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REGULAR PAPER

Introgressive hybridization between wild and domestic individuals and its relationship with parasitism in brook charr *Salvelinus fontinalis*

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The effects of introgression on parasitism in brook charr *Salvelinus fontinalis* were investigated in 28 lakes with various levels of stocking in Québec, Canada. No effect of genetic background on parasitism was found at the individual level. Body length seemed to explain most of the variation observed at this level, with largest fish being more infected. However, lakes with the greater average domestic genetic background were found to display significantly lower parasite prevalence and diversity. Since our results indicate no effect of domestic genes at the individual level, the negative association with introgression found at the population level may be mainly attributed to differences in intrinsic environmental quality of lakes (*e.g.* fishing pressure, availability of food resources, abiotic characteristics).

KEYWORDS

admixture, host–parasite relationship, hybridization, salmonids, stocking, trout

1 | INTRODUCTION

Modern day human activities are a major threat to natural populations worldwide and are recognized as one of the main causes of decline in many species (Goudie, 2013; Halpern *et al*., 2008; Sanderson *et al*., 2002). These declines can occur because of multiple factors related to human activities including habitat loss, introduction of invasive species, pollution or overexploitation (Wilcove *et al*., 1998). As a result, conservation actions are widely applied to counteract these negative effects (Sanderson *et al*., 2002). For instance, stocking is a practice widely used to prevent collapses of exploited fish populations (Laikre *et al*., 2010; Soorae, 2013). It often relies on using hatchery-reared fish to supplement wild populations. However, these farmed fish are affected by domestication, which is defined by Price (1999) as "the process by which a population of animals becomes adapted to man and to the captive environment by genetic changes occurring over generations". Domestication is caused by artificial selection, deliberate or not (Perry *et al*., 2005; Uusi-Heikkilä *et al*., 2017), which is due the selective pressures encountered in artificial environments (*e.g.* hatcheries) and can happen very quickly, sometimes after only one or two generations of captivity (Christie *et al*., 2012; Fraser *et al*., 2018).

Stocking with farmed fish often leads to hybridization and genetic introgression of exogenous alleles in wild populations (Laikre *et al*., 2010; Rhymer & Simberloff, 1996). While introgressive hybridization can sometimes increase genetic diversity (Marie *et al*., 2010), it is generally perceived as a threat to natural populations. For instance, introgression can reduce the fitness of hybrids (Araki *et al*., 2007, 2009), cause the loss of local adaptations (Allendorf *et al*., 2001; Laikre *et al*., 2010) and ultimately compromise the viability of wild populations (Araki *et al*., 2009; McGinnity *et al*., 2003; Muhlfeld *et al*., 2014;

Rhymer & Simberloff, 1996). Thus, the cost–benefit of stocking is widely debated in the literature because it can ultimately impede the recovery of supplemented populations, despite its conservation purpose (Brown & Day, 2002; Laikre *et al*., 2010; Rhymer & Simberloff, 1996).

A fitness component of fish that should be greatly affected by stocking is immunity. First, parasitism and diseases cause high mortality in hatcheries and thus medication is extensively used to limit the presence and effect of pathogens (Duston & Cusack, 2002; Scholz, 1999). Such intense use of medication can lead to a relaxed selection on pathogens resistance and greater susceptibility to parasitic infection (Bakke & Harris, 1998; Lamaze *et al*., 2014; Naish *et al*., 2008; van Oosterhout *et al*., 2007). Domestic and introgressed fish can thus be more vulnerable to diseases and parasites than wild individuals (Consuegra & de Leaniz, 2008; Naish *et al*., 2008; van Oosterhout *et al*., 2007). Also, domestic fish grow larger and faster than wild fish, since growth is a trait under strong selection in hatcheries (Solberg *et al*., 2013; Thorpe, 2004) and could thus have poorer immunity because of a trade-off among these components (Lamaze *et al*., 2014; Mangel & Stamps, 2001).

At the population-level, stocking should also affect host–parasite relationships in different ways. Domestic individuals brought in the wild can become vectors for the introduction of new parasites (Naish *et al*., 2008; Valtonen & Koskivaara, 1994; Wootten, 1973) and create favourable conditions for their establishment (Krkošek, 2017; Krkošek *et al*., 2006). Additionally, since supplementing a lake implies increased density of fish (*i.e*., potential hosts), the transmission of parasites can be facilitated and prevalence of infection (*i.e*., the proportion of infected hosts in a population) could increase (van Oosterhout *et al*., 2007). Yet, despite the importance of parasitism in the dynamics and viability of populations, the effects of stocking on parasite communities have rarely been monitored in supplemented populations and the relationship between parasitism and genetic introgression has received very little attention in the literature. Previous studies conducted at the interspecific level showed equivocal results, with hybrid fish displaying either a poorer (Dupont & Crivelli, 1988), intermediate (Bakke *et al*., 1999; Kalbe & Kurtz, 2006; Le Brun *et al*., 1992) or better (Krasnovyd *et al*., 2017; Šimková *et al*., 2012, 2013) resistance to parasites than the parental strains. At the intraspecific level, some studies aimed at understanding how hybridization between host strains belonging to different geographic areas shapes parasitism (*e.g*., Kalbe *et al*., 2016; Kalbe & Kurtz, 2006) and others showed that domestication could negatively affect the parasite resistance of farmed fish (Consuegra & de Leaniz, 2008; van Oosterhout *et al*., 2007), yet only a few investigated the effects of genetic introgression of domestic genes on parasitism. For instance, Currens *et al*. (1997) showed that introgression of exogenous genes through farmed fish stocking decreased the individual resistance to a myxosporean parasite in a population of rainbow trout *Oncorhynchus mykiss* (Walbaum 1792). Also, Lamaze *et al*. (2014) suggested that, after stocking with farmed fish, individuals with a more domestic background were more heavily infected by parasites in brook charr *Salvelinus fontinalis* (Mitchill 1814). These results suggest that introgression could lower the individual resistance to parasites after stocking.

