Genetic variability in reaction norms between farmed and wild backcrosses of Atlantic salmon (*Salmo salar*)

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Abstract: Adaptive responses to environmental heterogeneity may vary among populations. Genetic variability in reaction norms might account for population differences in the ability to respond to environmental change and may reflect local adaptation. Reaction norms for early life history traits were compared among three population crosses of Atlantic salmon (*Salmo salar*). Two comprised second-generation backcrosses introgressed with either farmed or wild genes; the third comprised individuals from a second-generation, pure wild cross. Using a common-garden experimental protocol, each cross was exposed to three temperature regimes. Plasticity in embryonic development, growth, survival, and body size was measured from fertilization up to 24 weeks of exogenous feeding. Reaction norms differed markedly among crosses, irrespective of whether individuals interbred with those whose genes originated from another wild population or from a cultured population. We find that introgression involving individuals with comparatively few genetic differences can change reaction norms. If plasticity represents an adaptive response to local environments, then changes to reaction norms resulting from interbreeding between populations are unlikely to have a beneficial effect on fitness.

Résumé : Les réactions adaptatives à l'hétérogénéité de l'environnement peuvent varier d'une population à une autre. La variabilité génétique des normes de réaction peut expliquer les différences entre les populations dans leur capacité à réagir aux changements environnementaux et peut représenter une adaptation locale. Nous avons comparé les normes de réaction des traits du début du cycle biologique chez trois populations croisées de saumons atlantiques (*Salmo salar*). Deux des populations comprenaient des individus rétrocroisés de seconde génération avec introgression de gènes de pisciculture ou de gènes sauvages; la troisième comprenait des individus de seconde génération issus d'un croisement sauvage pur. Dans un protocole expérimental de jardin commun, chaque croisement a été exposé à trois régimes thermiques. Nous avons mesuré la plasticité du développement embryonnaire, de la croissance, de la survie et de la taille corporelle depuis la fécondation jusqu'après 24 semaines d'alimentation exogène. Les normes de réaction varient de façon marquée d'un croisement à l'autre, indépendamment du fait que les individus aient été croisés avec d'autres dont les gènes provenaient d'une autre population sauvage ou d'une population d'élevage. Nous observons que l'introgression, qui implique des individus avec comparativement peu de différences génétiques, peut modifier les normes de réaction. Si la plasticité représente une réaction adaptative aux environnements locaux, alors les changements de normes de réaction dus aux croisements entre les populations sont peu susceptibles d'avoir un effet bénéfique sur la fitness.

[Traduit par la Rédaction]

Introduction

Phenotypic plasticity reflects the ability of individuals to respond to environmental change (Bradshaw 1965), a characteristic of presumed fundamental importance to the persistence of natural populations (Schlichting and Pigliucci 1998). Given that the direction of selection can vary in both space and time in heterogeneous environments (Via and Lande 1985), the ability of a genotype to produce different phenotypes can allow for short-term, potentially adaptive responses to environmental change (Pigliucci 2001).

Plasticity can be heuristically and graphically represented by a norm of reaction, defined as the profile of phenotypes produced by a given genotype across an environmental gradient (Schmalhausen 1949). Reaction norms provide information on the magnitude of trait plasticity, the presence of genotype × environment interactions on the phenotypic expression of a given trait, and the extent to which the additive genetic variance of a trait changes with the environment (de Jong 1990; Falconer and Mackay 1996). Population-level differences in reaction norms may explain why populations respond differently to natural or anthropogenic changes in the environment (Schlichting and Pigliucci 1998; Dieckmann and Heino 2007) and might reflect local adaptation. If true, then changes to either the elevation or slope of reaction norms could have negative consequences for fitness.

Within this context, we explored the degree to which interbreeding alters the shapes of reaction norms in Atlantic salmon (*Salmo salar*), a species whose life history varies considerably throughout its geographical range (Hutchings

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and Jones 1998). Although differences in the average expression of various traits have been hypothesized to reflect local adaptation (Taylor 1991; McGinnity et al. 2003; Garcia de Leaniz et al. 2007), population differences in life-history reaction norms have not been previously examined in this species, with the exception of those recently documented for male parr maturity (Piché et al. 2008).

