

The role of ecotype-environment interactions in intraspecific trophic niche partitioning subsequent to stocking

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Abstract. Worldwide, stocking of fish represents a valuable tool for conservation and maintenance of species exploited by recreational fishing. Releases of hatchery-reared fish are more and more recognized to have numerous demographic, ecological, and genetic impacts on wild populations. However, consequences on intraspecific trophic relationships have rarely been investigated. In this study, we assessed the impacts of supplementation stocking and resulting introgressive hybridization on the trophic niches occupied by stocked, local, and hybrid lake trout (*Salvelinus namaycush*) within populations of piscivorous and planktivorous ecotypes stocked from a wild piscivorous source population. We compared trophic niches using stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and trophic position among the three genetic origins. Putative genetic effects were tested with phenotype-genotype association of “life history” ecological traits (body size, growth rate, condition index, and trophic niche) and genotypes (RADseq SNP markers) using redundant discriminant analysis (RDA). Results showed that sympatry resulting from the stocking of contrasting ecotypes is a risk factor for niche partitioning. Planktivorous populations are more susceptible to niche partitioning, by competitive exclusion of the local fish from a littoral niche to an alternative pelagic/profundal niche. Observed niche partitioning is probably a manifestation of competitive interactions between ecotypes. Our results emphasize that ecotypic variation should be considered for more efficient management and conservation practices and in order to mitigate negative impact of supplementation stocking.

Key words: genotype-by-sequencing; introgressive hybridization; lake trout; life history; phenotype-genotype association; RADseq; salmonids; stable isotopes; supplementation stocking.

INTRODUCTION

The goals of human-mediated translocation of fish are manifold, as exemplified by the diverse terminology (i.e., put-and-take, conservation, fishery enhancement) developed to classify stocking activities (Utter and Epifanio 2002, Arahamian et al. 2003). Population declines or low productivity of species being exploited either by commercial or recreational fisheries (Post et al. 2002) have been commonly compensated by supplementation stocking. Specifically, objectives of supplementation may be defined as aiming to increase or maintain targeted fish stock at sustainable exploitation levels, a situation particularly common in anglers’ seeking after salmonid populations (Cowx 1994, Arahamian et al. 2003, Araki et al. 2008).

Hatchery and stocking practices may vary among jurisdictions or be species specific, but are generally based on an artificial hatchery production of the target species preceding their release into the wild. While supplementation may represent an efficient method for preservation of wild populations, concerns about its potential negative impacts have long been raised (Allendorf et al. 2001, Araki et al. 2009, Vandersteen et al. 2012, Hutchings 2014).

One of the main concerns regarding supplementation stocking consists in the potential genetic and ecological interactions between stocked and local fish. Hatchery-produced fish could exhibit pronounced ecological or genetic differences compared to their wild counterparts, even when they are progeny of wild broodstock (Weber and Fausch 2003, Christie et al. 2016). In the short term, enhancement of top-predator density could alter trophic networks (Eby et al. 2006). Furthermore, addition of stocked fish may induce deleterious density-dependent phenomena on local populations (Hunt et al. 2014). In the long term, introgressive hybridization between

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stocked and wild fish may affect the integrity of the local populations depending on the extent of reproduction between them (Evans and Willox 1991, Allendorf et al. 2001, Valiquette et al. 2014). Introgression can cause the disruption of coadapted genes and loss of local adaptation (McGinnity et al. 2003, Araki et al. 2009, Muhlfeld et al. 2009, Bourret et al. 2011, Renaut and Bernatchez 2011, Lamaze et al. 2013). Such genetic alteration can have negative consequences on the productivity and the viability of stocked populations (Berejikian et al. 2009, Fraser et al. 2010). However, long-term intraspecific impacts of stocking on trophic niche have seldom been studied. As a consequence, it remains unclear whether divergence between local and stocked fish is sufficient to cause trophic alterations, comparable to the consequences resulting from species introduction (e.g., ecological exclusion or species extirpation). Moreover, the role of introgression in this mechanism is yet to be defined.

Lake trout (*Salvelinus namaycush*) is a large and long-lived salmonid from deep and cold lakes of the Canadian Boreal Shield and the northern United States (Martin and Olver 1980, Scott and Crossman 1998). In its natural distribution range, lake trout exhibit extensive life history variations in terms of trophic niche, growth, maturation time, and body size (Muir et al. 2015). These variations likely reflect the combined influence of environmental conditions, niche availability, and genetics (McDermid et al. 2010, Bernatchez et al. 2016). In small boreal lakes, the two most common ecotypes are tightly linked with the available prey communities. The piscivorous ecotype is observed in lakes hosting large pelagic prey (forage fish or *Mysid* shrimps). Lake trout from the piscivorous ecotype are reaching large size (>600 mm) and are maturing later in life (>9 yr). Whereas trout of the planktivorous ecotype, which are occurring in lakes lacking large pelagic prey (Rasmussen et al. 1990, Shuter et al. 1998), are shown to be smaller fish (~400 mm) with a faster maturation time (>6 yr). There is no record of intraspecific trophic consequences subsequent to supplementation of lake trout. However, a striking case of lake trout trophic niche modification has been reported by Vander Zanden et al. (1999), showing that the introduction of the invasive small-mouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) have profoundly modified the fish community and caused a shift in the trophic niche of this local top predator through competitive interactions (Vander Zanden et al. 2004).

Next-generation sequencing (NGS) now makes possible the rapid sequencing of thousands of single-nucleotide polymorphism (SNP) genetic markers at a more affordable cost, opening the possibility to assess the potential genetic architecture of any given phenotype (Gagnaire and Gaggiotti 2016). This in turn enables the possibility to investigate the consequences of interactions between polygenic traits and habitat variation for conservation and management purposes, namely in the context of stocking (Bernatchez et al. 2016, Laporte

et al. 2016). For instance, in a previous study, we showed that body condition of lake trout hybrid (stocked \times local) is negatively correlated to the proportion of their genotype related to stocked fish (Morissette et al. 2018). This suggested that body condition is a complex polygenic trait affected by multiple genes of small effect rather than few genes of large effect, potentially linked to the ecological incompatibilities between stocked populations and the habitat where it is introduced.

The goal of this study was to assess the intraspecific consequences of supplementation stocking on the trophic niche of lake trout populations of either piscivorous or planktivorous ecotypes from small Boreal Shield lakes. We combined stable isotope analysis and population genomics to test for potential differences in the observed trophic niche of three genetic groups (stocked, hybrid, and local fish) within stocked populations. We tested the hypothesis that the ecotype of the stocking source and recipient populations has an influence on the Lake Trout trophic niche, even years after the last supplementation events. Finally, using genotype information obtained from RADseq genotyping, we tested for a possible genotype–phenotype association resulting in variations of individual fish ecological traits and occupied trophic niche.

METHODS

Study design

Every sampled lake is hosting a single allopatric lake trout population of either planktivorous or piscivorous ecotype. We selected populations based on their known stocking history (or absence of stocking). Selected stocked populations have experienced at least one stocking event during the last 12 years, with a stocking history ≥ 20 yr (Table 1). We also based our selection of populations on hybridization data from a previous study (Valiquette et al. 2014) to avoid highly admixed populations (>75% of stocked genetic background), thus ensuring to collect enough fish to represent the three genetic groups (pure stocked, pure local and hybrids). For comparison, we also sampled unstocked lakes hosting population of both ecotypes.

