LETTER

Transgenerational Effects of Parental Rearing Environment Influence the Survivorship of Captive-Born Offspring in the Wild

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Abstract

As natural populations decline, captive breeding and rearing programs have become essential components of conservation efforts. However, captive rearing can cause unintended phenotypic and/or genetic changes that adversely impact on population restoration efforts. Here, we test whether the exposure of captive-reared Atlantic salmon (*Salmo salar*) to natural river environments (i.e., "wild exposure") during early life can serve as a mitigation technique to improve the survivorship of descendents in the wild. Using genetic pedigree reconstruction, we observed a two-fold increase in the survivorship of offspring of wild-exposed parents compared to the offspring of captive parents. Our results suggest that harnessing the influence of transgenerational effects in captive-rearing programs can improve the outcomes of endangered species restoration efforts.

Introduction

As natural populations decline, captive-rearing programs have become important components of conservation and management efforts (Williams & Hoffman 2009). These programs are largely aimed at preserving the genetic integrity of a threatened species ex situ and providing demographic support to wild populations until the external factors contributing to declines can be mediated (Frankham 2008; Allendorf *et al.* 2013). However, wild population supplementation or rehabilitation efforts are complicated by the phenotypic differences that may arise in captive compared to wild populations. Indeed, captive-reared individuals face relaxed natural and sexual selection pressures relative to wild individuals and/or "domestication" selection for phenotypes that carry high fitness in captivity but low fitness in natural environments (Waples 1991; Gall 1993; Lynch & O'Hely 2001; Ford 2002; Williams & Hoffman 2009). Moreover, developmental phenotypic plasticity may drive trait divergence between wild and captive individuals (Lorenzen *et al.* 2012) and these "acquired" traits passed to wild descendants via nongenetic mechanisms of inheritance mediated by DNA methylation patterns or maternal effects (Jablonka *et al.* 1995; Jonsson *et al.* 1996; Day & Bonduriansky 2011; Bonduriansky *et al.* 2012; Salinas & Munch 2012). Collectively, transgenerational effects arising from exposure to captivity, and driven by genetic and/or nongenetic mechanisms of inheritance, have the potential to influence the performance of captive-reared individuals, and their descendants, in the wild (Araki *et al.* 2009; Christie *et al.* 2012).

More than 300 fish species are now reared in captivity for fisheries supplementation or conservation purposes, with billions of individuals released into the wild annually (Brown & Day 2002). Despite this massive investment, population sizes for many captive-reared and

supplemented species remain at historically low levels (Brown & Day 2002; Fraser 2008). A growing number of studies of salmonid fishes have demonstrated that captive-reared individuals experience poor survival and reproductive success in the wild compared to wild-origin individuals (Araki *et al.* 2007; Christie *et al.* 2012; Anderson *et al.* 2013; Milot *et al.* 2013). Furthermore, introgression between hatchery origin and wild fish may contribute to decreased productivity of wild populations (Lynch & O'Hely 2001; Ford 2002; Araki *et al.* 2009). Thus, while captive-rearing programs for salmon are capable of minimizing loss of genetic variation resulting from the action of neutral genetic processes (Eldridge & Killebrew 2007), their efficacy as mechanisms of supportive breeding for wild populations has been called into question (Brown & Day 2002; Fraser 2008). However, for populations at risk of imminent extinction, including many native populations of Atlantic salmon (*Salmo salar*) in North America and Europe, the use of captive-rearing programs appears unavoidable (Snyder *et al.* 1996). Ultimately, the effectiveness of such programs, depends on their ability to produce "wild" phenotypes capable of contributing to population productivity (Fleming 1994; Brown & Day 2002; Lorenzen *et al.* 2012).