The potential for populations to differ in their ability to respond to environmental change may be particularly important from a conservation perspective. There is considerable evidence that deliberate or inadvertent introduction of cultured (e.g., farmed, hatchery) salmon to the wild can lead to evolutionary change in native populations (reviewed by Hutchings and Fraser 2008). As a consequence, cultured salmon may significantly alter the genetic composition of native populations and affect their ability to respond adaptively to their local environments (Hindar et al. 1991; Gharrett and Smoker 1993). For example, interbreeding between populations may result in the breakdown of co-adapted gene complexes, leading to a reduction in fitness within hybrid lineages attributable to outbreeding depression (Granath et al. 2004; McClelland et al. 2005; Edmands 2007).

One means of exploring the degree to which interbreeding might affect plasticity, and thus fitness, would be to compare the shapes of life history reaction norms between a pure population cross and those hybridized with the pure cross, using a common-garden experimental protocol. We adopted this approach, using three population crosses of Atlantic salmon. The pure cross was one generation removed from the wild. The others were second-generation backcrossed populations possessing introgressed genes from either a cultured or a nonlocal wild population. Backcrossed salmon were used because this particular genetic makeup can be considered representative of what may be evident in the wild given the potential for escaped farmed or introduced nonlocal salmon to interbreed successfully with native populations (Lura and Sægrov 1991; Crozier 1993, 2000).

Few studies on fishes have distinguished genetic and environmental variation in the average expression of traits among second-generation hybrids (McGinnity et al. 2003; Smoker et al. 2004; Tymchuk et al. 2007) and only one — Fraser et al.'s (2008) study of acidity tolerance — has examined the effects of introgression on the shapes of reaction norms. Given its influence on development in early life in ecotherms in general (Einum and Fleming 2000; Ojanguren and Braña 2003) and in salmonid fish in particular (Alderdice and Velsen 1978; Beacham and Murray 1987; Hebert et al. 1998), we use variation in temperature to construct an environmental gradient against which reaction norms for life history traits can be compared.

The objectives of the present study are twofold: (*i*) to determine the effects of introgression on the expression of early life history traits across temperatures, and (*ii*) to examine whether introgression affects the shapes of reaction norms for early life history traits in Atlantic salmon.

Material and methods

Establishment of population crosses

The second-generation (F_2) experimental fish were derived from first-generation (F_1) progeny whose parents originated from three different populations. Two of these consisted of wild Atlantic salmon in Stewiacke River (S; 44°59′N, 64°05′W) and Tusket River (T; 43°53′N, 65°56′W), Nova Scotia, Canada. The salmon inhabiting Stewiacke River are among those comprising the Inner Bay of Fundy unit (more than 30 rivers in total; Fisheries and Oceans Canada (DFO) 2003), which has been assessed as endangered by Canada's national science advisory body on species at risk (Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2006). Water temperatures experienced by salmon in the Inner Bay of Fundy rivers are considerably cooler than those experienced by salmon in Tusket River. Based on data recorded during the summer (15 June – 5 September) in either 2000 or 2001, average water temperature in four Inner Bay rivers is 2.5 to 5.8 °C cooler than that in Tusket River (MacMillan et al. 2005).

The third population was of cultured, or farmed (F), origin and was obtained from the Atlantic Salmon Broodstock Development Programme (St. Andrews, New Brunswick (NB)). The progenitors of these salmon were from the Saint John River, NB (45°22′N, 66°01′W) (Glebe 1998). It has been estimated that these fish have been subjected to artificial and domestication selection for four generations (Glebe 1998). Empirical genetic data indicate that these populations are genetically distinct from one another (McConnell et al. 1997; Verspoor et al. 2002). The original crosses from which the F_1 progeny were produced were made in November 2001, at which time three pure (T × T, S × S, and F × F) and three hybrid crosses (T × S, T × F, S × F) were created in the Aquatron Facility at Dalhousie University (Lawlor et al. 2009). Crosses were then reared in a common environment for one generation, which served to eliminate the potential for residual environmental effects to generate population differences. Each of these six population crosses was the product of 10 different full-sib families, as described by Lawlor et al. (2009).

The F_2 crosses used in the present study were produced in the Aquatron Facility on 1 and 9 December 2004. The three populations consisted of one pure cross and two backcrosses. The pure population was an F_2 laboratory population that originated from the Tusket River (TT × TT). The first backcross comprised Tusket River salmon and F_1 hybrids from Tusket and Stewiacke rivers (TT × ST). The second backcross comprised Tusket River salmon and F_1 hybrids of Tusket River and farmed salmon (TT × FT). Eight males and eight females (all of the same age) from the F_1 populations were randomly selected to create each population cross (for details, see Table 1). Upon fertilization, the eight individual families were combined by population cross in incubator trays, and unfertilized eggs were discarded. They were held in the dark, undisturbed in flowing water, for 1 day. Thereafter, 4200 eggs counted from each cross were randomly selected, using a cup to collect multiple eggs at once, and moved to their assigned tanks. At the time of fertilization, individual parental data (length and weight) were recorded, and 50 fertilized eggs were randomly sampled from each population to determine egg size at fertilization.