Stocking history

According to the lakes stocking history (Appendix S1), all stocking events have been conducted using first-generation progeny (F1) of wild breeders. Parents were captured on known spawning sites in source lakes (e.g., Blue Sea Lake and Trente-et-un-Miles Lake, both hosting the piscivorous ecotype). Eggs and milt were mixed on site and transferred back in hatcheries to be reared until stocking. No breeders were maintained in hatchery. Age at stocking varied between a few months (fry stage) to a year (1+). Therefore, neither domesticated strains nor

TABLE 1. Study design and key information for each lake, including the year that each lake was stocked for the last time, lake area, and average annual air temperature and design groups.

Lake	Latitude (°N)	Longitude (°W)	Last year stocked	Lake area (ha)	Air temperature (°C)†	Length (mm)†	Age (yr)†	Design group
Desert	46.573	76.322	NA	329	3.08	483.3	11.5	wild, piscivorous
Marguerite	47.029	75.804	NA	662	2.34	491.5	11.8	wild, piscivorous
Opeongo	45.688	78.363	NA	5,154	NA	485.3	10.5	wild, piscivorous
Antoine	46.370	76.986	NA	435	3.33	417.4	11.4	wild, planktivorous
Bondy	47.083	75.851	NA	531	2.18	372.4	12.9	wild, planktivorous
Cayamant	46.106	76.277	2011	725	3.93	484.8	10.4	stocked, piscivorous
Muskoka	45.054	79.491	2014	12,205	NA	502.0	12.2	stocked, piscivorous
Cedres	46.305	76.111	2011	282	3.84	539.9	10.6	stocked, piscivorous
Louisa	45.772	74.417	2006	440	3.98	418.4	11.9	stocked, planktivorous
McFee	45.715	75.623	2001	93	4.03	408.0	13.6	stocked, planktivorous

NA, not applicable.
†Means.

adult fish have been involved in the stocking history (Quebec Ministère des Forêts, de la Faune et des Parcs [MFFP] and the Ontario Ministry of Natural Resources and Forestry [OMNRF]; *personal communications*). According to the otolith's back-calculated length-at-age (see data from Morissette et al. 2018), there was no significant difference in total length at age 1 (time of stocking) among stocked, hybrids, and local fish (one-way

ANOVA, $F_{2,274} = 0.297$, $P = 0.743$, average total length [TL] = 84.96 ± 15.31 mm).

Sampling

A total of 342 lake trout were sampled in 10 selected lakes throughout Quebec and Ontario (Canada) (Fig. 1). Fish were captured with gill nets, in collaboration with

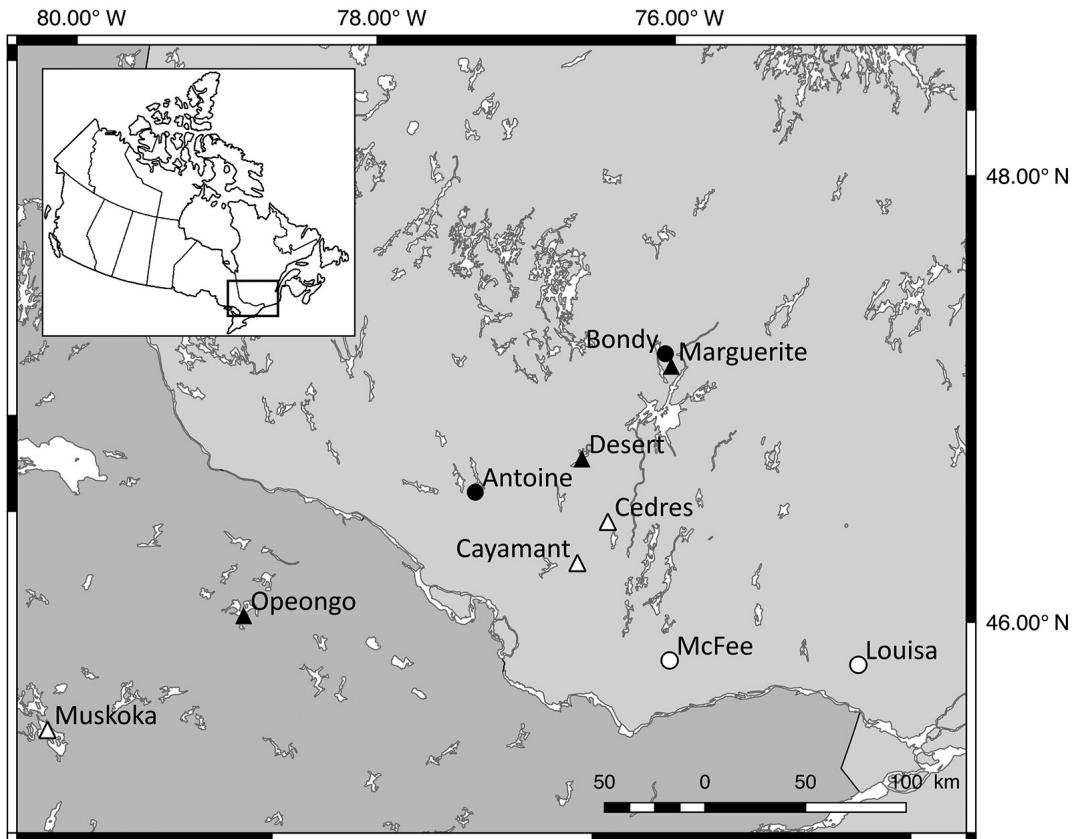


Fig. 1. Map of studied lakes, symbols are representing either piscivorous (triangle) and planktivorous (circle) ecotypes of stocked (open symbols) and wild (filled symbols) populations.

MFFP and OMNRF. Both MFFP and OMNRF followed the same normalized sampling protocol, where putative summer habitat volumes (water temperature 12°C or less and a dissolved oxygen concentration of 5 mg/L or more) were randomly sampled. For two lakes (Cayamant and Cedres), seven voluntary anglers sampled fish in the same period of time to complement our sampling efforts. A provincial angler and hunter federation (Fédération québécoise des chasseurs et pêcheurs) selected anglers based on their knowledge of targeted lakes. Anglers kept every captured fish (any size) and followed the same field processing procedure as our scientific team, they kept fish heads frozen before shipping them at the end of the sampling period. Additionally, MFFP provided 30 adipose fins from each of two stocking source populations (Lakes Blue Sea and Trente et Un Milles) for genetic group assignment.

Pelagic zooplankton samples (potential pelagic prey) were obtained at the deepest point of every lakes. A zooplankton net (mouth opening 20 cm and 200 µm mesh) was horizontally towed for 5–10 min at a depth between 0 to 10 m (oblique tow). Samples were then filtered on a sieve of the same mesh size (200 µm), stored, and frozen immediately.