The main objective of this study was to investigate how stocking and genetic introgression affected the host–parasite relationships in *S. fontinalis* from 28 lakes in Québec, Canada. *Salvelinus fontinalis* is the most important species for recreational angling in Québec and several lakes are heavily stocked each year (Marie *et al*., 2010). Lakes with different stocking intensity and introgression levels were selected and different variables related to parasitism were evaluated at the individual and population level. More specifically, at the individual level, the relationship between introgression and infection status (*i.e*., being infected or not) and intensity of the infection (*i.e*., number of parasites carried by infected individuals) was investigated. At the population level, the variation of diversity of parasite communities and prevalence among lakes were analysed as a function of introgression level and environmental variables.

2 | MATERIALS AND METHODS

2.1 | Sampling sites and procedures

Sampling was conducted in three wildlife reserves (Portneuf, Mastigouche and Saint-Maurice) in Québec, Canada (Figure 1) in 2015 (all reserves) and 2016 (Saint-Maurice only). *Salvelinus fontinalis* were sampled in 28 lakes (4 in Portneuf, 6 in Mastigouche and 18 in Saint-Maurice) using experimental gill nets in May, June and July 2015 and in June and July 2016. Lakes that were sampled had a known history of stocking since 1964 (provided by the Ministère des Forêts, de la Faune et des Parcs). Some of these lakes were stocked intensively for decades while others were not stocked for years (Table 1). The number of sampled fish per lake varied between 32 and 67 (Table 1) with a total of 731 fish sampled in 2015 and 509 in 2016. Fish were euthanized with clove oil immediately after their capture. Each fish was weighed (M, ± 1 g), measured (total length, L_T, ± 1 mm) and sexed by observation of the gonads during dissection in the field. Individuals for which sex could not be determined were recorded as indeterminate since they were mostly very small and had not reached the stage of gonad development. Digestive tracts were preserved in 4% formaldehyde until being dissected in the laboratory for parasites analyses. Adipose-fin tissue of each fish was preserved in 95% ethanol until DNA extraction and genotyping. All protocols and procedures employed were reviewed and approved by the Ministère des Forêts, de la Faune et des Parcs.

2.2 | Parasitism analyses

In the field, each fish was inspected for the presence of external parasites when captured. In the laboratory, the digestive tract of each fish was dissected to investigate the presence of internal parasites. Parasites were identified to genus (Northcote, 1957). All parasites (internal and external) were pooled together for all analyses (analyses conducted on separate groups provided similar results; Tables S1, S2 in Appendix S1). Prevalence was estimated for each lake and intensity of infection for each parasitized individual, according to the definitions of Bush *et al*. (1997). Infection status was defined as a binary (0 or 1)

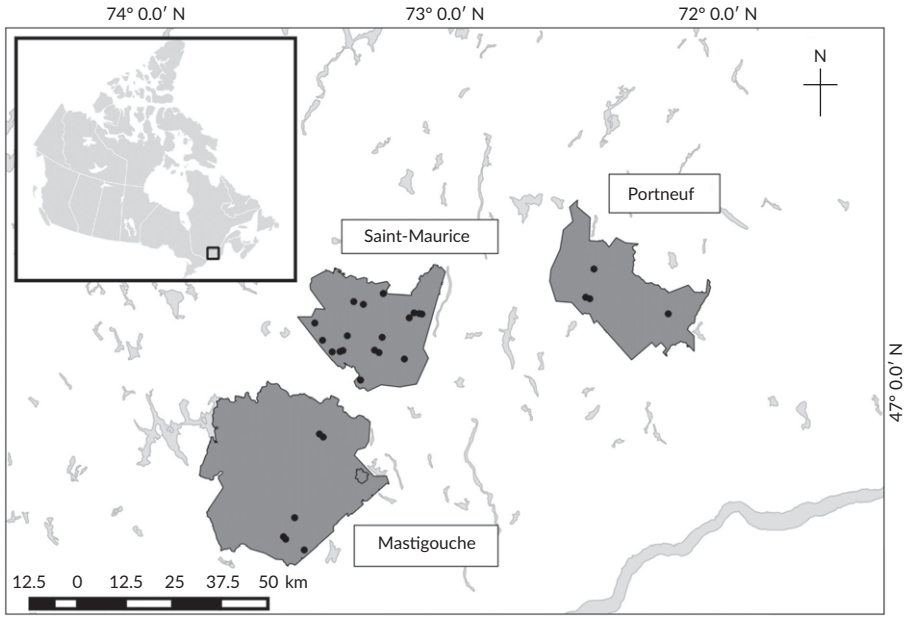

FIGURE 1 Location of lakes sampled (•) in the wildlife reserves of Portneuf, Mastigouche and Saint-Maurice in Québec, Canada

variable indicating whether a fish was infected or not by at least one parasite.