Reaction norms were constructed during two separate common-garden experiments. The first was undertaken dur-

Table 1. Breeder framework for the second-generation crosses of Atlantic salmon: Tusket pure cross and Tusket × (Stewiacke × Tusket) performed 1 December 2004; Tusket × (farmed × Tusket) backcross performed 9 December 2004.

Tusket pure cross	Tusket × (Stewiacke × Tusket) backcross	Tusket × (farmed × Tusket) backcross
TT♀1 × TT♂1	ST♀1 × TT♂1	FT♀1 × TT♂1
TT♀2 × TT♂2	ST♀2 × TT♂2	FT♀2 × TT♂2
TT♀3 × TT♂3	ST♀3 × TT♂3	FT♀3 × TT♂3
TT♀4 × TT♂4	ST♀4 × TT♂4	FT♀4 × TT♂4
TT♀5 × TT♂5	TT♀1 × ST♂5	TT♀1 × FT♂5
TT♀6 × TT♂6	TT♀2 × ST♂6	TT♀2 × FT♂6
TT♀7 × TT♂7	TT♀3 × ST♂7	TT♀3 × FT♂7
TT♀8 × TT♂8	TT♀4 × ST♂8	TT♀4 × FT♂8

ing the embryonic stage, which extended from fertilization until absorption of the yolk sac. The second experiment focused on the early life feeding stages of development, i.e., during the first 24 weeks of exogenous feeding. To a first approximation, the temperatures to which the salmon were exposed during the embryonic and early life feeding experiments encompassed those that these fish might reasonably be expected to experience in the wild during these developmental stages.

Experimental protocol: embryonic stage

Eggs from each population cross were reared under identical conditions in twenty-four, 85 L circular tanks (0.48 m wide, 0.47 m high) at three different temperature regimes (mean ± standard deviation, SD): low (5.3 ± 0.1 °C), medium (9.2 ± 0.1 °C), and high (11.7 ± 0.1 °C). There were three replicate tanks, each containing 300 eggs, for each cross at the high- and medium-temperature treatments and two replicates for each cross at the low-temperature treatment. Eggs were held in the dark to mimic the light conditions that they would be expected to experience in the natural environment. Temperatures were recorded daily and dead eggs were removed periodically, with care taken to minimize disturbance.

To quantify egg size, 50 eggs from each population cross were randomly collected at the time of fertilization, evenly distributed into 10 containers, and dried at 40 °C for 4 days. We then compared the mean dried egg weight per container among crosses.

Survival during the embryonic stage was defined as the proportion of fertilized eggs that survived until the date on which the last eggs hatched (17 March 2005). Eggs were checked after fertilization approximately once weekly and dead eggs were removed periodically. Once the embryos had reached the eyed stage, dead eggs were removed daily to prevent the spread of fungus. Upon hatching, in addition to recording the date and time of hatch, individuals were euthanized with eugenol (Sigma-Aldrich, Oakville, Ontario), and a maximum of four alevins were placed in 1.5 mL microtubes and preserved in 65% ethanol for similar time periods prior to analysis. Preserved individuals were measured and weighed to determine body length at hatch and yolk sac weight at hatch. Fifty individuals were measured from each replicate tank. Length at hatch was measured with vernier calipers to the nearest 0.1 mm. Yolk sac weight at hatch was measured to the nearest 0.001 g. To measure yolk sac weight, the yolk sac was removed from the rest of the body and weighed separately.