Fish processing

For every fish, total length (TL, mm) was measured in the field as well as mass (g), using a portable digital scale. The adipose fin was sectioned and stored in 95% ethanol in individual plastic vials (Eppendorf, Mississauga, Ontario, Canada). In the laboratory, a sample of dorsal muscle without skin and bones was cut from the fresh fish and immediately frozen; the knife was sterilized with 95% ethanol between each sample. To test for the agreement of stable isotope ration between dorsal and neck muscles, we also sampled near-head (neck) muscle tissue on 30 individuals from Lake McFee during the standardized sampling. Muscle samples were collected accordingly in the neck region from thawed heads of the angler-collected fish.

Genomic data and genotyping

Genomic DNA was obtained with the salt-extraction protocol (Aljanabi and Martinez 1997) from adipose fins. Sequencing was performed on an Illumina HiSeq2000 (Illumina Inc., San Diego, CA, USA) (100 base pair [bp] length single reads). Adapters were removed from sequencing raw data with cutadapt v1.8.2 (Martin 2011) in the single-end mode. Sequences were demultiplexed and 80 bp-trimmed with process_radtags in STACKS v 1.35 (Catchen et al. 2013). Individual reads were aligned and de novo potential polymorphic loci were aligned with ustacks. A catalog of single nucleotide polymorphism (SNP) loci was assembled with cstacks using default parameters. Genotyping was performed with sstacks by matching individual reads against our catalog.

Markers quality and filtering

The populations module of STACKS ($r = 0.5$, $m = 3$) and a subsequent quality filtering process of SNP markers were applied to either pairs of source–target populations or, in one case, trio (Louisa Lake was stocked once by Blue Sea in 1998 and Trente et Un Milles otherwise, Appendix S1). We filtered loci with too low minimum coverage ($m < 5$) but a maximum coverage of 30 and a maximum proportion of heterozygous individuals of 0.7. We retained loci present in at least 70% of individuals within populations. We also removed individuals with percentage of missing loci $>30\%$, identified with the missing_vizualisation function from stackr R package (Gosselin and Bernatchez 2016). Loci with more than two alleles were also identified with the function summary_haplotype in stackr and removed from the database to filter for putative paralogs or sequencing artifacts. After these filtration steps, the populations module (STACKS software) and filtering steps were rerun. The filtering procedure is part of the STACKS workflow, available on Github website (*available online*).⁵ All module parameters used are listed in the supporting information (Appendix S2).

Individual genetic group assignment

Individual assignment to one of the three genetic groups was based on admixture proportion (Q), estimated for source of stocking population using the Bayesian clustering method implemented in the software ADMIXTURE v 1.3 (Alexander et al. 2009). This value is the individual proportion of genotype related to user-specified number of genetic clusters (K) identified without a priori information. ADMIXTURE analyses were realized including one stocked population and the source population for stocking (Lake Blue Sea, Trente et un Milles, or both). The assumed number of genetic clusters was either $K = 2$ or $K = 3$, according to stocking history data, but an extended range of probable K was tested ($K = 1–6$). The most probable K was inferred with cross-validation error. Standard error was estimated from 2,000 bootstrapped replicates. Stocked fish were assigned when $Q_{\text{stocking source}} + \text{SE} \geq 90\%$, local fish when $Q_{\text{stocking source}} + \text{SE} \leq 10\%$, whereas others were classified as hybrids (Q values ranging from 10% to 90%).

Stable isotopes ratios quantifications

Pelagic zooplankton samples were thawed and sorted under a LEICA MZ12 dissecting microscope (Leica microsystems, Wetzlar, Germany). Roughly 200–700 individuals of *Daphnia* sp. or *Bosmina* sp. (depending on their sizes) were sorted in triplicate for each lake. Frozen muscle samples were thawed and 1-cm³ samples were

⁵ https://github.com/enormandeu/stacks_workflow

sectioned with clean scissors. Zooplankton and muscle samples were dried at 60°C for 48 h. A mortar and pestle were used to grind samples into a fine powder. Using a digital scale, powder was encapsulated in pressed tin capsules (3.5×5 mm) to a mass of 1 ± 0.05 mg.

Carbon and nitrogen stable isotope ratios were produced using a varioEL III Isotope Cube (Elementar America, Philadelphia, PA, USA). The procedure first implies a flash combustion and the resulting gases are carried by ultra-pure helium to the columns and successive absorption traps to separate the gases (“trap and purge procedure”). A thermoconductivity detector (TCD) measures the gases as they are released. Stable isotope results were expressed in delta (δ) notation (as part per thousand, or permil ‰) as the normalized ratios of the sample in relation to international standards. The standards used for the measurements were Vienna Pee Dee Belemnite (VPDB) limestone for carbon isotopes ($\delta^{13}\text{C}$) and atmospheric nitrogen (air) for nitrogen isotopes ($\delta^{15}\text{N}$).

Stable isotope analysis

Isotopic values of dorsal and neck muscle tissue within same individuals of lake McFee were compared by single factor analysis of variance (ANOVA). The comparison between dorsal and neck muscle tissue revealed no difference for $\delta^{13}\text{C}$ (ANOVA, $F_{1,58} = 0.0004$, $P = 0.99$) and $\delta^{15}\text{N}$ (ANOVA, $F_{1,58} = 1.91$, $P = 0.17$). Slopes of linear relationships were 0.87 and 0.91 and

$R^2 = 0.77$ and 0.79 , respectively. Isotopic values of $\delta^{13}\text{C}$ were a posteriori normalized for fat content by the C:N ratio, as suggested by Post et al. (2007). Trophic position was calculated based on a fractionation factor of 3.4 and the following equation: trophic position = $((\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}})/3.4) + 2$ (Vander Zanden et al. 1999). Since $\delta^{13}\text{C}$ of pelagic zooplankton prey varied widely among lakes (Table 2), we calculated individual fish distance from lake-specific pelagic baseline as $\Delta\delta^{13}\text{C}_{\text{pelagic}} = \delta^{13}\text{C}_{\text{fish}} - \delta^{13}\text{C}_{\text{zooplankton}}$ to enable between-lakes comparison.

We assessed trophic niche breadth by calculating the standard ellipse area (SEA) from isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of all genetic groups within every lake (three groups in stocked lake [local, hybrid, and stocked] and one group in unstocked lakes). SEA is based on an estimation of the Bayesian multivariate normal distribution of every group within the data set. SEA is calculated on the posterior distribution of the covariance matrices for each group. The calculations of SEA are integrated in the R package SIBER (Jackson et al. 2011). We modeled the effects of ecotype and genetic origin on SEA (response variables) within populations using mixed effect models. Factors of the model were ecotypes (fixed, two levels: piscivorous and planktivorous) and genetic origins (fixed, four levels: wild, local, hybrid, and stocked) nested within ecotypes. Populations (lakes) were treated as a random factor, to account for among-lakes variability. SEAs were log-transformed to meet normality assumption.

TABLE 2. Mean and standard deviation (SD) of stable isotope ratios of each genetic group (local, hybrid, stocked and wild) within lakes, number of fish by groups, convex hull total area (TA), and 95% standard ellipse area (SEA) of the group niches.