Here, we test experimentally whether the exposure of captive-reared salmon to natural river environments during early life can serve as a technique to improve the survivorship of descendants in the wild. Our study system was the Big Salmon River (BSR) population of Atlantic salmon in New Brunswick, Canada. Inner Bay of Fundy (iBoF) Atlantic salmon populations, including the BSR, were federally listed as "endangered" in 2001. The iBoF population assemblage was historically composed of at least 32 salmon-bearing rivers that produced >40,000 breeding adults—today the iBoF harbors fewer than 250 adults and is largely sustained via a pedigree-supported captive-rearing program that seeks to preserve the remnant genetic diversity and differentiation found among iBoF populations (Department of Fisheries and Oceans Canada 2010). These efforts appear to have halted or at least postponed the extirpation of iBoF Atlantic salmon, as rivers supplemented through captive rearing, including the BSR, have maintained small populations in contrast to unsupplemented rivers, albeit natural productivity remains extremely low (Department of Fisheries and Oceans Canada 2010).

Methods

Experimental crosses and offspring wild releases

We generated monogamous crosses (i.e., each male and female was used only once) between parents born and raised entirely in captivity (C; $N = 8$ crosses) and parents that were born in captivity but exposed to the wild ("wild-exposed") via release to a natural river environment for either 1 (WE1 $N = 10$ crosses) or 2 (WE2 $N = 9$ crosses) years during development. These fish were released as unfed fry (at the start of exogenous feeding, roughly 5–6 months following egg fertilization) and remained in the wild to 1+ or 2+ years of age, at which point survivors were recaptured, and then reared to sexual maturity in captivity. Further detail on the rearing conditions for the parental treatment groups can be found in the supporting information. The majority of mortality across the Atlantic salmon life cycle is experienced during freshwater residency; fry-to-smolt survival in the BSR, for example, averaged 2.5% in the years 2001 to 2004 (Flanagan *et al.* 2006). Our experimental design thus exposed captive broodstock to environmental conditions and selection pressures naturally found during freshwater development in iBoF Atlantic salmon. We also generated crosses between parents that were born in the wild, collected as 1+-year-old juveniles (W1; $N = 11$ crosses) from the BSR, and subsequently reared in the hatchery as captive broodstock. These W1 crosses represent an approximate "baseline" with which the fitness effects of experimental exposure of captive-origin fish, particularly the WE1 fish, to wild environments may be compared. Since 2000, all iBoF salmon used in supportive breeding programs have been genotyped at a suite of microsatellite loci (O'Reilly & Doyle 2007; O'Reilly & Harvie 2010), and this information is used to identify origin via pedigree analysis (i.e., captive or wild; Houde *et al.* 2011a, 2011b; DeMestral *et al.* 2012, 2013). The majority of juveniles collected from the BSR for captive broodstock from 2003 to 2010 did not assign genetically to known hatchery crosses (Flanagan *et al.* 2006; DeMestral *et al.* 2013), indicating that their parents, and therefore the grandparents of all salmon analyzed for survivorship in the wild in this study, were likely to have been produced by wild-spawning parents from the BSR.

All crosses were conducted during 20–28 November 2007 at the Mactaquac Biodiversity Center in Fredericton, New Brunswick, Canada. Adipose fin clips were collected from all parents used in the crosses and stored in 95% ethanol. The known pedigree of the captive-origin broodstock was used to avoid crosses between full- or half-sibs. Across the treatments, the parents used for the crosses were 4–6 years of age and thus conceived in different years in the hatchery. However, there was no effect of male or female conception year on (log+1 transformed; see statistical methods below) offspring survival (ANOVA: male year: $F_3 = 0.87$, $P = 0.460$; female year: $F_2 = 0.71$, $P = 0.492$). Furthermore, neither male nor

female length were significant predictors of offspring survivorship (ANOVA: male length: $F_1 = 0.001$, $P = 0.975$; female length: $F_1 = 0.001$, $P = 0.978$).