The intensity of infection was determined by counting all parasites observed for each fish. When too many parasites of one genus were present to be counted accurately, a fixed value of 500 for external parasites and 300 for internal parasites was attributed. These values were chosen to be slightly greater than the maximum number of parasites counted in each category (maximum count of 432 for external parasites, 220 for internal parasites). Owing to important overdispersion in the distribution of the intensity of infection variable, it was treated as a categorical variable rather than as a continuous one. To do so, infected fish were divided in two categories according to the median number of parasites per fish (the median was 14.5 so the limit was set to 15 parasites). Thus, the heavily infected group included fish that carried ≥ 15 parasites, whereas the lightly infected group comprised fish that carried < 15 parasites.

Stocked fish in the sampled lakes came from different hatcheries and consisted either of strains kept in captivity for multiple generations (*e.g.*, Jacques Cartier hatchery) in the Portneuf reserve or of hybrid strains (*e.g.*, Lac des Écorces and Saint-Alexis des Monts hatcheries: crosses using domestic fish and wild fish collected each year from Bourassa Lake, which is located in Mastigouche Reserve) in the Mastigouche and Saint-Maurice Reserves. Samples were collected from each hatchery [Jacques Cartier (JC), n = 53; Saint-Alexis des Monts (A), n = 80; Lac des Écorces (ECO), n = 40) and from lake Bourassa (BOU, n = 40).

2.3 | Genetic analyses

DNA was extracted from clips of adipose fins (3 mm^2) using a slightly modified version of Aljanabi and Martinez (1997) salting out method. In brief, 44 μl of 20% sodium dodecyl sulphate (SDS; 1.75% final concentration) and 20 μl of proteinase K (790 μg ml^{-1} final concentration) were used for tissue digestion and samples were incubated overnight at 60°C. A volume of 300 μl of saline solution (5 M) was added and samples were vortexed 1 min. Samples were then centrifuged 30 min at 10157*g*. DNA precipitation was performed using 600 μl isopropanol for 30 min. Samples were then centrifuged 20 min at 16363*g* at the room temperature. A solution of −20°C ethanol 70% was used to wash the pellets twice with a 10 min centrifugation at 16363*g* between these two steps. The pellets were finally diluted in 200 μl of sterile water. The quality and concentration of DNA in the samples were then controlled on 1% agarose gel.

All sampled individuals from lakes and hatcheries were genotyped at 20 microsatellite loci (Table S3). GeneAmp PCR 9700 and SimpliAmp thermocyclers (ThermoFisher Scientific; www.thermofisher.com) were used to amplify microsatellites with the following 10 μl reaction mixture: 10 mM Tris-HCl (pH 9.0); 50 mM KCl; 0.1% Triton X-100; 1 or 1.2 or 1.5 mM $MgCl_2$ (Table S3); 0.2 mM of each deoxynucleotide triphosphate (dNTP); 0.4 mg bovine serum albumin (BSA); 0.6 mM fluorescent forward primer; 0.6 mM reverse primer; 0.25 U μl^{-1} Taq and 5 ng DNA template. PCR conditions consisted of an initial denaturation step of 6 min at 96°C; then 30–35 cycles of 45 s at 96°C, an annealing phase of 30 s at 48–62°C (Table S3) and 45 s at 72°C; and finally after the last cycle an elongation step of 7 min at 72°C.

Microsatellite loci were analysed using four multiplexes (Table S3). PCR products of loci from a same multiplex were pooled and 1 μl of this mixture was used for genotyping with 0.15 μl of GeneScan 600 LIZ size standard (Applied Biosystem; www.appliedbiosystem) and 8.85 μl of Formamide Hi-Di (Applied Biosystem). PCR products were visualized on an AB3130xl automated DNA sequencer (Applied Biosystem) and alleles lengths were determined using Genemapper 4.1 (Applied Biosystem).