Ecotype and lake	Genetic group	<i>n</i>	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		TA	SEA
			Mean	SD	Mean	SD		
Piscivorous								
Desert	wild	15	-28.18	0.27	12.18	0.36	0.85	0.29
Marguerite	wild	15	-26.66	0.62	10.44	0.85	3.51	1.57
Opeongo	wild	25	-25.99	0.87	10.60	1.94	20.0	4.93
Cayamant	local	8	-29.59	1.30	12.25	0.52	3.49	1.97
Cayamant	hybrid	5	-29.85	2.24	12.62	0.58	1.50	1.44
Cayamant	stocked	10	-29.60	2.42	12.53	0.68	7.20	3.37
Cèdres	local	21	-28.54	0.33	11.69	0.48	1.47	0.49
Cèdres	hybrid	13	-28.56	0.27	11.84	0.18	0.31	0.15
Cèdres	stocked	9	-28.28	0.83	11.76	0.62	1.31	0.83
Muskoka	local	24	-26.87	0.49	16.04	1.40	6.86	2.02
Muskoka	hybrid	25	-26.91	0.60	16.18	1.04	5.55	1.52
Muskoka	stocked	25	-26.92	0.53	15.88	1.65	9.60	2.29
Planktivorous								
Antoine	wild	15	-27.13	0.88	10.90	1.03	5.67	2.86
Bondy	wild	10	-25.91	0.37	8.60	0.71	1.81	0.82
Louisa	local	2	-28.35	0.17	11.68	0.11	ND†	ND†
Louisa	hybrid	6	-28.65	0.67	12.11	0.48	1.05	0.86
Louisa	stocked	9	-28.20	2.98	11.85	0.41	8.16	4.32
McFee	local	13	-34.23	1.48	11.06	0.66	13.9	2.66
McFee	hybrid	18	-33.65	2.18	11.05	0.75	8.25	2.37
McFee	stocked	36	-32.80	2.08	11.16	0.89	13.4	5.39

†Data number not sufficient to estimate.

Linear mixed models were fitted using the function `lme` in the R package `nlme` (Pinheiro et al. 2016). Post-hoc contrasts among predictors (genetic groups) were realized using a least-square mean procedure provided by the R function `lsmeans` (`lsmeans` R package, [Lenth 2016]).

We also modeled the effects of ecotypes, genetic origin, and total length on trophic position and distance from pelagic baseline ($\Delta\delta^{13}\text{C}_{\text{pelagic}}$), again with a linear mixed-effects model. The model was the same for both response variables. Model factors were ecotypes (fixed, two levels: piscivorous and planktivorous), genetic origin (fixed, four levels: wild, local, hybrid, and stocked) nested within ecotypes, and total length nested within ecotypes, to account for size difference among ecotypes. Populations (lakes) were treated as a random factor to account for among-lakes variability. Response variables were normally distributed then no transformation was required.

Genotype–phenotype association

Individual polygenic association with observed life-history traits was assessed using multivariate analyses. We tested for an association between genomic (SNP) individual variations and five individual ecological metrics. Those ecological metrics were trophic niche ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), growth (asymptotic length L_{inf} and early life growth rate ω) and body condition (relative mass condition index W_r), and will be referred as life history traits thereafter for simplicity. L_{inf} and ω were estimated by regression for each individual fish using typical Von Bertalanffy growth models (VBGM) fitted with a nonlinear regression of back-calculated total length in function of age. Individual length-at-age was back-calculated using otolith measures and age estimation under the body-proportional hypothesis (Francis 1990). VBGM modeling was performed using the `nls` function implemented within the FSA R package (Ogle 2016). The model $L_t = L_{\text{inf}} [1 - e^{-K(t-t_0)}] + \varepsilon$ describes back-calculated length at time t (L_t) as a function of asymptotic length (L_{inf}), the Von Bertalanffy growth parameter (K), the theoretical length at age 0 (t_0), and additive process error (ε). Omega (ω) growth rate was calculated for each individual as $\omega = L_{\text{inf}} \times K$, as suggested by Gallucci and Quinn (1979). This parameter is corresponding to the slope of the growth curve at its origin measured in mm/year. It can be biologically interpreted as the growth rate early in life.

The relative mass condition index was estimated as $W_r = 100 \times (W/W_s)$, where W is the mass of fish at the time of capture and W_s is a standard mass, calculated from a species-specific equation, as first suggested by Wege and Anderson (1978). These authors suggested that W_r relates not only to “fish plumpness,” but also fish general health when calculated from a standard equation encompassing the entire geographic range of a given species (Blackwell et al. 2000). Hence, we calculated standard mass based on lake trout total length

(TL) and using the published equation derived from 58 lake trout populations throughout the native range of distribution; $\log_{10}W_s = -5.681 + 3.2462 \log_{10}\text{TL}$ (Piccolo et al. 1993). We observed no significant linear relationship between W_r and total length ($t_{20,153} = -1.45$, $P = 0.147$) or age ($t_{20,146} = -0.8$, $P = 0.425$) in wild fish from unstocked populations. This absence of relationship opens the possibility to compare W_r between size classes as well as within and among populations (Blackwell et al. 2000).

We limited the genotype–phenotype analysis on stocked planktivorous populations, as we observed no significant variation of life history metrics between genetic origins among piscivorous populations (Morissette et al. 2018). Life history and individual SNP genotype variations were expressed as composite variables resulting from two principal component analyses (PCA); PCA for life history metrics (continuous quantitative values) was conducted on a standardized correlation matrix since those variables are based on different scales (see Legendre and Legendre [2012] for further details). PCA for SNP genotypes were realized on a covariance matrix. As PCA does not tolerate missing data, SNP alleles were imputed to avoid missing data using a Random Forest algorithm included within `vcf_imputation` function of `stackr` package. The procedure imputed respectively 31.2% and 21% of the loci from McFee and Louisa lake populations. Life history principal component (PC) axes were retained for subsequent analyses based on the broken stick distribution (Legendre and Legendre 2012). Because genetic variance is usually well distributed among PC axes and differences among them are not sufficient to retain axes according to the broken-stick distribution criteria, we consider for analysis every PC axes explaining $>1.5\%$ of genetic variance. This percentage of variance corresponds to one-half the maximum percentage of variance explained by the first PC axis (3.2%). We chose this criterion to include the most informative genetic variations while remaining parsimonious and to avoid adding unnecessary variance.

Association between life history PCs (response variables) and genotypes PCs (explanatory variables) was assessed using a redundant discriminant analysis (RDA), a variant of canonical correlation analysis (CCA), included in the R package `vegan` (Oksanen et al. 2017). Selection of the best explanatory variables (genotypes PCs) for the RDA model was conducted using automatic permutation tests of the ordination model (function `ordisep` in the `vegan` package). Loci showing association with life history were selected within the significant PCs of the RDA model, based on variable loadings. The loadings of the loci within PCs were transformed to standard deviations from the mean, then loci with values >2.5 (positive correlation) or <-2.5 (negative correlation) were selected, as in Uva et al. (2009). To avoid the possible confounding effect of population structure, the above analyses were realized on population-specific data sets.