The family groups resulting from the crosses were reared at the Mactaquac hatchery until 6 June 2008, when offspring reached the exogenous feeding stage. At this point, offspring from each family group were collectively weighed, counted, and evenly distributed into four groups for release at two sites (each ~ 400 m long) of Bonnell Brook (~ 5 km apart), a tributary of the BSR, hereafter referred to as the upper and lower Bonnell. Juveniles were distributed across the sites every 50 m. The upper and lower sites showed qualitative differences. The upper site is located above a beaver dam, and shows consistent aquatic vegetation throughout and exhibits a wet width range of 2–5 m. The lower site is located below a waterfall, has little to no observable aquatic vegetation, and exhibits a wet width range of 4–10 m. Neither site had been stocked historically. Overall, a total of 6,046 offspring were released per site (see Table S1 for release numbers by family).

Offspring survivorship in the wild

In the fall of 2008 (25 September–8 October), we used electrofishing to sample a total of 368 young-of-the-year (0+ offspring) from lower Bonnell Brook and 341 0+ offspring from upper Bonnell Brook. During 25–29 August 2009, an additional 350 parr (1+ offspring) were collected from lower Bonnell Brook (Table S1). The upper site was not sampled in 2009 due to logistical constraints. Each site was sampled using standard multiple-pass backpack electrofishing techniques, both up and downstream of the release locations and until zero fish were captured for 100 m of sampling, which extended approximately 0.5 km up- and downstream of each site. All sampled juveniles were weighed and photographed with a size standard. In addition, we collected adipose fin clips from each individual and stored the tissues in 95% ethanol. Following processing, fish were returned to the stream near their location of capture. The fork length of each juvenile was measured to the nearest millimeter from the digital photographs using Image J (NIH, Bethesda, MD, USA).

We used genetic pedigree analysis to assign juvenile salmon collected from Bonnell Brook to one of the 38 families. DNA Wizard (Promega Corp., Madison, WI, USA) or DNAeasy blood and tissue (Qiagen Inc., Valencia, CA, USA) kits were used to isolate DNA from the tissues of parents and offspring. Offspring and parents were then genotyped at six microsatellite markers, *Ssa*202 and *Ssa*197 (O'Reilly *et al.* 1996) and *SSsp*2201, *SSsp*2215, *SSsp*2216, and *SSsp*1G7 (Paterson *et al.* 2004). Each locus was amplified in 10 μl PCR reactions comprising: 1 × PCR buffer, 2.5 mM $MgCl_2$, 0.5 mM dNTP, 1 mM of forward and reverse primer, and 0.5 U *Taq* DNA polymerase. The PCR products for offspring were visualized on the ABI 3730 DNA analyzer and scored in GeneMapper v. 4.1 (Life Technologies Inc., Burlington, ON, Canada). Parents were genotyped on an FMBIO, an MJ Base station, or an ABI 3130XL as described in Herbinger *et al.* (2006). A common size standard and allele binning algorithm was applied across the platforms in order to minimize discrepancies in allele size determination.

The microsatellite loci were highly variable, exhibiting between 12 and 23 alleles (Table S2). Combined, the six loci resulted in an average nonexclusion probability for a candidate parental pair of 1.3×10^{-7}, as calculated in CERVUS v. 3.0 (Kalinowski *et al.* 2007). Analyses of allele frequencies in parents in Genepop v. 4.2 (Raymond & Rousset 1995) indicated that all but two loci, *SSsp*2201 and *SSsp*1G7, were in Hardy–Weinberg equilibrium. The parents showed slight heterozygote deficits at these loci, possibly related to low-frequency null alleles (Table S2). Thus, to be conservative in our parentage assignments, we did not exclude a candidate parental pair based on allelic mismatches with offspring at either of these loci on their own.

We compared the multilocus microsatellite genotypes of all offspring to the genotypes of the known parental pairs and excluded candidate parental pairs based on mismatches between parents and offspring at the loci. We then used COLONY v. 2.0 (Jones & Wang 2010) to construct full-sib kinship groups based on offspring genotypes. These groups were used to ensure consistency in matches between a given parental pair and offspring identified as full-sibs. Kinship groups were assigned in COLONY using a medium run length and the monogamous male and female setting. Allele dropout and general error rates were set to 1% for each locus. Survivorship for each family is presented as the percentage of offspring assigned to a family out of the total number of offspring from that family initially introduced into the wild environment (Table S1).

