates using microsatellites

Effective population size (N_e) was calculated by a point estimation method using linkage disequilibrium (Hill 1981; Waples 2006) and a temporal method using moments-based *F*-statistics (Waples 1989) in NeESTIMATOR v2 (Do et al. 2013). For the temporal method implemented, the year 1986 was considered generation 0 and 1999 was considered generation 5, based on a generation time of 3 years in Lake Whitefish (Nei and Tajima 1981). A conservative estimation of generation time of 3 years in Lake whitefish was chosen because the time to first reproduction is indicative of the speed at which a population could change (by selective or neutral processes) in a given time period (Campbell and Bernatchez 2004). In both methods, 0.01 was the lowest

Fig. 2 Phenotypic size variation for length and weight of Lake Whitefish caught in multi-mesh test netting surveys (MMTN) as well as for different ages. Dots outside the whiskers represent outliers defined by 1.5 times the inter-quartile-range. Note that commercial fishery nets have a mesh size of 127 mm



allele frequency permitted in the analysis. Multiple methods were employed since alternative methods may lead to different estimates of N_e , and congruence between methods must be checked (Fraser et al. 2007).

F_{ST} outlier analysis

F_{ST} outlier analyses were performed for each cohort on all SNP loci using LOSITAN which implements Fdist to evaluate the relationship between F_{ST} and expected heterozygosity under an island model of migration with neutral markers (Lewontin and Krakauer 1973; Beaumont and Nichols 1996; Antao et al. 2008). The null distributions were created by running 50,000 simulations and the observed data were plotted against this distribution in order to locate outlier loci above the 95 % confidence intervals. Neutral mean F_{ST} values were calculated after an initial set of 50,000 simulations removed loci found to be outside of 95 % confidence intervals in order to reduce bias (Beaumont and Nichols 1996). Any locus located above the confidence intervals when comparing MMTN and gill net fishery populations, for each cohort, was considered an F_{ST} outlier, and a candidate under divergent selection (Antao et al. 2008).

Results

Phenotypic variation

Phenotypic variation in sizes of Lake Whitefish samples was observed with standard deviations of weight and length, respectively, ranging from 18.29 g and 17.57 mm

for one year olds to 486.41 g and 43.91 mm in sixteen year old fish. Size variation in association with mesh size catches highlighted the relative catch biases of commercial nets as smaller mesh sizes catch smaller fish on average (127 mm was the mesh size of commercial fisheries during the period of study and MMTN surveys include all mesh sizes, Fig. 2). Commercial fisheries captured individuals ranging in size from 460–1500 g and 319–475 mm in weight and length, respectively. In contrast, MMTN using various mesh sizes, captured individuals ranging in size from 30–2210 g and 115–532 mm in weight and length, respectively (Fig. 2). Overall, the coefficient of variation for weight in MMTN survey individuals (0.56) was over three times greater than that of individuals caught in 127 mm commercial fishery nets (0.16). The same is true in lengths of individuals where the coefficient of variation for MMTN survey individuals (0.24) was nearly five times greater than that of individuals caught in 127 mm commercial fishery nets (0.05) (Fig. 2).

Genotyping

DNA was isolated for 100 % of the samples (n = 384) with an amplification of microsatellite loci success rate of 83.0 % (6371/7680). The lowest amplification success rate (81.6 %) occurred in 1986 samples and the highest (84.3 %) occurred in the 1999 samples. Out of 276 archived samples assayed on the SNP chip, 257 (93.1 %) passed sample performance quality checks with greater than 80 % call rates on SNP loci. DNA concentrations of samples that passed quality checks ranged from 0.045 to 24.99 ng/μL. Fifty one out of 80 markers (63.8 %) passed

Table 2 Expected and observed heterozygosity for each SNP locus with allele frequency for most common allele as well as F_{IS} and HWE test p values before multiple test correction (values in bold are significantly deviated from HWE expected values after multiple test correction)