Data were checked for genotyping errors and an error rate was calculated for each locus. Hardy-Weinberg equilibrium and linkage disequilibrium were assessed with a Bonferroni correction using GENEPOP 4.3 (Rousset, 2008). The presence of null alleles for each locus,

TABLE 1 Summary of *Salvelinus fontinalis* stocking and sampling information for lakes sampled in this study

Year	Reserve	Lake	*n*	Y_{FS}	Y_{LS}	Y_{SS}	N_{SE}	N_{ST}	Area (ha)	N_{ST} ha^{-1}	$q \pm$ s.d.	Strain
2015	MAS	Demarest (DEM)	66	1999	1999	16	1	1,000	5.2	192.31	0.01 ± 0.02	ECO + BOU + A
2015	MAS	Head (HEAD)	46	1972	1972	43	1	2,500	9.7	257.73	0.05 ± 0.07	ECO + BOU + A
2015	MAS	Cerné (CER)	67	NS	NS	NS	0	0	13.2	0	0.06 ± 0.09	ECO + BOU + A
2015	MAS	Chamberlain (CHAMB)	41	1972	2006	9	9	17,250	18.4	937.50	0.16 ± 0.27	ECO + BOU + A
2015	MAS	Deux Étapes (DETP)	40	1972	2012	3	22	44,861	12.3	3,647.24	0.28 ± 0.4	ECO + BOU + A
2015	MAS	Pitou (PIT)	40	1971	2013	2	23	20,971	8	2,621.38	1 ± 0	ECO + BOU + A
2015	PN	Sorbier (SOR)	46	NS	NS	NS	0	0	5	0	0.01 ± 0.02	JC
2015	PN	Langoumois (LANG)	41	NS	NS	NS	0	0	10	0	0.01 ± 0.02	JC
2015	PN	Main de Fer (MDF)	38	NS	NS	NS	0	0	16	0	0.02 ± 0.13	JC
2015	PN	Caribou (CAR)	32	2008	2013	2	11	2,850	5	570.00	0.2 ± 0.26	JC
2015	STM	Corbeil (CORB)	43	1969	1971	44	2	5,000	9.5	526.32	0.02 ± 0.04	ECO + BOU + A
2015	STM	Brown (BRO)	63	1966	1975	40	4	31,250	273	114.47	0.03 ± 0.04	ECO + BOU + A
2016	STM	Courbé (COUR)	40	1968	2015	1	22	218,965	105.1	2083.40	0.06 ± 0.09	ECO + BOU + A
2015	STM	Portage (PORT)	40	1979	1990	25	11	48,964	46.9	1,044.01	0.07 ± 0.09	ECO + BOU + A
2016	STM	Clairval (CLAI)	40	1973	2015	1	21	61,595	24.9	2,473.69	0.15 ± 0.26	ECO + BOU + A
2015	STM	Milord (MIL)	44	1969	2005	10	16	54,850	46.7	1,174.52	0.16 ± 0.27	ECO + BOU + A
2016	STM	Epervier (EPER)	40	1998	2015	1	9	14,900	12.8	1,164.06	0.18 ± 0.28	ECO + BOU + A
2016	STM	Plongeon-Huard (PLON)	40	1983	2015	1	16	14,932	5.3	2,817.36	0.22 ± 0.23	ECO + BOU + A
2016	STM	Ecarté (ECAR)	41	1979	2014	2	18	27,459	6.3	4,358.57	0.22 ± 0.28	ECO + BOU + A
2015	STM	Soucis (SOU)	41	1976	1976	39	1	750,000	267.5	2,803.74	0.25 ± 0.34	ECO + BOU + A
2016	STM	Est (EST)	40	1980	2015	1	14	27,398	12.2	2,245.74	0.46 ± 0.47	ECO + BOU + A
2015	STM	Perdu (PER)	43	1964	1990	25	16	50,668	22.1	2,292.67	0.49 ± 0.34	ECO + BOU + A
2016	STM	Bec-Scie (BEC)	41	1983	2015	1	20	28,850	9.7	2,974.23	0.66 ± 0.43	ECO + BOU + A
2016	STM	Sud (SUD)	40	1979	2015	1	18	18,868	6.4	2,948.13	0.77 ± 0.39	ECO + BOU + A
2016	STM	Pin (PIN)	64	1991	2015	1	13	14,897	5.9	2,524.92	0.81 ± 0.36	ECO + BOU + A
2016	STM	Boucher (BOUCH)	40	1964	2014	2	34	136,049	25.1	5,420.28	1 ± 0	ECO + BOU + A
2016	STM	Cardinal (CARD)	40	1969	2014	2	24	57,726	7.1	8,130.42	1 ± 0	ECO + BOU + A
2016	STM	Hamel (HAM)	43	1965	2015	1	31	69,893	10.7	6,532.06	1 ± 0	ECO + BOU + A

Note. A: Saint-Alexis des Monts; area: lake area; BOU: Bourassa lake; JC: Jacques Cartier. NS: lake not stocked; MAS: Mastigouche; *n*: number of genotyped *S. fontinalis*; N_{SE}: number of stocking events; N_{ST} ha^{-1}: stocking density; N_{ST}: number of fish stocked; PN: Portneuf; *q*: mean *q*-value of each lake; STM: Saint-Maurice; strain: domestic strains used in analyses: ECO: Lac des Écorces; Year: Sampling year; Y_{FS}: year of first stocking event; Y_{LS}: year of last stocking event; Y_{SS}: number of years between last stocking event and sampling.

allelic richness and expected and observed heterozygosity were determined using CERVUS 3.0.7 (Kalinowski *et al.*, 2007).