Statistical analysis

The survivorship and body size data conformed to log distributions (Shapiro–Wilk test: $P > 0.88$) and thus we log transformed these data prior to statistical analyses. We examined relationships between offspring survivorship (log+1 transformed) per family group and the four types of parental rearing environments/crosses (C, WE1, WE2, W1) using ANOVA. For the ANOVA model examining 0+ offspring survivorship, parental

Table 1 Results of ANOVA models examining the influence of parental rearing environment on Atlantic salmon offspring survivorship in Bonnell Brook, New Brunswick

	Factors	R^2	F	DF	P	Parameter	β	βSE	t	P
0+ survivorship	Model	0.14	2.82	4,75	**0.031**	Intercept	1.76	0.06	28.98	**<0.001**
	Transplant site		1.26	1	0.265	Lower Bonnell	−0.07	0.06	−1.12	0.265
	Parent environment		3.34	3	**0.024**	C	−0.32	0.11	−2.85	**0.005**
						W1	0.03	0.10	0.33	0.745
						WE1	0.03	0.10	0.32	0.748
1+ survivorship	Model	0.04	0.42	3	0.740	Intercept	1.74	0.09	19.81	<**0.001**
	Parent environment		0.42	3	0.740	C	−0.13	0.16	−0.80	0.431
						W1	−0.07	0.14	−0.46	0.647
						WE1	0.11	0.15	0.72	0.479

The survivorship of the offspring of parents exposed to captive (C) or wild environments (WE, W; see methods) during development was estimated using parentage analysis of 0+ juveniles collected in 2008 from lower and upper Bonnell release sites and 1+ juveniles collected in 2009 from the lower Bonnell site. Estimates of the magnitude of the effect of each parameter on offspring survivorship (β) and its SE (β SE) are indicated. The hypothesis that each parameter's effect on survivorship is zero was tested with the t-statistic. Degrees of freedom (DF) for each factor, and numerator and denominator DF for the model, are also indicated. P-values falling below the critical α (0.05) are boldfaced.

environment, transplant site (lower Bonnell or upper Bonnell), and the interaction between parental rearing environment and transplant site were included as fixed factors. The interaction term was ultimately excluded from the model as it was not a significant predictor of variance in offspring survivorship (see Table S3 for results of full model). For the model examining 1+ offspring survivorship (log+1 transformed) at the lower Bonnell site, parental rearing environment was included as fixed factor.

We examined differences in the initial (estimated from family group weight and offspring counts) log-transformed mass of juveniles from each family released at Bonnell Brook using one-way ANOVA. Generalized linear mixed models (GLIMM) were used to examine relationships between log-transformed mass or length of offspring and parental-rearing environment. For 0+ offspring, the models incorporated parental rearing environment and transplant site, and their interactions, as fixed factors and family ID as a random factor to account for the nonindependence of mass or length within families. However, as for the 0+ offspring survivorship model, the interaction was not a significant predictor of either body size estimator and was excluded from final models (Table S3). We also examined variation in log-transformed body mass and body length of 1+ offspring from lower Bonnell using GLIMM, with parental rearing environment and family ID included as fixed and random factors, respectively, in the model.

Means are reported ±1 SE throughout. We used the critical value $\alpha = 0.05$ for all statistical tests. All statistical analyses were performed in JMP v. 10 (SAS Institute Inc., Cary, NC, USA).