Experimental protocol: early life stage

At fertilization, 1500 eggs from each population were randomly selected and divided evenly among five 100 L circular tanks (n = 15 tanks of 0.66 m diameter and 0.43 m height). Throughout the embryonic stage, eggs were held in the dark at approximately 5 °C. Once all the eggs had hatched, but prior to swim-up, individuals were transferred to twenty-four, 85 L circular tanks (diameter, 0.48 m; height, 0.47 m). Temperature in all 24 tanks was increased to 13.7 ± 0.4 °C to initiate swim-up. After 1 week, three different temperature regimes were established: low (15.4 ± 1.3 °C), medium (18.6 ± 0.7 °C), and high (21.8 ± 0.7 °C). There were three replicates at each of the high- and medium-temperature regimes, and two replicates at the low-temperature regime. Temperature in each tank was recorded daily. Individuals were divided evenly into the designated tanks, resulting in initial population sizes of 102 fish in each of the TT × TT tanks, 125 in each of the TT × ST tanks, and between 75 and 100 fish in each of the TT × FT tanks.

Throughout the early life stage, fish were exposed to a 12 h light – 12 h dark photoperiod cycle. The diet consisted of a commercial fish feed (Corey High Pro starter diet; Corey Aquafeeds, Fredericton, NB). Fish in each tank were initially fed six times daily during daylight hours, a frequency that was reduced gradually to three times daily by the 45th day after the initiation of exogenous feeding. The size of each food item gradually increased from 0.5 to 1.0 mm; the volume of food was based on ensuring that all fish were fed to satiation. Fish were considered satiated if there was evidence of uneaten food at the bottom of the tanks; uneaten food and other waste materials were removed once daily.

Survival during the early life stage was quantified from the onset of exogenous feeding until 11 weeks thereafter. Although the experiments continued until the end of the 24th week, a mass-mortality event during the 11th week in one of the TT × FT low temperature treatment tanks (a consequence of nonbiological factors) necessitated the quantification of survival from the onset of feeding until this date.

Fish were measured for length and weight approximately once monthly (six sampling periods in total). Sampling was performed by lightly anaesthetizing (with eugenol) 50 individuals from each of the 24 tanks and then obtaining an image of two to four individuals at a time, using a Sony Mavica digital camera located at a constant distance from the fish. To minimize handling time, 15 of the 50 fish were randomly subsampled and individually weighed to the nearest 0.1 g. Following recovery, fish were returned to their designated tanks. Following Ricker (1979) and Haugen and Vøllestad (2000), specific growth rates were calculated for each individual as

$$(1) \qquad G = (\ln(L_2 - L_1)/(t_2 - t_1)) \times 100$$

where L_x is fork length (mm) at time t_x (estimated from the digital images to the nearest 0.1 mm) and t is measured in days.

Table 2. Mean (± standard deviation, SD) parental fork length, weight, and egg weight of female breeders used to produce the experimental, second-generation crosses of Atlantic salmon (T, Tusket River; S, Stewiacke River; F, farmed salmon).

	TT females 1–4	TT females 5–8	ST females 1–4	FT females 1–4
Fork length (cm)	57.25±2.87	54.75±0.50	53.00±3.56	55.25±2.36
Weight (g)	2867.00±437.28	2279.50±70.24	2530.00±671.08	2393.50±325.46
Egg dry weight (g)*	$3.8\times10^{-2}\pm0.2\times10^{-2}$		$3.6\times10^{-2}\pm0.8\times10^{-2}$	$4.4\times10^{-2}\pm0.2\times10^{-2}$

*Calculated as TT × TT, ST × TT, and FT × TT egg dry weight (g).

Fig. 1. Reaction norms for (*a*) proportion surviving to hatch, (*b*) days to 50% hatch, (*c*) length at hatch, (*d*) yolk sac weight, (*e*) survival from hatch until 11 weeks after the initiation of exogenous feeding, (*f*) fork length at week 24, (*g*) weight at week 24, (*h*) specific growth rate for three population crosses of Atlantic salmon (*Salmo salar*) reared at three temperature regimes: low (5.3 °C for *a* through *d*; 15.4 °C for *e* through *h*), medium (9.2 °C for *a* through *d*; 18.6 °C for *e* through *h*), and high (11.7 °C for *a* through *d*; 21.8 °C for *e* through *h*). Population abbreviations: T, Tusket River; S, Stewiacke River; F, farmed origin. The reactions norms, showing population means ±1 SE, corresponding to each population are indicated as follows: TT × TT, ■; TT × ST, ●; TT × FT, ▲.