The gene ontology (performed by a BLAST [blastn] query) of loci most associated with life history traits was investigated by alignment of the 80 bp sequences surrounding each relevant SNP to the rainbow trout (*Oncorhynchus mykiss*) genome (Berthelot et al. 2014). We kept only alignment hits with an expected value (E , number of times similar observation is made by chance) $< 10^{-20}$. If multiple hits from the same loci were present, the loci with lowest E value within the significant hits were retained. The gene ontology of the identified sequences was annotated according to (Berthelot et al. 2014) and principal known function assessed using the Uniprot database.

RESULTS

Population genomics and genetic groups assignment

The total number of raw reads obtained by sequencing was 2,057,139,965, averaging 3,590,122 reads/individual. After filtering, we retained an average of 600 SNP markers (range = 553–700) for pairwise comparisons between the source and stocked populations. Thus, in all cases, the most probable number of clusters was $K = 2$ when stockings were from only one source population and $K = 3$ when stockings were from two different source populations. This confirmed the accuracy of the stocking history records (Appendix S1). As expected, all five stocked populations were made up of trout from stocked, local, and hybrid origins, with a proportion of local individuals accounting between 18% and 55% of the samples.

Trophic niche size

The linear mixed effects model showed that genetic origin (i.e., wild, stocked, hybrid, and local) was the only factor significantly affecting SEA sizes (Table 3). Stocked fish occupied a significantly broader isotopic niche than hybrid and local fish. Trophic niche breaths of wild populations were highly variable and not significantly different from any other groups. Increases of trophic niche size were significant for both ecotypes (Fig. 2). In every stocked population, except Muskoka Lake, stocked fish showed a larger SEA niche size (Table 2). Trophic niche sizes of stocked fish within piscivorous populations were twice as large as local/hybrids, and four times larger within planktivorous populations.

Group-specific trophic positions

Average trophic positions by ecotypes ranged from 4.29 ± 0.54 (planktivorous) to 5.15 ± 0.43 (piscivorous). Accordingly, the linear mixed-effects model showed a significant effect of ecotypes on trophic position (ANOVA, $F_{1,3} = 110.99$, $P < 0.04$). Among all studied lake trout populations (both ecotypes), there was no significant effect of genetic origin on trophic position (Table 4). Total length had a significant effect

TABLE 3. Linear mixed effect model for standard ellipse area (SEA), where columns present the estimates of differences (positive or negative) of group response variables with the intercept (piscivorous ecotype), standard error and P values of the factor.

Coefficient	SEA response		
	Estimate	SE	P
Fixed parts			
Intercept	0.94	0.24	<0.001
Ecotype (planktivorous)	0.29	0.38	0.60
Ecotype (piscivorous), local	0.23	0.10	0.07
Ecotype (planktivorous), local	0.19	0.17	0.29
Ecotype (piscivorous), stocked	0.48	0.10	0.005
Ecotype (planktivorous), stocked	0.97	0.13	<0.001
Ecotype (piscivorous), wild	0.40	0.48	0.44
Ecotype (planktivorous), wild	0.25	0.53	0.66

Notes: Significant P values are in boldface type. The two term coefficients (separated by commas) represent the nested factors. Number of tested groups, $N_{\text{grp}} = 11$. Number of observations = 20.

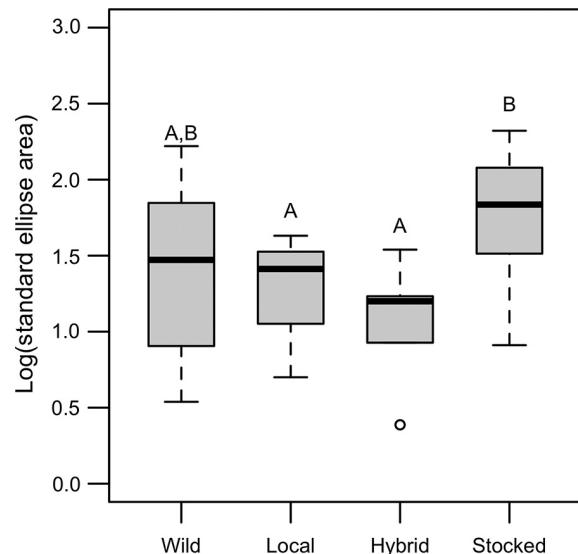


FIG. 2. Distribution of the square root of standardized ellipse area (SEA) among the three genetic origins (local, hybrid, stocked) within stocked populations and wild populations. Letters are representing significant differences from post-hoc least-square mean contrast. Box plot components are midline, median; box edges, 25th and 75th percentiles; whiskers, min/max values within 1.5 interquartile range; points, outliers.

only on trophic position for piscivorous ecotypes. Larger fish were at a higher trophic position than smaller ones. Within stocked planktivorous populations, however, 20% of stocked lake trout showed a higher trophic position than all other fish (one way ANOVA, $F_{1,98} = 15.67$, $P = 0.01$). The mean difference of trophic position was 0.4 higher than other stocked fish and nearly one trophic level higher than local planktivorous trout (Tukey HSD, $P = 0.01$).

TABLE 4. Linear mixed effect models for the response variables trophic position and distance of pelagic prey where Columns present the estimates of differences (positive or negative) of group response variables with the intercept (piscivorous ecotype), standard error and *P* values of the factor.

Coefficient	Response					
	Trophic position			Distance pelagic prey		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
Fixed parts						
Intercept	4.91	0.28	<0.001	0.699	0.90	0.45
Ecotype (planktivorous)	-0.78	0.46	0.14	-0.25	1.58	0.88
Ecotype (piscivorous), hybrid	0.05	0.06	0.45	-0.08	0.26	0.75
Ecotype (planktivorous), hybrid	-0.03	0.10	0.76	0.08	0.40	0.83
Ecotype (piscivorous), local	0.02	0.06	0.73	-0.08	0.25	0.73
Ecotype (planktivorous), local	-0.01	0.09	0.88	-1.00	0.38	0.008
Ecotype (piscivorous), wild	-0.08	0.35	0.82	2.14	1.14	0.11
Ecotype (planktivorous), wild	0.05	0.44	0.92	1.71	1.41	0.27
Total length, piscivorous	0.0004	0.0002	0.04	-0.001	0.001	0.26
Total length, planktivorous	-0.0002	0.0004	0.66	0.004	0.002	0.004

Notes: Significant *P* values are in boldface type. The two terms coefficients (separated by commas) represent the nested factors. Number of tested groups, $N_{\text{grp}} = 10$; number of observations = 301.

Group-specific distance from pelagic prey

The linear mixed-effect model showed no significant effect of ecotypes on distance from pelagic prey ($\Delta\delta^{13}\text{C}_{\text{pelagic}}$). Genetic origin and total length had a significant effect on distance from pelagic prey, but only within planktivorous populations (Table 4). Thus, fish of local genetic origin had a significantly more negative (pelagic) $\Delta\delta^{13}\text{C}_{\text{pelagic}}$ value (-0.30‰) than wild (2.41‰), hybrid (0.78‰), and stocked fish (0.70‰), showing a higher than expected reliance on pelagic/profundal trophic resources. Total length was positively correlated to distance from pelagic prey only within populations of the planktivorous ecotype. Hence, larger hybrid and stocked fish displayed $\delta^{13}\text{C}$ values linked to a diet comprising a larger proportion of littoral prey compared to local fish. There was no significant effect of any factor on distance from pelagic preys within piscivorous populations (Fig. 3).