Results

We assigned 356 of 368 (97%) and 296 of 341 (87%) 0+ offspring sampled from the upper and lower Bonnell sites, respectively, to a parental pair (cross). For the 1+ offspring collected in 2009 from the lower Bonnell site, we were able to assign 297 of 350 (85%) to a parental pair. Offspring from C (pure captive parents) crosses showed significantly lower survivorship than the other three treatments (Table 1), with 4% of the released offspring having been recaptured as 0+ juveniles, an observation that was replicated at both the upper and lower Bonnell sites (Table 1, Figure 1A). This survivorship rate was approximately half that observed for 0+ offspring from WE2 (i.e., captive parents exposed to wild for 2 years) crosses, who exhibited 7% and 8% survival at the lower and upper Bonnell release sites, respectively (Figure 1a). Overall, there was a trend toward higher offspring survivorship through the 0+ juvenile stage the longer parents were exposed to wild environments (Figure 1a). The offspring from WE1 (i.e., captive parents exposed to the wild for 1 year) and W1 (i.e., wild-origin parents) crosses showed equivalent survivorship in the wild and their survivorship was intermediate to that of offspring from C and WE2 crosses. We found no effect of parental rearing environment on the survivorship of 1+ offspring, although the general trend toward the offspring of WE2 crosses exhibiting the highest survivorship remained (Table 1, Figure 1B).

The initial mass of offspring at the time of release to the wild did not differ among the C, WE1, WE2, or W1 families (one-way ANOVA: $F_{3,34} = 0.730$, $P = 0.541$). For the 0+ and 1+ juveniles, parental rearing environment

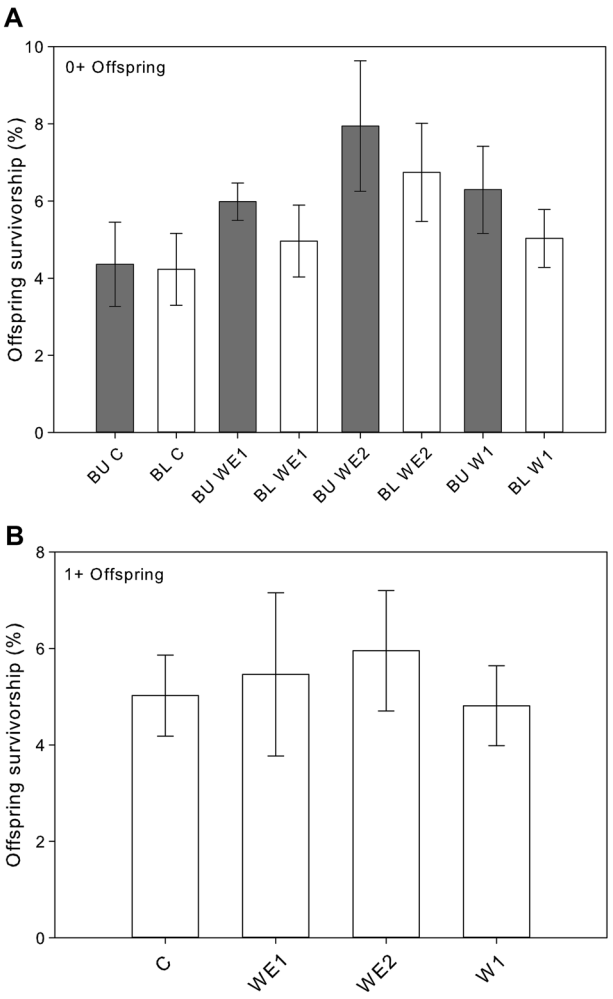

Figure 1 Survivorship of Atlantic salmon offspring released at Bonnell Brook, New Brunswick, Canada. The survivorship of 0+ (A) and 1+ (B) offspring (±1 SE) of parents that were reared entirely in "captive" hatchery environments (C), parents of captive origin but who were exposed to a wild environment for 1 year (WE1) or 2 years (WE2) during development, or parents of true "wild" origin (i.e., from wild spawning) that reared for 1 year in the wild before capture and subsequent captive rearing (W1) is shown. Survivorship of the offspring was followed at two sites, the upper (BU; gray bars) and lower Bonnell (BL; white bars).

was not a significant predictor of either body mass or body length (Table 2, Figure 2). However, the body size of 0+ juveniles differed between the two sites, with the lower Bonnell juveniles showing significantly larger body masses and lengths compared to juveniles sampled from the upper Bonnell (Table 2, Figure 2), suggesting that the release sites exhibit differences in productivity. Overall, there was no effect of an interaction between release site and parental rearing environment on survivorship, body mass, or body length, indicating that the influence of parental rearing environment on offspring performance is independent of any differences in release site productivity.