Locus	Accession Number	N	Alleles			Heterozygosity			HWE
			Major	Minor	Major Freq.	He	Ho	F_{IS}	p value
BU965641_re5_27	BU965641	254	A	G	0.650	0.456	0.630	-0.382	< 0.001
CA037452_re5_29	CA037452	256	A	G	0.778	0.347	0.336	0.032	0.592
CA038170_NDBC	CA038170	239	A	G	0.887	0.201	0.209	-0.042	0.747
CA038790_re5_57	CA038790	256	C	T	0.926	0.138	0.148	-0.078	0.373
CA042792_622 W	CA042792	256	A	T	0.650	0.456	0.418	0.083	0.218
CA042951_ND	CA042951	251	A	C	0.757	0.369	0.375	-0.016	0.864
CA044550_ca20_4	CA044550	254	T	G	0.825	0.290	0.287	0.008	>0.999
CA044613_NDBC	CA044613	225	G	T	0.620	0.472	0.600	-0.271	< 0.001
CA049476_re5_101	CA049476	253	A	G	0.557	0.494	0.830	-0.681	< 0.001
CA051860_BC	CA051860	244	C	T	0.695	0.425	0.520	-0.225	< 0.001
CA052650_148 M	CA052650	234	C	A	0.797	0.324	0.380	-0.173	0.008
CA054079_re5_14	CA054079	248	G	T	0.682	0.435	0.629	-0.447	< 0.001
CA054630_BC	CA054630	257	C	A	0.940	0.114	0.121	-0.062	0.609
CA054959_380R	CA054959	256	C	T	0.500	0.501	1.000	-1.000	< 0.001
CA058958_re5_26	CA058958	254	C	T	0.866	0.232	0.220	0.051	0.418
CA060324_154 M	CA060324	247	C	A	0.502	0.501	0.891	-0.781	< 0.001
CA062071_NDBC	CA062071	240	G	T	0.821	0.295	0.350	-0.188	0.002
CA063046_219 W	CA063046	248	T	A	0.567	0.492	0.488	0.009	0.896
CA063623_352 M	CA063623	247	T	G	0.541	0.498	0.595	-0.196	0.002
CB492682_re5_136	CB492682	247	G	T	0.935	0.121	0.121	-0.001	>0.999
CB492813_188 K	CB492813	232	G	T	0.761	0.365	0.341	0.067	0.371
CB496486_re5_37	CB496486	225	A	C	0.816	0.302	0.324	-0.076	0.371
CB497584_re3_2	CB497584	254	A	G	0.612	0.476	0.760	-0.599	< 0.001
CB497894_re5_154	CB497894	256	C	T	0.584	0.487	0.707	-0.454	< 0.001
CB498771_re5_67	CB498771	255	C	T	0.967	0.065	0.067	-0.033	>0.999
CB511030_339 K	CB511030	252	G	T	0.853	0.251	0.254	-0.012	>0.999
CB516686_131R	CB516686	256	G	A	0.951	0.093	0.098	-0.049	>0.999
CX030416_re5_72	CX030416	248	T	C	0.998	0.004	0.004	0.000	>0.999

N number of samples, He expected frequency of heterozygotes, Ho observed frequency of heterozygotes

quality checks with greater than 80 % call rates on DNA. Out of 51 loci that passed quality checks, 28 loci were polymorphic and genotypes for these were retained for further analyses (Table 2).

Genetic and genotypic variation

From samples caught by MMTN surveys, the number of microsatellite alleles ranged from 2 to 24 with an average of 7.5 alleles per locus. HWE exact tests for 1986 and 1999 samples suggested nine and five loci were not in HWE ($n = 40$, $\alpha_{\text{corr}} = 0.05$) after multiple test correction, respectively. Linkage disequilibrium tests for 1986 and 1999 populations found no pairs of loci exhibiting linkage disequilibrium ($n = 380$, $\alpha_{\text{corr}} = 0.05$) after multiple test correction. Tests for allelic dropout, null alleles and allelic

scoring errors at each locus revealed that 4 out of 20 loci showed evidence for null alleles by homozygote excess, 0 out of 20 loci showed evidence for scoring errors due to stuttering and 0 out of 20 loci showed evidence for allelic dropout. HWE exact tests found 11 SNP loci that were not in HWE ($n = 28$, p value <0.05) after multiple test correction (Table 2). Frequencies of major alleles ranged from 0.502 to 0.998. Linkage disequilibrium tests found one pair of SNP loci (CA054079_re5_14 and CA062071_NDBC) in linkage disequilibrium ($n = 351$, p value <0.05) after multiple test correction.