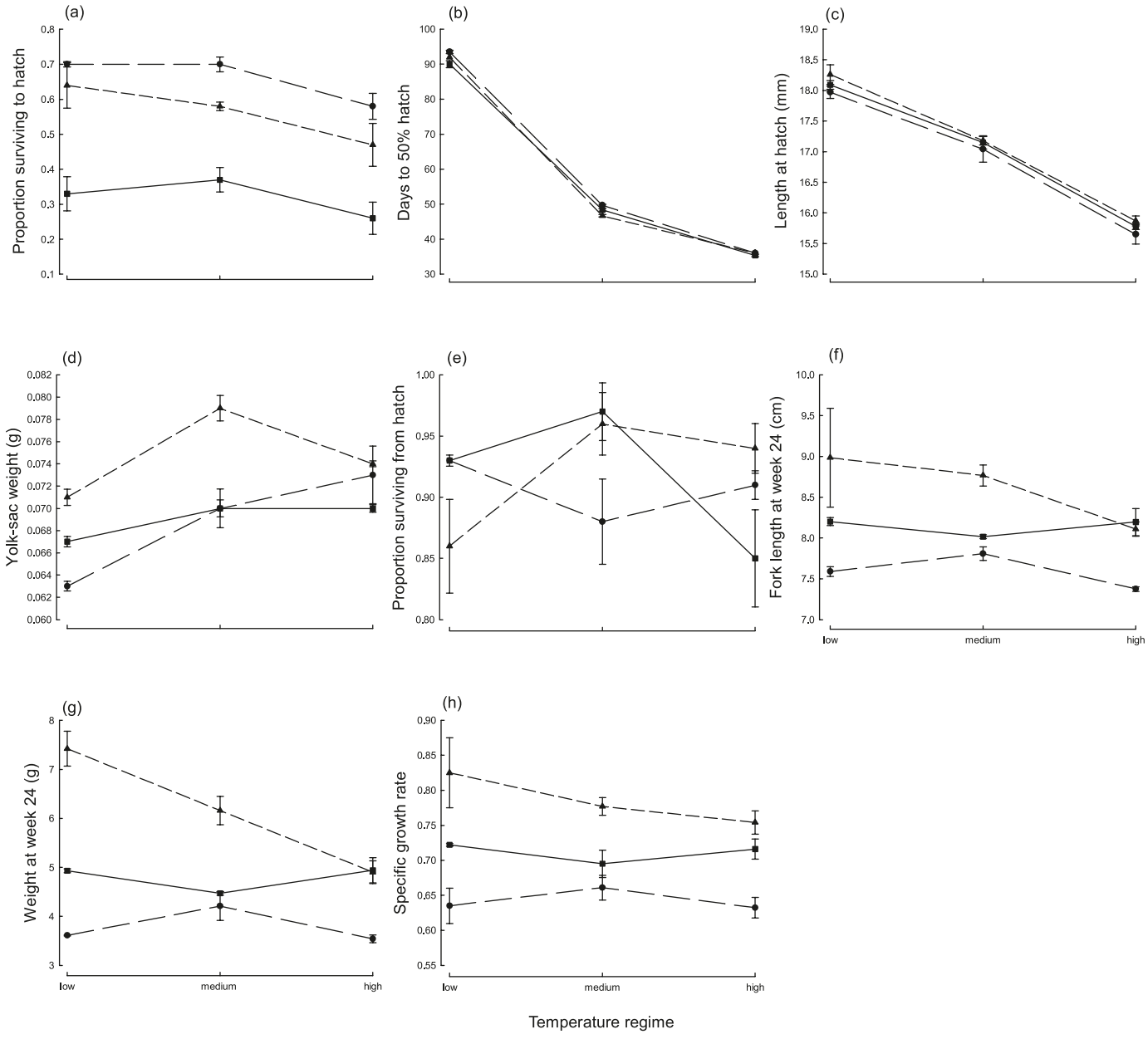


Table 3. Summary of two-way analysis of variance (ANOVA) statistics (F value with degrees of freedom in parentheses) for the effects of population, temperature, and population–temperature interactions (Pop × Temp) on several phenotypic traits.

	Effect		
Trait	Population	Temperature	Pop × Temp
Proportion hatched	60.54 (2, 19)*	9.39 (2, 19)*	0.35 (4, 15)
Days to 50% hatch	18.99 (2, 15)*	17233.57 (2, 15)*	9.94 (4, 15)*
Length at hatch	1.98 (2, 19)	259.24 (2, 21)*	0.11 (4, 15)
Yolk sac weight	19.58 (2, 15)*	12.63 (2, 15)*	4.04 (4, 15)*
Survival from hatch to week 11	0.66 (2, 15)	1.51 (2, 15)	2.71 (8, 15)*
Fork length at week 24	15.61 (2,21)*	3.45 (2, 15)	2.92 (6, 15)
Weight at week 24	10.39 (2, 21)*	1.49 (2, 15)	1.64 (6, 15)
Specific growth rate	32.55 (2, 21)*	1.13 (2, 15)	1.43 (6, 15)

*$P < 0.05$.