Discussion

To our knowledge, this is the first study to experimentally demonstrate that transgenerational effects can be harnessed to improve the performance of a captive-reared fish species in the wild. For the endangered iBoF Atlantic salmon, our results have revealed that offspring of parents exposed to the wild for 2 years experienced a two-fold increase in survivorship over the first 4 months of freshwater residency compared to offspring of purely captive-reared parents. The offspring of parents exposed to the wild for 1 year (WE1) exhibited survivorship that was intermediate to that of offspring of pure captive parents and parents exposed to the wild for 2 years, suggesting that increased length of parental exposure to the wild during freshwater residency increased descendent survivorship in the wild. Moreover, the offspring of wild (W1) and WE1 parents showed equivalent survivorship despite differences in fertilization regimes (natural vs. captive), and subsequent rearing environments to the fry stage (i.e., when captive-origin parents were released to the wild). This suggests that sexual selection and variation in parental rearing environment prior to the onset of exogenous feeding has less of an impact on descendents' performance than wild exposure at later developmental stages. This is not to say that sexual selection is unimportant, but rather that the beneficial effects may not be realized for several generations (Pélabon *et al.* 2014; Whitlock & Agrawal 2009). Overall, our results indicate that transgenerational effects driven by parental rearing environment can positively impact Atlantic salmon juvenile survival following their release to the wild from captive-breeding programs. Recovery teams for endangered salmon should therefore consider exposing captive broodstock to wild environments following their emergence as fry and incorporate the use of wild-exposure periods in excess of 1 year in order to yield the greatest improvements to descendant performance.

At one of our experimental release sites, lower Bonnell Brook, we were able to assess offspring survivorship across an additional 11 months (to summer 2009) following our initial assessment of survivorship in the fall of 2008. While patterns of offspring survivorship remained similar to those observed over the first 4 months following their wild release, we did not find that parental rearing environment remained a significant predictor of survival. This result may indicate that any heritable effects, including epigenetic and/or nongenetic, driven by

Table 2 Results of generalized linear mixed models examining the influence of parental rearing environment on Atlantic salmon offspring body size in Bonnell Brook, New Brunswick

	Factors	R^2	*F*	DF (num, denom)	*P*
0+ body mass	Model	0.26			
	Transplant site		90.77	1, 638.5	<**0.001**
	Parental rearing environment		0.34	3, 33.9	0.800
1+ body mass	Model	0.14			
	Parental rearing environment		0.77	3, 28.2	0.519
0+ body length	Model	0.27			
	Transplant site		82.40	1, 565.4	<**0.001**
	Parental rearing environment		0.60	3, 33.1	0.619
1+ body length	Model	0.14			
	Parental rearing environment		0.61	3, 27.8	0.614

Body mass and fork length was examined for 0+ juveniles collected in 2008 from the lower and upper Bonnell release sites and 1+ juveniles collected in 2009 from the lower Bonnell site that assigned as offspring of captive- and wild-reared parents using genetic parentage analysis. R^2 indicates the fit of the overall model to the data. The influence of each factor on log-transformed body mass or body length was tested using the *F*-statistic. Numerator (num) and denominator (denom) degrees of freedom (DF) are shown for each factor. *P*-values falling below the critical α (0.05) are boldfaced.