Population structure

Bayesian clustering analysis as implemented in STRUC-TURE suggested an absence of genetic population

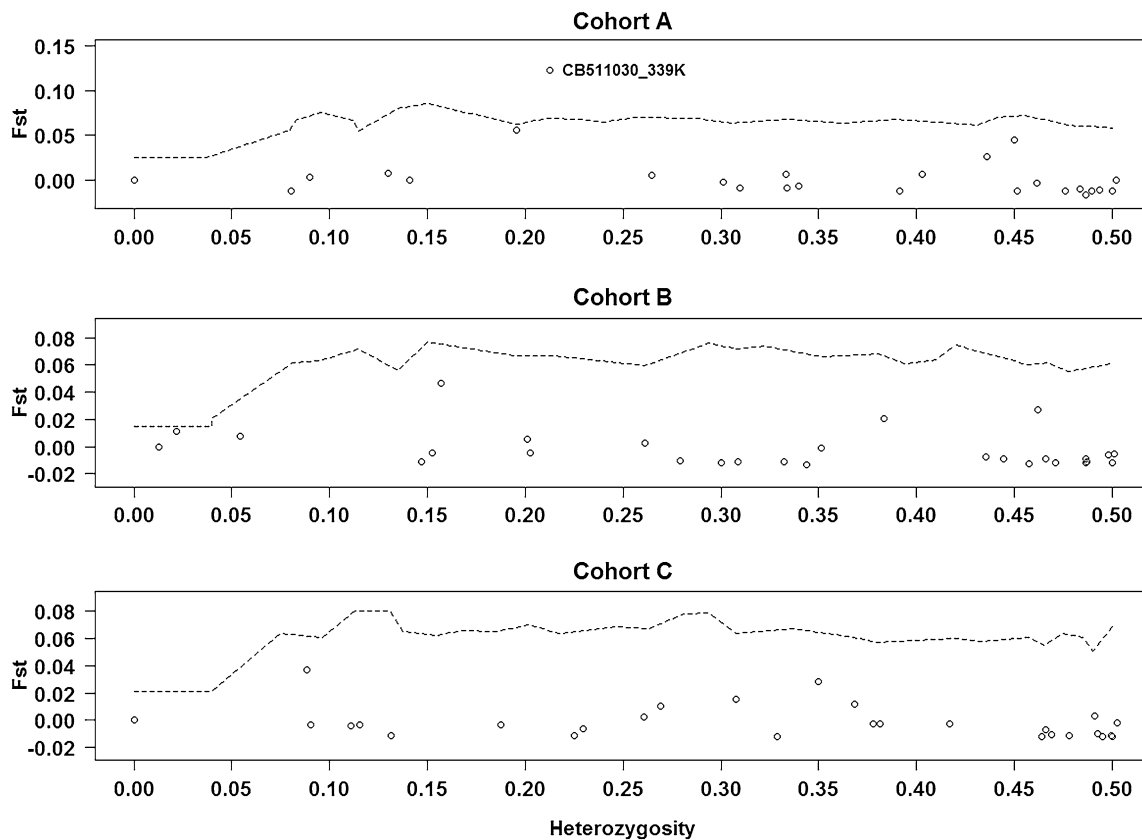


Fig. 3 F_{ST} outlier analyses results showing SNP loci and 95 % CI for divergence between multi-mesh test netting surveys (MMTN) and commercial fishery samples in three separate cohort analyses. The outlier locus shown to be under divergent (positive) selection is labelled

structure in the 1986 ($K = 1$) and weak evidence in the 1999 samples ($K = 1$ or 2). A population without structure was used for subsequent analysis since assignment of the 1999 samples to two putative K clusters was weak, did not reflect lake geography, and was not supported by genetic differentiation metrics ($\theta_{st} = 0.005$, 95 % CI 0.001–0.013). Temporal population differentiation between 1986 and 1999 was low, yet significant ($\theta_{st} = 0.023$, 95 % CI 0.001–0.066), suggesting that while Lesser Slave Lake Whitefish likely represent only one genetic stock, there have been temporal changes in the genetic composition of samples over the time period observed.