Statistical analysis

Among-population differences in trait means and population × temperature interactions (Pop × Temp) were examined using two-way factorial analyses of variance (ANOVAs; Zar 1999; Crawley 2002). Temperature (low, medium, and high), population (TT × TT, TT × ST, and TT × FT), and interactions among populations were set as fixed terms. Given that fish weight at week 24 was not normally distributed, we used a generalized linear model with a gamma distribution to analyse these data. Differences in egg size and parental female size were examined using a one-way ANOVA with a Tukey post-hoc test.

Results

Embryonic stage

The average size of egg from which the progeny were produced differed among population crosses. These differences, however, could not be attributed to differences in female body size, the primary correlate of egg size in fishes (Wootton 1998) (Table 2). Although eggs produced by TT × FT females were significantly heavier than those produced by females from the two other populations ($F_{[2,27]}$ = 21.70, $p < 0.0001$), neither maternal length nor weight differed among populations (one-way ANOVA for TT females 5–8, ST females 1–4, and FT females 1–4; length, $F_{[2,11]}$ = 0.91, $p = 0.44$; weight, $F_{[2,11]} = 0.34$, $p = 0.72$).

Survival to hatch differed significantly among populations (Fig. 1*a*; Table 3), being lowest at all temperatures among TT × TT progeny and highest among the TT × ST progeny (low temperature, $F_{[2,5]} = 16.86$, $p = 0.023$; medium temperature, $F_{[2,8]} = 46.95$, $p < 0.001$; high temperature, $F_{[2,8]}$ = 10.76, $p = 0.01$). Survival varied with temperature (Table 3), although the Pop × Temp term was not significant. Thus, although the elevation of the reaction norms differed among crosses, the slopes did not.

Elapsed time until 50% hatching was influenced by temperature, population, and an interaction between temperature and population (Fig. 1*b*; Table 3). Within each population, the elapsed time was inversely related to water temperature (TT × TT, $F_{[2,7]} = 2800$, $p < 0.0001$; TT × ST, $F_{[2,7]}$ = 8851, $p < 0.0001$; TT × FT, $F_{[2,7]} = 15\,080$, $p < 0.0001$). Time to 50% hatch was also significantly influenced by a population–temperature interaction ($p = 0.003$), indicating that the slopes of the reaction norms differed among crosses.

At hatching, length did not differ among population crosses (Fig. 1*c*; Table 3). Yolk sac weight, however, was significantly influenced by an interaction between population and temperature ($p = 0.02$; Fig. 1*d*; Table 3), indicative of differences in reaction norm slopes for yolk sac weight among crosses. In general, TT × FT individuals possessed the largest yolk sacs.