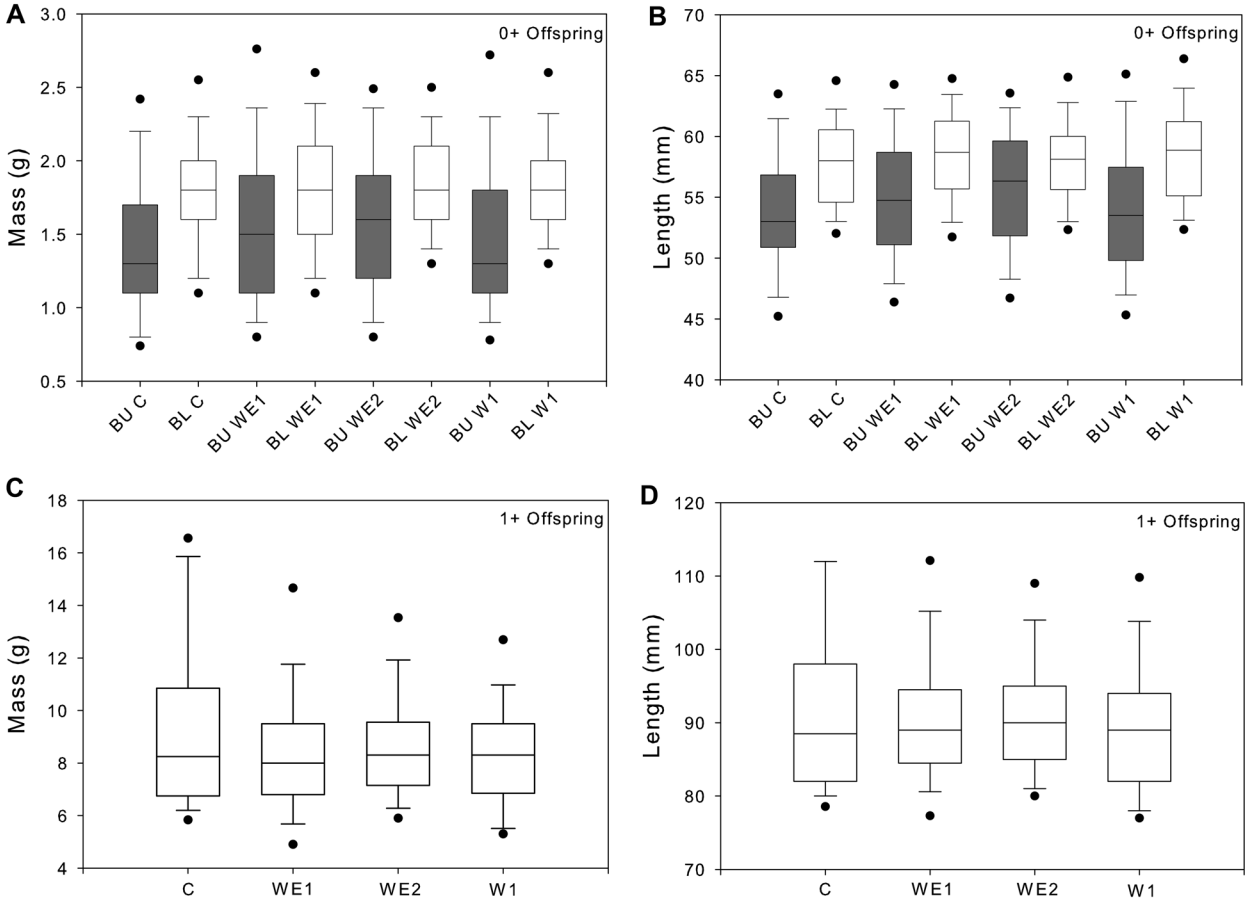

Figure 2 Body mass and length of Atlantic salmon offspring introduced into Bonnell Brook, New Brunswick, Canada. Mass and length distributions for offspring of parents reared in captivity (C), captive parents exposed to a wild environment for 1 year (WE1) or 2 years (WE2) during development, or parents of wild origin (i.e., from wild spawning) that reared for 1 year in the wild before capture and subsequent captive rearing (W1) are shown using boxplots. Offspring were followed at two sites, the upper (BU; gray boxes) and lower Bonnell (BL; white boxes). We obtained estimates of 0+ offspring mass and fork length in the BU and BL in 2008 (A and B, respectively) and 1+ offspring mass and fork length in the BL in 2009 (C and D, respectively). The boxplots show median mass (horizontal line in box) surrounded by the upper and lower quartiles (boxes representing 50% of the datapoints). Lower and upper error bars indicate the 5th and 95th percentiles, respectively. Points represent outliers.