The genetic origin and level of introgression (*q*-value) of each individual was determined using Structure 2.3.4 (Pritchard *et al.*, 2000). The *q*-values vary between 0 and 1, respectively designating pure wild and pure domestic individuals. Analyses were performed for each lake using the fish sampled and hatchery fish used to stock the lake (Table 1). The number of populations (*K*) was fixed according to the number of populations (defined as: lake + number of hatcheries used for stocking) probably present in a given lake (*K* = 2 for Portneuf lakes, *K* = 4 for Mastigouche and Saint-Maurice).

2.4 | Model variables and statistical analyses

Seven different types of parasites were found (Table S4) in sampled lakes. The number of parasite genera per lake was used as an indicator of parasite diversity. Catch per unit effort has been widely used to estimate fish abundance and has been shown to be a reliable predictor of density with different fishing methods and in different species (Sanders & Morgan, 1976) including *S. fontinalis* (Bergman *et al.*, 2011). Therefore, the catch per unit effort was used as a proxy of the density of fish in the sampled lakes and calculated it as:

$$D_{is} = n_s (f_i t_i)^{-1} \quad (1)$$

where D_{is} is the proxy of density for lake i for species *s*, n_s the number of fish of the species s caught, f_i the number of nets used on the lake *i* and t_i the cumulative fishing time on the lake i.

White suckers *Catostomus commersonii* Lacépède 1803 were also caught as bycatches. This species is a well-known competitor of *S. fontinalis* that can affect host–parasite relationships when present (Dubois *et al.*, 1996). The presence of *C. commersonii* was recorded for each lake and their density was estimated using Equation 1.

The L_T and *M* of each individual were used to estimate body condition using the Fulton index: $K_F = 100\ M(L_T^3)^{-1}$ (Cone, 1989; Fulton, 1904). This index correlates with visceral fat and relative liver glycogen in *S. fontinalis* (Crespel *et al.*, 2013) and is therefore a reliable indicator of energy storage.

Infection status, intensity of infection and prevalence data were analysed using generalized linear mixed models (GLMM) with a

binomial error distribution. The diversity of parasites (*i.e.*, number of parasites genera per lake) was analysed using a generalized linear model (GLM) with a Poisson error distribution. All models were simplified using a backward stepwise model selection approach. For individual analyses (*i.e.*, infection status and intensity of infection), M, L_T, q-value, sex and K_F were included as fixed effects. An interaction between sex and K_F was also included as an additional fixed effect, since body condition can vary differently in males and females (Sutton *et al*., 2000). Lake and reserve identities were used as random effects to account for hierarchical data structure. For population analyses (*i.e.*, prevalence and diversity of parasites), lake area, *S. fontinalis* population density, *C. commersonii* density, mean q-value of the lake (mean of the q-values of all *S. fontinalis* in a given lake), mean L_T of *S. fontinalis* and mean K_F of *S. fontinalis* were included as fixed effects and reserve identity was included as a random effect. Since the random effect was not significant for the number of parasite species model, it was removed and this variable was analysed with a GLM. All continuous independent variables were standardized (mean = 0, variance = 1). Multicollinearity was accounted for and, as a result, M was removed from analyses at the individual level because of strong collinearity with L_T (all variance inflation factor, VIF < 3; Graham, 2003). All analyses were performed using R 3.3.2 (www.r-project.org) and the packages lme4 to fit GLMMs (Bates *et al*., 2015) and piecewiseSEM to calculate R^2 (Lefcheck, 2016).

3 | RESULTS

The mean genotyping error rate was 0.62% with a range of 0% (for 11 loci) to 2.5%. All loci were polymorphic with allelic richness ranging between six and 41 alleles, with an average of 15.85 alleles. Linkage disequilibrium (LD) was significant for 1.2% of loci pairwise LD measurement for all lakes. On the 28 sampled lakes, 16 showed significant deviation from Hardy-Weinberg equilibrium. Expected and observed heterozygosity are given in Table S5. The mean overall proportion of null alleles was 4.74%. Loci *Sfo-12* and *Sfo*C88 showed high proportion of null alleles (above 10%). Genetic analyses were performed with and without these two loci and the q-values obtained were highly correlated (Pearson, d.f. = 1,359, r = 0.99 [0.994–0.995], P < 0.001). Thus, the q-values obtained with the 20 loci were used in all analyses. For several lakes (*e.g.*, Boucher, Hamel, Cardinal and Pitou), all fish shared the same genetic cluster as one of the hatcheries, so they were considered as being pure domestic and a q-value = 1 was attributed to them.