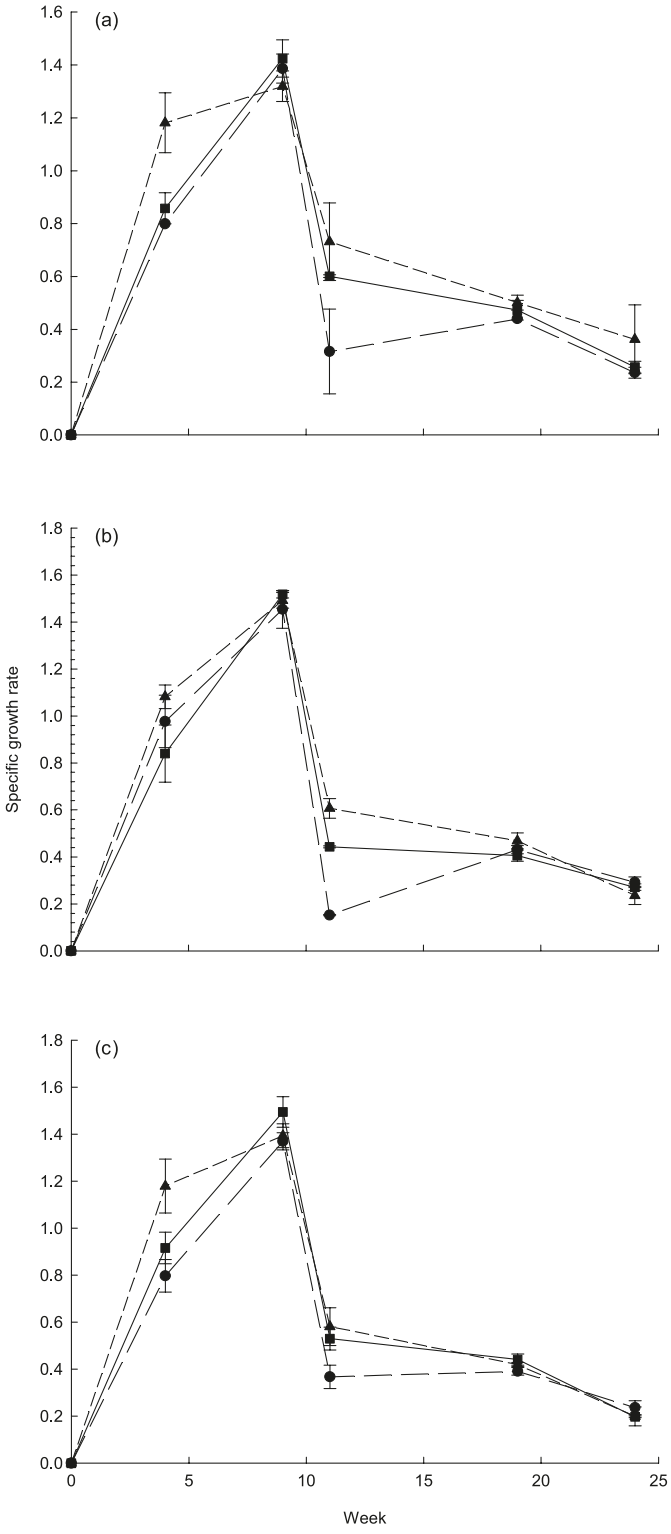
Early life stage

Reaction norms for posthatch survival differed among population crosses, as reflected by a significant interaction between population and temperature ($p = 0.015$; Fig. 1*e*; Table 3). These among-population final differences in survival could not be attributed to final differences in density (r = 0.024, $N = 23$, $p = 0.47$).

After yolk sac absorption, the average length of individuals from the TT × FT population was marginally, albeit significantly, less than that of the other two populations (TT × TT = 2.6 ± 6.7 × 10^{-3} cm; TT × ST = 2.6 ± 6.8 × 10^{-3} cm; TT × FT = 2.5 ± 6.2 × 10^{-3} cm; $F_{[2,1199]} = 17.41$, $p <$ 0.0001). At 24 weeks after hatching, there were significant differences in the elevation of reaction norms for body size. Progeny from the TT × FT population cross possessed the greatest length and weight at both the low- and medium-temperature regimes (Figs. 1*f*, 1*g*), but not at the high-temperature regime (body length: low temperature, $F_{[2,3]}$ = 4.32, $p = 0.13$; medium temperature, $F_{[2,6]} = 24.15$, p = 0.0014; high temperature, $F_{[2,6]} = 19.58$, $p = 0.002$; body weight: low temperature, $F_{[2,3]} = 1.84$, $p = 0.3$; medium temperature, $F_{[2,6]} = 19.74$, $p = 0.0023$; high temperature, $F_{[2,6]} = 15.03$, $p = 0.0046$; Table 3).

Measured on a monthly basis, specific growth rate differed among populations and was highest, at every temperature, for progeny from the TT × FT population (low temperature, $F_{[2,3]} = 10.25$, $p = 0.046$; medium temperature, $F_{[2,6]} = 12.4$, $p = 0.0074$; high temperature, $F_{[2,6]} = 16.93$, $p = 0.0034$; Fig. 2). Reaction norms for growth differed in elevation among population crosses but not in slope (Fig. 1*h*; Table 3). There was no influence of density on growth rate (i.e., length at age) based on the results of a three-way ANOVA treating density as a fixed effect ($F_{[1,8]}$ =

Fig. 2. Temporal variation in specific growth rate experienced by three Atlantic salmon (*Salmo salar*) population crosses (TT × TT, ■; TT × ST, ●; TT × FT, ▲; T, Tusket River; S, Stewiacke River; F, farmed origin) from the 1st to the 24th week of exogenous feeding: (*a*) low temperature regime, 15.4 °C; (*b*) medium temperature regime, 18.6 °C; (*c*) high temperature regime, 21.8 °C.