Bottlenecks

Wilcoxon sign tests revealed no significant deviations from expected heterozygosity frequencies under any of the assumptions of IAM, SMM and TPM (p value = 0.636 for IAM, p value = 0.999 for SMM, and p value = 0.999 for TPM) in the 1986 population. Nor were there any significant deviations in the 1999 population (p value = 0.115 for IAM, p value = 0.999 for SMM, and p value = 0.989 for TPM).

Effective population size estimates

Point-based linkage disequilibrium methods revealed a smaller N_e estimate in 1986 (437.1, 95 % CI 302.5–748.4) than in 1999 (5008.2, 95 % CI 847.5–Infinite), respectively. Temporal based methods using both the 1986 and 1999 data (as the generation time difference is expected to be informative based on our sample size and number of alleles present, Wang and Whitlock 2003) resulted in a lower N_e estimate (113.6, 95 % CI 77.7–165.7).

F_{ST} outlier analysis

F_{ST} outlier analysis between MMTN and gill net individuals revealed that one SNP out of 28 (3.6 %) was a significant outlier beyond the computed 95 % confidence intervals after an FDR of 0.05 was applied. CB511030_339K diverged above the 95 % confidence intervals when Cohort A (corresponding to the 1985 year class) was analyzed with an F_{ST} value of 0.123 compared with the median F_{ST} value of -0.006 (Fig. 3). When the full sequence was compared (BLASTn) against NCBI’s GenBank, CB511030_339K matched a cloned sequence from Zebrafish (*Danio rerio*) (e-

value = $7E-12$) and a Unigene EST cluster from Atlantic salmon (*Salmo salar*) encoding nucleoside diphosphate kinase A (e -value = $4E-9$).

Discussion

Our main objective was to gain insight on the potential population genetic consequences of selective harvesting in a commercially fished population of Lake Whitefish. We discovered that the commercial mesh-sizes used by the Lesser Slave Lake commercial fishery captured a fraction of the variation in size of individuals (less than half of the weight variation and even less in length variation) compared to what was captured with MMTN. These results suggest that Lake Whitefish become vulnerable to commercial mesh sizes as they near 400 mm in length. Interestingly, this result was also reflected in Handford et al. (1977), where the size-structure had become truncated at essentially the same length by 1975. Collectively, these results provide evidence that this commercial fishery selected against larger fish.

By elucidating the genetic population structure of Lake Whitefish in Lesser Slave Lake, we investigated temporal stability in genetic diversity and effective population sizes over time. We further performed an outlier analysis to compare SNP loci associated with growth and reproduction in Lake Whitefish between MMTN surveys and gill net fishery to test the prediction that gill net fishing and the removal of large fish was associated with a non-random removal of genetic variation at functional SNPs within generations of three cohorts. No genetic population structure was found between basins in the 1986 or 1999 individuals, which was surprising when considering the size of the lake and previous estimates of microgeographic population structure for salmonids within in intra-lacustrine environments (Dupont et al. 2007; Hale et al. 2012). While a narrow, shallow channel separates both basins (Fig. 1), our results suggest that this channel does not act as a barrier to dispersal. The philopatric nature of salmonids, including Lake Whitefish (e.g., Scheerer et al. 1985; Walker et al. 1993), could potentially limit gene flow between these basins similar to other lacustrine salmonids (Fraser et al. 2004; Hendry et al. 2004; Ramstad et al. 2004; Golder Associates 2006), yet such population genetic patterns were not evident over two distinct time periods in our study. Additionally, microsatellites revealed more temporal than spatial variation in allele frequencies, which may be significant in the context of our inferred changes in N_e (Coltman 2008).