3.1 | Individual analyses

Sex and L_T were significantly related to the infection status with the largest fish being more likely to be infected (Table 2). To untangle the effect of sex, a post hoc test using pairwise comparisons with a Tukey adjustment for P-values was performed using the package lsmeans in R (Lenth, 2016). There was no difference in infection status between males and females (P > 0.05), but individuals with undetermined sex identification were less likely to carry parasites than males (P < 0.01) and females (P < 0.01). Body length was the only variable related to the intensity of infection, larger individuals being more likely to be in the highly infected group (GLMM, n = 734, d.f. = 730, estimate = 1.25, S.E.M. = 0.14, z = 8.71, P < 0.001, marginal R^2 = 0.128, conditional R^2 = 0.730).

3.2 | Population analyses

All variables, except *C. commersonii* population density, were significantly related to the parasite prevalence (Table 2). More specifically, the proportion of infected fish was higher in larger lakes, in lakes with higher population densities of *S. fontinalis* and those with the higher mean body condition of fish. However, the proportion of infected fish was lower in lakes with the smaller mean L_T and in lakes with the most domestic genetic background [*i.e.* the highest q-values; Figure 2(a)].

Only lake area and introgression level were related to the number of parasite species (Table 2). The largest lakes displayed a higher number of parasite species, whereas a lower parasite diversity was found in lakes with higher domestic genetic backgrounds (Figure 2(b)).

4 | DISCUSSION

The main objective of this study was to understand how supplementation with hatchery-reared fish and the introgression of their genes in wild populations could affect the host–parasite relationships in *S. fontinalis*. At the individual level, no evidence for an association between the genetic background and either infection status or intensity of infection was detected. Both variables were explained by L_T, with the largest individuals being more likely to be infected. At the population level however, it appeared that lakes with a greater proportion of domestic genes displayed lower parasite prevalence and less diversified parasite communities.

4.1 | Individual level

The proportion of domestic genes carried by individuals was not related to infection status or parasite load in the present study. These results are rather surprising given that resistance to parasites was shown to have a genetic basis in fishes, including in *S. fontinalis* (Eizaguirre *et al*., 2012; Glover *et al*., 2004; Kolstad *et al*., 2005; Perry *et al*., 2005) and that it was suggested that domestic fish were more susceptible to parasites. For instance, van Oosterhout *et al*. (2007) showed that after only four generations of captive breeding, guppies *Poecilia reticulata* Peters 1859 reintroduced in the wild displayed higher parasite prevalence and a higher mortality due to infection than wild fish. The results of the present study are also somewhat different from those of Currens *et al*. (1997), who showed that local adaptation was critical for parasite resistance in *O. mykiss* and with results from Lamaze *et al*. (2014) who showed that parasite infection increased with introgression of domestic genes in *S. fontinalis*.

Other studies suggested that hatchery-reared fish may not be more susceptible to infection than their wild counterparts. Indeed, Glover *et al*. (2004) found that among domestic and wild strains of Atlantic salmon *Salmo salar* L. 1758 exposed to sea lice *Lepeophtheirus salmonis*, the most heavily infected strain was from a wild group. Some

TABLE 2 Results of generalized linear mixed models at the individual (infection status) and population (prevalence) level and of generalized linear model at the population level (number of parasite species) in populations of *Salvelinus fontinalis*

Dependent variables	Distribution	*n*	d.f.	Fixed factors	Estimate	s.d.	z	*P*
Infection status	Binomial	1,240	1,224	L_T	0.69	0.13	5.33	<0.001
Marginal R^2 = 0.037				Sex (indeterminate)	−1.03	0.31	−3.29	<0.01
Conditional R^2 = 0.842				Sex (male)	0.02	0.20	0.08	>0.05
Prevalence	Binomial	28	21	Lake area	0.35	0.10	3.32	<0.001
Marginal R^2 = 0.241				Brook charr density	0.60	0.11	5.62	<0.001
Conditional R^2 = 0.382				Mean *q*−value	−0.67	0.09	−7.58	<0.001
				Mean L_T	−0.51	0.09	−5.93	<0.001
				Mean Fulton index	0.63	0.13	4.98	<0.001
Number of parasite species	Poisson	28	25	Lake area	0.20	0.10	2.06	<0.05
R^2 = 0.445				Mean *q*−value	−0.45	0.18	−2.44	<0.05

Note. Lake and wildlife reserve were used as random factors in the infection-status model and wildlife reserve was used as random factor in the prevalence model. Only variables from the final models are presented here. In the infection-status model, sex has three levels and females are the reference level. R^2 estimated with the package piecewiseSEM for GLMMs (infection status and prevalence) and R^2 of the GLM (number of parasite species) is the McFadden's pseudo-R^2.