Genotype-phenotype association

After the second filtering, we retained, respectively, 1,248 and 5,119 SNP markers for the McFee and Louisa planktivorous populations. A population-specific PCA for life history and genotype metrics was performed prior to RDA analysis. In the McFee population, we kept the first two life history PCs according to the broken-stick distribution, which together explained 66.6% of the life history variation, and the first 31 genotype PCs each explaining $>1.5\%$ of variation, and which collectively explained 65.3% of all genetic variation. In the Louisa population, we also kept two life history PCs and 31 genotypes PCs, which represented 79.8% and 66.7% of the life history and genetic variance, respectively. Stepwise selection of the RDA model using the ordistep

R function identified five genotype PCs (PC1, PC14, PC19, PC25, and PC31) for the McFee population. The model was globally significant ($P = 0.007$) and explained 65.5% of the life history variation (adjusted $R^2 = 10.13$; Fig. 4). In the Louisa population, stepwise RDA construction retained three genotype PCs (PC1, PC2, and PC8). The model was globally significant ($P < 0.001$) and explained 46% of the life history variation (adjusted $R^2 = 10.15$; Fig. 4). After selection of loci showing association with life history, based on PC loadings, 135 and 341 loci were respectively retained for the McFee and Louisa populations.

Gene ontology

The BLAST alignment analysis on the 135 (McFee Lake) and 341 (Louisa Lake) loci identified as putatively associated with life history metrics returned five and 14 significant ($E < 1 \times 10^{-20}$) and unique alignments that were located within genes. Those genes were mainly associated with biological functions related to growth, immunity, metabolism, and oogenesis (Table 5).

DISCUSSION

Risk assessment and prediction of the consequences resulting from supplementation represent a major challenge in the management of exploited fish stocks (Ham and Pearsons 2001, Aprahamian et al. 2003). In particular, introductions of predators from the same trophic guild, deliberated or not, have been shown to modify food webs (Sharma and Borgström 2008, Schulze et al. 2012, Bašić and Britton 2016). Accordingly, our data showed an increased niche breadth in stocked populations of both ecotypes, but individual segregation in resource utilization only for populations of

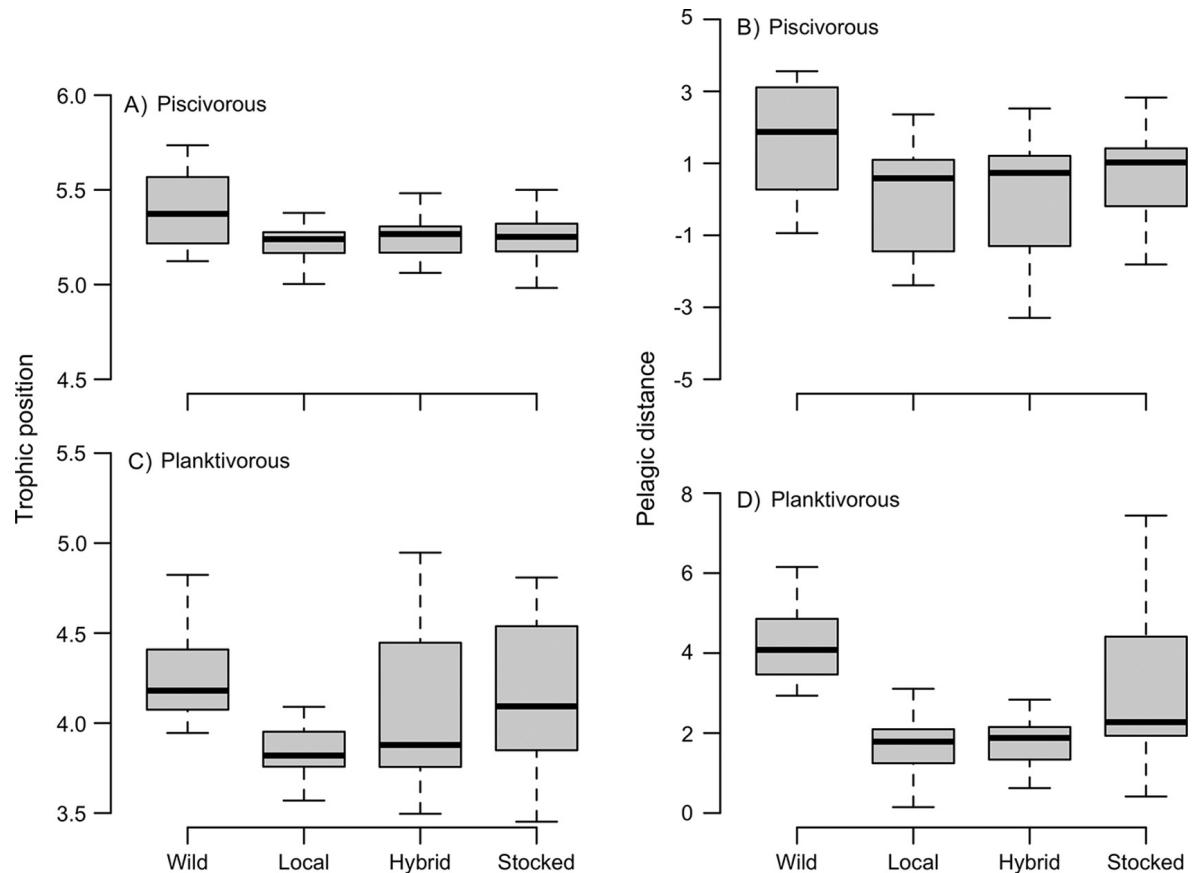


FIG. 3. Distribution of trophic position and distance from pelagic preys of wild populations and three genetic groups (pure stocked, pure local, hybrid) within stocked populations of (A, B) piscivorous and (C, D) planktivorous ecotypes; note that axis scales differ among graphics.

planktivorous ecotype. To our knowledge, our results are the first to show the underlying potential to induce intraspecific niche partitioning as a consequence of supplementation stockings. In contrast, a study of supplementation stockings using a domesticated hatchery strain of brook trout (*Salvelinus fontinalis*) showed no impact on utilized trophic niche of stocked, hybrid, and local resident fish (Lachance and Magnan 1990). The wider trophic capacity of lake trout (a large apex predator) compared to brook trout, along with the striking variations in life-history traits observed in lake trout (Muir et al. 2015), could explain the more pronounced food web modifications observed in this study. We are suggesting community complexity, niche availability, and the resulting competitive interactions between divergent groups of individuals as probable explanations for the observed niche partitioning within planktivorous populations.

Community as niche partitioning susceptibility factor

In this study, trophic niche sizes of stocked fish were significantly larger in population of both ecotypes.

Trophic niche widening could be caused by a generalist feeding strategy as well as individual specialization in response of intraspecific competition (Bolnick et al. 2003, Svanback and Persson 2004). Both of these strategies may cause the same manifestation of an apparent niche widening at the population level. Assessing individual utilization rather than population averages was thus critical to understand the underlying processes of those niche expansions. Hence, analyses of individual trophic position and distance from pelagic prey had a unique contribution to address this question.