By using SNPs characterized in sympatric Lake Whitefish ecotypes, we identified one outlier SNP exhibiting within-generation selection in the 1985 year class. The proportion of outlier loci detected (3.6 %) is consistent to

other studies that have examined recent population divergence in other systems (Nosil 2008), including in other Lake Whitefish populations (Bernatchez et al. 2010; Renaut et al. 2011). This SNP is part of an EST cluster encoding nucleoside diphosphate kinase A, a necessary enzyme for the catabolic production of adenosine triphosphate (ATP) (Rise et al. 2004). Interestingly, this SNP was also under strong selection between dwarf (slow growing) and normal (fast growing) ecotypes of Lake Whitefish in Eastern North America (Renaut et al. 2011; Gagnaire et al. 2013). Given that higher metabolic rates require more upregulation of ATP biosynthesis genes, including nucleoside diphosphate kinase A, such findings offer at least some initial evidence that commercially selected Lake Whitefish fish may exhibit distinct resource allocation and metabolism rates. Overall, non-random size selection associated with gill nets was reflected at the genetic level in our samples, and may be associated with unintended phenotypic effects from fishing that have been previously documented in Lesser Slave Lake, i.e., slower growing fish that mature earlier (Handford et al. 1977). These results are consistent with recent observations in fishes that such selection can occur and be measured in at little as a generation (Bourret et al. 2014). To this end, more thorough genome scans and direct links to putatively selected phenotypes (e.g., body size and growth) and fitness are required to understand the evolutionary genetic consequences of harvest.

One of the main criticisms of F_{ST} outlier methods is that they assume that populations with gene flow have gene frequencies that are independent of each other and that their distributions are approximately normal (Lewontin and Krakauer 1973; Beaumont 2005). In our study, Lake Whitefish share the same history and constitute a single population. Also, there may be some upward bias of the null distribution of genetic markers due to the types of SNP ascertained. A small fraction (25 %) of the SNPs were developed based on genes identified from microarray data as differentially expressed between whitefish ecotypes (Renaut et al. 2011). This may have increased our upper outlier threshold, potentially excluding other true outliers. Our SNP assay was employed as a preliminary method for detecting loci under selection, but future studies would benefit from genome-wide coverage using genotyping-by-sequencing methods (De Wit and Palumbi 2013; Gagnaire et al. 2013; Narum et al. 2013). Finally, the lack of theoretical models for measuring changes in the distribution of a trait using within-generation genome scans renders the disentanglement of direct selection on a trait with indirect selection on correlated traits (or both) more difficult (Endler 1986; Brodie et al. 1995; Hoekstra et al. 2001; Kingsolver and Pfennig 2007).

In summary, despite the relatively low numbers of markers used, we characterized genetic structure and

detected an F_{ST} outlier SNP divergent between MMTN surveys and commercially harvested gill net individuals, suggesting that selection from harvest can occur rapidly, i.e., within a generation, in a commercial fishery. Large size-selective gill nets remove faster growing fish that are larger at a given age and retain slow growing fish whose phenotypes are reminiscent of the dwarf ecotype (Hamley 1975; Enberg et al. 2012). In addition, significant temporal variation of microsatellite allele frequencies in this genetic stock occurred between 1986 and 1999. However, we cannot elucidate whether harvest or other environmental changes may be affecting population demographic structure (e.g., age structure, sex ratio, Coltman 2008), which in turn may impact effective population size and genetic diversity in Lesser Slave Lake Whitefish. Collectively, these results support the hypothesis that gill nets are likely a selective force associated with evolutionary change in this population, consistent with Handford et al. (1977). Future studies will benefit from the closer examination of within-generation selection to account for drift and other population genetic consequences that may be associated with N_e and structured stocks in cases of potential fisheries-induced evolution.

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Data accessibility Raw data for this study are available upon request and will be archived in Dryad. Accession number for outlier loci on NCBI nucleotide database was CB511030.

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Compliance with Ethical Standards

Conflict of interest We declare no conflict of interest.

Ethical standards The study was certified by the Life and Environmental Science Animal Care Committee (Rogers AC13-0040) in accordance with the Canadian Council for Animal Care ethical standards.

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