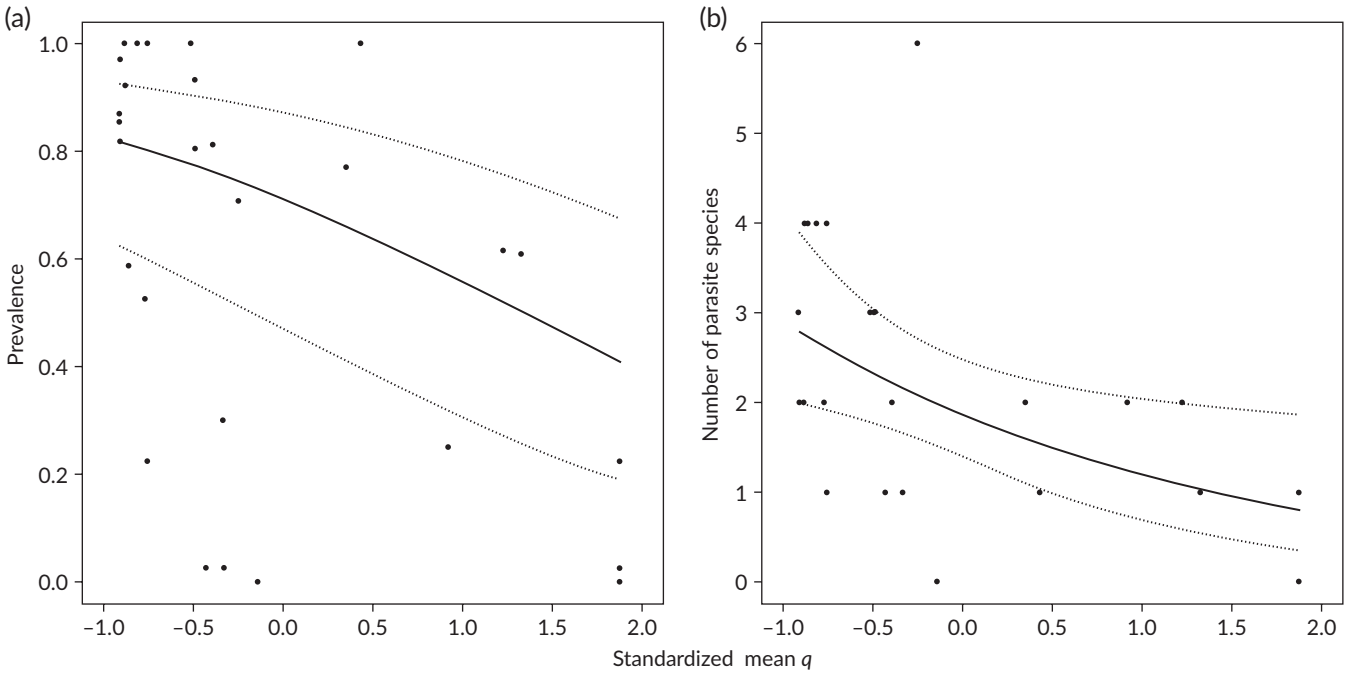

FIGURE 2 Relationships between the mean *q*-value (standardized, mean = 0, σ^2 = 1) of lakes and (a) parasite prevalence and (b) number of parasite species in *Salvelinus fontinalis*. ·····, the predictions of the models; ●, 95% C.I.; , raw data. The higher the q-value, the more domestic the genetic profile of the lake

authors suggested, therefore, that the differences of parasite resistance observed among different fish strains were more likely to be explained by genetic differences in susceptibility (Glover *et al*., 2004) and by local adaptation (Currens *et al*., 1997) rather than by intrinsic differences of resistance between wild and domestic fish. Furthermore, a recent study suggested that domestic fish could actually achieve similar or even better parasite resistance than wild individuals, for instance when they come from an enriched rearing environment (*e.g*., physical structures added into the tanks; Karvonen *et al*., 2016). Moreover, some studies have shown that domestic fish were tolerant to stress (Solberg *et al*., 2013; Woodward & Strange, 1987), which is an important determinant of the immune response, as higher stress results in greater secretion of cortisol, a hormone with immunosuppressive effects (Bakke & Harris, 1998). A higher tolerance to stress could thus improve the capacity of domestic fish to cope with infections. Furthermore, hatchery conditions may not directly affect the parasite resistance of fish, but rather increase the pathogenicity of parasites (Pulkkinen *et al*., 2010; Suomalainen *et al*., 2005). This could explain the existence of parasite outbreaks in hatcheries, without implying that domestic fish are less immunocompetent. Finally, the composition of the parasites assemblage in a given study can strongly influence its results since the level of virulence can shape probability of establishment of parasites (Dobson & May, 1987), for example, or host prevalence and intensity of infection (Bakke & Harris, 1998). Therefore, the number of parasite species and their characteristics such as life cycle or pathogenicity levels

should be accounted for when comparing the results of different studies.