4.21, $p = 0.07$), although density did influence final body weight ($F_{[1,6]} = 118.37$, $p < 0.0001$).

Discussion

The present study provides evidence of genetic variability in fitness-related traits and their plastic responses to changes in temperature between second-generation backcrossed Atlantic salmon and one of the original parental populations. These differences in plasticity are consistent with the hypothesis that introgression can affect population responses to environmental change by altering the elevation and slopes of reaction norms for survival, growth, and metrics thereof in early life. By altering the shapes of reaction norms, interbreeding between first-generation hybrids and their parental population, a level of introgression involving comparatively small genetic differences between parents, has the potential to influence individual fitness in wild populations (Fraser et al. 2008).

Changes to reaction norms are evident irrespective of whether individuals interbreed with those whose genes originate from other wild populations or from populations that have been reared in a cultured environment. Nonetheless, there was some consistency in the disparity in reactions norms among crosses. For several traits (e.g., yolk sac weight, size at week 24, specific growth rate), the reaction norm for the pure TT × TT cross was intermediate relative to those of the two second-generation backcrosses. Among these same traits, reaction norms expressed by the wild hybrid population (TT × ST) tended to reflect lower trait values across temperature regimes relative to those expressed by the other two crosses. However, these patterns were not consistent among all traits, underscoring the unpredictability of the effects of hybridization on fitness-related traits.

Some of the differences in reaction norms resulting from introgression may be attributable to outbreeding depression, although a direct comparison between pure parental and second-generation backcrosses would be required to test this hypothesis (Lynch and Walsh 1998; McClelland et al. 2005; Tymchuk et al. 2007). All else being equal, outbreeding depression is expected to reduce fitness within hybrid populations, relative to the pure parental populations, because of the breakdown of co-adapted gene complexes. This might provide an explanation for the lower-elevation reaction norms — resulting in smaller sizes, longer hatching times, and slower specific growth rates — observed among TT × ST salmon. The absence of a similar response among TT × FT salmon might be attributable to strong directional selection resulting from domestication practices that typically select for increased growth and body size in culture environments (Einum and Fleming 1999; Hutchings and Fraser 2008).

Nongenetic influences on offspring size can translate into differences in offspring size and survival, resulting in an overestimation of genetic variance and the interpretation of environmentally based maternal effects as genetic effects (Falconer and Mackay 1996). Although we cannot entirely discount the possibility that our results might have been influenced by maternal effects, our experimental protocol was intended to minimize their influence. Firstly, the body size of parental females, a primary correlate of differences in

egg size (Wootton 1998), did not differ among population crosses. Secondly, half of the females involved in each cross were involved in all other crosses, reducing further the possibility that differences among populations could be attributable to individual female effects. Although the TT × FT eggs were significantly larger than those produced by the other parental females (despite the absence of differences in female body size), there were no significant differences among crosses in length at hatch, the developmental stage at which maternal effects are expected to be most pronounced (Heath et al. 1999; Einum and Fleming 2000). Furthermore, the average length of TT × FT individuals at first feeding was significantly less than those of the other two populations, indicating that the increased yolk sac size of the TT × FT population did not contribute to an increased size prior to the beginning of exogenous feeding.

The existence of genotype × environment interactions, reflected herein by interactions between population and temperature, implies that there can be genetic variation for plasticity among fish populations (Dieckmann and Heino 2007; Hutchings et al. 2007; Piché et al. 2008). The existence of such genetic variability might facilitate adaptation by populations to their local environments. Evidence that populations "perform" best (e.g., experience the fastest growth rate, highest survival) at the temperatures that they are most likely to experience in the wild would provide indirect evidence of such local adaptation (Haugen and Vøllestad 2000; Hutchings et al. 2007; Fraser et al. 2008).

In summary, we find that introgression can change the shapes of life history reaction norms in Atlantic salmon. Although these changes could potentially affect the ability of populations to respond adaptively to environmental change, our results underscore the difficulty in reliably predicting the demographic consequences of interbreeding (Weir and Grant 2005), irrespective of whether the introgression occurs with cultured individuals. Nonetheless, our observation that comparatively small genetic differences between breeding individuals can significantly affect reaction norms for traits closely related to fitness does raise questions from a conservation perspective. If their shapes in wild populations represent adaptive responses to local environments, then one might reasonably predict that changes to reaction norms are unlikely to have a positive influence on fitness (Fraser et al. 2008).

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