parental environment are experienced early in the life cycle of offspring, and become diluted by other factors contributing to variance in survivorship over time. It is also possible that our inability to detect a relationship between parental rearing environment and offspring survival reflects decreased statistical power given as we were only able to sample one release site in 2009. Long–term studies, across the entire life cycle, are needed to fully assess the power of parental exposure to the wild as a technique for improving the performance of future generations of captively bred organisms for reintroduction.

The observed increase in offspring survivorship was achieved after one generation of parental exposure to the wild indicating that strong selection against maladaptive phenotypes may be occurring during the parental generation's freshwater residency. Domestication selection for phenotypes that experience low fitness in the wild has been demonstrated in steelhead trout (*Oncorhynchus mykiss*) within a single generation of captive rearing (Christie *et al.* 2012), and therefore our survivorship results may indicate that the experimental wild release of captive-origin parents is selecting for traits that are adapted to natural conditions.

While adaptation may occur via the inheritance of genetically based traits selected during minimal exposure to the wild, the potential for nongenetic inheritance of traits arising from plastic responses to environmental variation has also been suggested as a likely mechanism of rapid phenotypic divergence of captive-reared and wild salmon (Araki *et al.* 2009). For instance, nongenetic inheritance could be driven by differential patterns of DNA methylation or maternal effects arising from environmental variation experienced by parents (Jablonka *et al.* 1995; Jonsson *et al.* 1996; Day & Bonduriansky 2011; Bonduriansky *et al.* 2012). The only study to have examined a potential mechanism of nongenetic inheritance in salmonid fishes—overall levels of methylation in the steelhead genome—did not uncover any differences related to captive and wild environments (Blouin *et al.* 2010), albeit gene-specific patterns of methylation remain to be examined. Indeed, a recent study of sheepshead minnows (*Cyprinodon variegates*) demonstrated transgenerational plasticity in physiological response to temperature, suggesting that parents can adaptively program the genomes of offspring in order to match their environment (Salinas & Munch 2012). Our work, combined with the results of previous studies, has shown that transgenerational effects, mediated through genetic and/or nongenetic inheritance mechanisms, can lead to rapid and adaptive changes to offspring phenotype.

Overall, our results have demonstrated experimentally that captive rearing can have a pronounced effect on the survival of future generations, and have provided a potential mechanism—the wild exposure of parental generations—for mediating such effects, in this case, for recovery programs of endangered Atlantic salmon. Our results also indicate that increased parental exposure to the wild increases rates of survivorship for offspring following their release to the wild. Therefore, minimizing parental exposure to captivity and maximizing exposure to the wild, but even for short time periods and within generations, should be an important component of captive-rearing planning for endangered species and populations, such as the salmon of the iBoF. This may require trading off survivorship in the parental generation (i.e., mortality is likely to be higher in the wild than in captivity for the period of exposure) for improved performance in future generations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Total number of Atlantic salmon offspring released per site and recovered, as estimated from genetic parentage assignment, by family (cross) at Bonnell Brook, New Brunswick.

Table S2. Microsatellite loci used to assign parentage in Atlantic salmon from Bonnell Brook, New Brunswick.

Table S3. Results of full statistical models examining the influence of parental rearing environment, rearing site within Bonnell Brook (lower or upper), and their interactions on the survivorship and body size (mass and length) of Atlantic salmon juveniles.

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