Infection status and parasitic load were mostly explained by L_T, with larger individuals being more likely to carry at least one parasite and to be more infected. Such results are common in fish studies (Glover *et al*., 2001, 2004; Pennycuick, 1971; Poulin *et al*., 1991) and are probably due to the fact that larger individuals are generally older and can have different feeding habits (Hanek & Fernando, 1978; Pennycuick, 1971; Poulin *et al*., 1991). For instance, they can eat more and can feed on a wide array of different prey resulting in potentially higher probabilities of being exposed to parasites (Pennycuick, 1971). Also, older individuals probably have a longer exposure period to parasites, thus increasing their chances of getting infected and of being more infected than younger (smaller) individuals (Poulin *et al*., 1991). Larger fish can also harbour more parasites because they present a larger contact surface (Glover *et al*., 2001; Poulin *et al*., 1991) and, more importantly, because they filter greater volumes of water through their gills (Poulin *et al*., 1991), thereby increasing their chances of getting infected by parasites. An effect of sex on infection status was also detected with indeterminate individuals being less likely to be infected than males and females. This effect is probably explained by the fact that immature fish are smaller and younger than sexually differentiated individuals. Infection levels have been shown to vary with age in fish (Hanek & Fernando, 1978) and the most common pattern is an increase of infection with age (Pennycuick, 1971; Hanek & Fernando, 1978; Valtonen & Koskivaara, 1994), which could partly explain the pattern observed in the present study.

4.2 | Population level

Prevalence and diversity of parasites were found to decrease with a greater proportion of domestic genes in lakes. This result was unexpected and somewhat contrasts with the idea that the introduction of farmed individuals into wild populations could increase the number and diversity of parasites (Krkošek, 2017; Naish *et al*., 2008; van Oosterhout *et al*., 2007; Wootten, 1973, but see Kennedy *et al*., 1991; Valtonen & Koskivaara, 1994) or increase prevalence through the introduction or attraction of new hosts (Dick *et al*. 1987, McGuigan & Sommerville 1985, van Oosterhout *et al*. 2007). A lower parasitism in stocked lakes could be partly due to the higher genetic diversity that is typical of stocked *S. fontinalis* in Québec (Marie *et al*., 2010). Indeed, a high genetic diversity is considered an important component of disease and parasite resistance (Coltman *et al*., 1999; Eszterbauer *et al*., 2015). Moreover, parasites can sometimes have a reduced infection success when they are confronted to non-local hosts (Kalbe *et al*., 2016; Voutilainen *et al*., 2009). Thus, they could be less successful in lakes where their hosts are more domestic, since they are presumably adapted to wild phenotypes. On the other hand, it is possible that the distribution of domestic individuals is a consequence of the distribution of parasites rather than the opposite. For instance, if hatchery-reared individuals are actually strongly affected by parasites (Naish *et al*., 2008; van Oosterhout *et al*., 2007), they could be less likely to survive in lakes with high prevalence and parasites diversity. Therefore, those lakes would display low levels of domestication because parasites limit the presence of farmed fish.

The absence of effect of introgression at the individual level and the significant association of introgression between prevalence and parasite diversity at the population level may reflect environmental differences among lakes. Lakes with the most domestic genetic background are the most heavily stocked in the system studied here (Létourneau *et al*., 2018; Marie *et al*., 2010). It has been suggested that intense stocking could alter environmental quality of habitats, for instance by altering zooplankton community structure and thus food resources (McNaught *et al*., 1999; Yang *et al*., 2005). Therefore, a more domestic genetic background could be confounded with poor quality environments, which could in turn influence the presence of parasites in lakes. Moreover, typically, intensively stocked lakes are supplemented because they are generally poorer environments in which populations are less productive (SÉPAQ, personal communication, 4th July 2016) and therefore would not sustain angling pressures without external supply. In the present study system, the presence of lakes with only pure domestic individuals suggests that either wild stocks have been replaced by domestic fish because of stocking (Evans & Willox, 1991) or that wild populations never managed to settle in these lakes in the first place, possibly because of poor environmental quality. In the present study, this possibility could not be tested because no detailed data on abiotic conditions (besides lake area which was positively related to prevalence and number of parasite species) were available for these lakes. Also, since lakes are supplemented to increase angling success, heavily stocked lakes are more likely to be exposed to stronger angling pressure. Those lakes could have depleted parasite communities because of the process of fishing out parasites through host density reduction, a phenomenon already described in marine systems in which the massive removal of hosts trough fishing leads to a global decline in parasites (Dobson & May, 1987; Krkošek, 2017; Wood *et al*., 2010). Furthermore, largest individuals that carry more parasites are also preferentially targeted by recreational anglers. Thus, it is possible that the removal of largest individuals in lakes that sustain important fishing pressures (*i.e.* heavily stocked lakes) lead to depleted parasites communities in these populations.

In conclusion, to our knowledge, no previous work addressed the consequences of introgressive hybridization of domestic fish on their wild conspecifics by documenting both individual and population measures of parasitism. The present results show no effect of the domestic genes at the individual level. At the population level, most introgressed populations are characterized by the occurrence of fewer parasites, but this could partly be explained by confounding environmental effects. To disentangle the effects of genetics and environment on the parasitism patterns of stocked lakes, additional environmental variables should be analysed, such as lake depth which is known to influence parasites communities in some cases (Bergeron *et al*., 1997; Dubois *et al*., 1996; Marcogliese & Cone, 1991).

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Authors' contributions

P. G. co-developed the ideas of the manuscript, collected and analysed data and wrote and edited all drafts. D.G. co-developed the ideas of the manuscript, helped analysing data, edited all drafts and provided funding. P.S. and L.B. edited drafts of the manuscript and provided funding.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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