Whereas our results indicate that niche diversification/expansion of stocked fish was a consistent consequence of supplementation stocking, the difference in effect size and the values of trophic metrics are suggesting that underlying mechanisms for this diversification were not the same among ecotypes. Within populations of piscivorous ecotype, individual trophic metrics only showed a simultaneous increase of trophic position alongside total length. This observation was consistent with the ontogenetic diet shift observed in natural populations (Trippel and Beamish 1989, France and Steedman 1996). Younger and smaller lake trout feeding on zooplankton

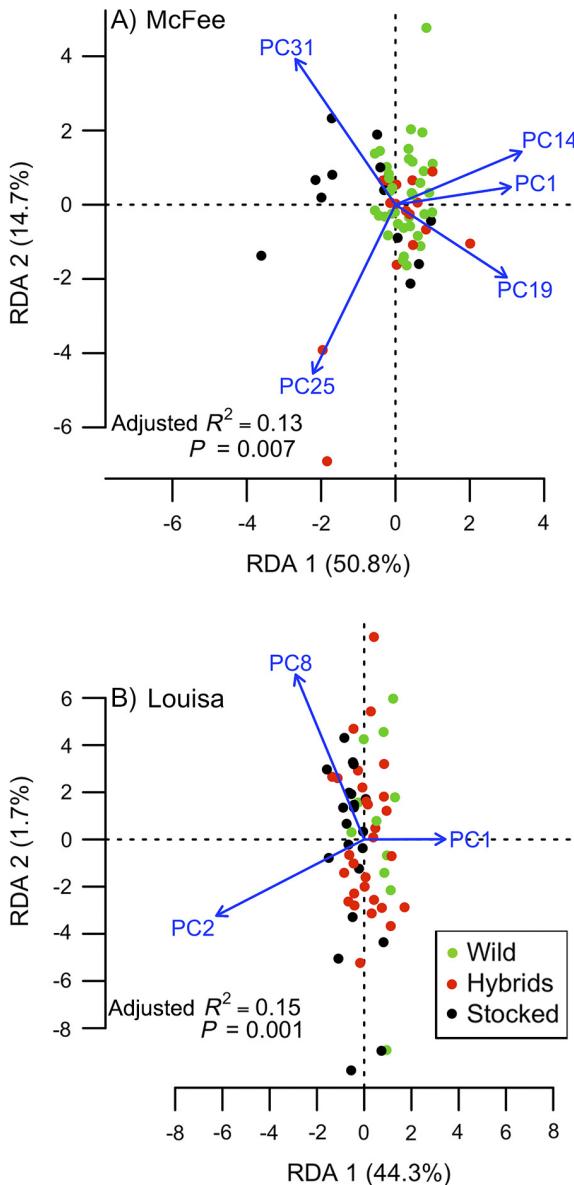


FIG. 4. Redundancy analysis (RDA) of the (A) McFee and (B) Louisa lakes showing the position of lake trout from stocked populations of planktivorous ecotypes according to a PCA of life history metrics (asymptotic length [Linf], early life growth rate [ω], relative weight condition index [Wr], and carbon [$\delta^{13}\text{C}$] and nitrogen [$\delta^{15}\text{N}$] stable isotope ratios) related to the selected axis of a PCA of SNP genotypes illustrated by blue arrows. Individual lake trout genetic groups are illustrated by colored dots as following: local (green), hybrid (red) and stocked (black) fish.

and macrobenthic invertebrates are gradually becoming more piscivorous or moving toward larger pelagic invertebrate prey (i.e., mysids) as they grow. This phenomenon is common in species with a gape limit and is generally operating at age 1–4 and/or TL > 200 mm in wild populations of large-bodied piscivorous lake trout (Martin 1951, Zimmerman et al. 2009). The uniformity

of other diet metrics among genetic groups suggested that only some atypical individuals were involved in the observed trophic niche expansion. Hence, broader niche size may be a consequence of a diet diversification fueled by plasticity of the newly stocked individuals exposed to a novel, potentially stressful habitat (Ghalambor et al. 2007, Amundsen et al. 2012). Hatchery rearing, even after one generation, could promote atypical behavioral characteristics (i.e., bolder and more aggressive fish), favoring establishment of new life history strategies (Tymchuk et al. 2006, Pearsons et al. 2007). However, the diversity of available trophic resources in lakes hosting large-bodied piscivorous ecotypes is probably sufficient to sustain those individuals, precluding population-wide deleterious trophic consequences.

The significant difference among genetic groups in planktivorous lakes suggests a much more complex mechanism. Stocked fish exhibited a broader, but also contrasting, individual niche use compared to the local and hybrid fish. Resident local fish appeared restricted to a limited trophic niche mostly based on pelagic/profundal prey. In comparison, stocked fish showed higher reliance on littoral resources of higher trophic position. The local pelagic/profundal trophic niche metrics showed practically no similarity with conspecifics from unstocked planktivorous populations, suggesting alteration of typical trophic niche subsequent to supplementation. This finding is in accordance with theoretical expectation of communities' susceptibility; consequences of exogenous introduction/invasion are higher in simpler food webs (Emmerson and Yearsley 2004). The presence of pelagic prey is expected to buffer against the impacts of introduction (Vander Zanden et al. 2004), by sustaining diet diversification and/or atypical ontogenetic shifts. This supports the hypothesis that lake community structure mediates the impacts of supplementation (Downing and Leibold 2010). Stocking-induced niche displacements are probably resulting from competitive exclusion between stocked and local lake trout, as well as genetic divergence from the local populations (McDermid et al. 2007).

Generalist/specialist competitive interactions

Intraspecific competitive interactions seem important between lake trout ecotypes newly found in sympatry following supplementation stocking. Indeed, our results show that local fish were displaced by stocked trout, a situation analogous to food web consequences observed following introduction of smallmouth bass (Vander Zanden et al. 1999). Similar results were also obtained in a study on sympatric brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) in Norway where species coexist. The most aggressive territorial trout relegate the less competitive to the inferior pelagic or profundal trophic niche (Langeland et al. 1991). This represents a clear case of niche differentiation caused by interspecific competitive asymmetry. Niche segregation observed

TABLE 5. BLAST hit sequences of genes putatively associated with life history metrics in the redundant discriminant analysis (RDA).

Locus ID	Transcript name	<i>E</i>	Gene name	Main known functions
McFee				
42417	AB258536.1	4.61×10^{-25}	onmy-LDA gene for MHC class I antigen	immune response (Berthelot et al. 2014)
63511	KF870466.1	9.98×10^{-22}	growth differentiation factor 11 (GDF11)	growth factor activity (Berthelot et al. 2014, de Mello et al. 2014)
83824	KF870468.1	2.78×10^{-22}	inhibin beta A subunit 2	growth factor activity (Berthelot et al. 2014, de Mello et al. 2014)
107567	NM_001124375.1	3.59×10^{-21}	vitellogenin receptor	oocyte development (Davail et al. 1998)
139470	AY883999.1	1.65×10^{-29}	toll-like receptor 3 gene	innate immunity (Berthelot et al. 2014)
Louisa				
25303	KF870466.1	4.90×10^{-24}	growth differentiation factor 11 (GDF11)	growth factor activity (Berthelot et al. 2014, de Mello et al. 2014)
44709	KF870470.1	1.36×10^{-24}	inhibin beta A subunit 4 (InhbetaA4)	growth factor activity (Berthelot et al. 2014, de Mello et al. 2014)
45875	HM208332.1	8.15×10^{-27}	zinc transporter (SLC39A7.B)	trans membrane transporter (Hansen and Dijkstra 2010)
53166	HF931026.1	8.20×10^{-22}	IFNc1 gene for type I interferon c1	defenses response to viruses (Zou et al. 2014)
58537	HE608241.2	3.76×10^{-30}	TPT1 gene for tumor protein	cellular function (i.e., apoptosis) (Verleih et al. 2010)
61853	GU228520.1	1.06×10^{-20}	Clock 1a protein (Clock 1a) gene	lipid metabolism (Betancor et al. 2014)
64924	KF870474.1	2.28×10^{-22}	transforming growth factor beta 2	growth factor activity (Berthelot et al. 2014, de Mello et al. 2014)
69865	DQ789362.1	1.05×10^{-25}	nonclassical MHC class I antigen (Onmy-LAA)	cell growth (Berthelot et al. 2014)
85094	AB162342.1	1.75×10^{-28}	MHC class I a region	immune response (Berthelot et al. 2014)
108678	KF870475.1	1.36×10^{-24}	transforming growth factor beta 3 (TGF-beta3)	growth factor activity (Berthelot et al. 2014, de Mello et al. 2014)
123037	AJ295231.1	2.93×10^{-26}	iNOS/NOS2 gene for inducible nitric oxide	nitric-oxide activity/defense responses (Wang et al. 2001)
126351	AB162343.1	2.95×10^{-21}	MHC class I b region, complete cds	immune response (Berthelot et al. 2014)
144100	FN545577.1	3.79×10^{-25}	Db-3 gene for defensin beta 3, exons 1–3	defenses response to bacteria (Berthelot et al. 2014)
224111	KF870464.1	1.75×10^{-28}	follistatin b1 (Fstb1) gene	growth factor activity (Berthelot et al. 2014, de Mello et al. 2014)

Notes: Statistical significance of the alignment is represented by the *E* value. Gene names and principal known functions are listed according to UniProt database and cited literature.

between Arctic char and brown trout has also been hypothesized to be a symptom of prey preference and foraging efficiency of both species (Jansen et al. 2002). Hence, stocked Lake Trout from source population of the piscivorous ecotype could be a more competitive generalist predator than the specialized local planktivorous trout.

Previous studies have shown that top consumers in high-latitude lakes feed preferentially on littoral rather than pelagic energy sources (Vadeboncoeur et al. 2002, Eloranta et al. 2010). Littoral habitat tends to provide more opportunities, but is also a habitat of higher competitive interactions (e.g., more pronounced light intensity, restricted vertical space) compared to the open pelagic habitat, which offers scarce and small prey (Schindler and Scheuerell 2002). Large-bodied piscivorous lake trout is an opportunistic generalist feeder, with energy acquisition coming from a trophic niche more or

less distributed between littoral and pelagic habitat (Vander Zanden et al. 2000). However, the simpler food webs of lakes hosting the planktivorous ecotype are limited in terms of possible energy sources and have driven evolution of trophic specialization, or ecotypes (Morbey et al. 2006, Zimmerman et al. 2007, McDermid et al. 2010). Thus, phylogeographic studies suggest that the planktivorous ecotype most likely results from local adaptation that evolved following postglacial colonization (i.e., ~8,000 B.P.; Wilson and Hebert 1996, 1998) and represent a specialized (and less competitive) form of the ancestral piscivorous ecotype (McDermid et al. 2010, Bernatchez et al. 2016). Trophic flexibility and larger size of stocked fish are probably favoring competitive exclusion of local trout, forcing them to decrease foraging on macro-benthic littoral prey. Interestingly, hybrid fish displayed intermediate trophic status between pure genetic groups, suggesting that the genetic basis of

ecotypic determination (Baillie et al. 2016, Bernatchez et al. 2016), may at least partially contribute to ecological outcomes of competitive interactions.

Contrasting ecotypic variation; a genetic predisposition to competitive interactions?

The high numbers of significant loci identified by RDA analyses corroborate the potential polygenic basis of life history traits, with a large set of small effect genes leading to important intrapopulation differences. This is in accordance with other salmonid alternative life history strategies shown to be under some genetic control (Rogers et al. 2002, Aubin-Horth et al. 2004, Gagnaire et al. 2013). According to our previous observations and hypotheses (Morissette et al. 2018), contrasting trophic niches could be related to intraspecific divergence in early life growth rate (ω) and asymptotic length (L_{inf}). Results of gene ontology showed that SNPs significantly associated with life history trait variations are mainly located within genes linked to growth functions and differentiation in various cell types (Growth differentiation factor 11, transforming growth factor beta 2 and 3, inhibin beta A2, and follistatin B1), including regulation of muscle growth and development (Berthelot et al. 2014, de Mello et al. 2014). All of these genes have been described as part of the transforming growth factor beta (TGF β) superfamily and represent a coherent complex of genes implied in growth as well as sexual maturation (notably inhibin beta A4) and immunity (de Mello et al. 2014).

We are aware that our BLAST alignment analysis does not cover the entire genome and should be taken with caution. However, parallel identification of genes from the same functional roles in two independent populations suggests a congruent mechanism of ecological differentiation observed in response to supplementation stocking of planktivorous populations. Hence, genetically based differences underlying ecotypic variation (piscivorous vs. planktivorous ecotypes) could be a factor of predisposition to contrasting life strategies by favoring fast early life growth rate and larger maximum length of the stocked piscivorous trout. In turn, this may increase intraspecific competition and promote niche partitioning. Hence, the small proportion of larger stocked fish feeding in high trophic position and hybrid individuals are probably the main drivers of the observed competitive exclusion (Fig. 4).

CONCLUSION

Considerations of the food web structure generally focus on a somewhat oversimplification of the species role and function within a given environment. Indeed, there is a tendency to consider each species as a homogeneous set of individuals, especially when planning supplementation stocking. Yet, most if not all species are characterized by intraspecific variation, including

generalist top predators. It is thus increasingly important to consider the individual variability of a species' trophic niche to assess potential inter- and intraspecific interactions. Our results showed that the intraspecific competitive interactions between contrasting ecotypes could be an important cause of trophic niche perturbation. Lake trout communities lacking pelagic fish prey seem more susceptible to such perturbations, and should be managed taking this information into consideration. Finally, natural variation among populations that evolved different life histories (e.g., planktivorous vs. piscivorous) as well as the community characteristics of their habitats should be considered in order to mitigate risk factors associated with competitive exclusion and food web alterations resulting from supplementation stocking.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1857/full>

DATA AVAILABILITY

All raw data file and R codes from this work are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.nt511dp>