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Hybridization effects on phenotypic plasticity: experimental compensatory growth in farmed-wild Atlantic salmon

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Abstract

Compensatory growth (CG) is a means by which organisms can increase their growth rate above their routine growth rate after a period of environmentally induced growth depression. Despite a focus on the implications of CG for aquaculture, little research has evaluated the effect of domesticated–wild hybridization on CG. Any deviation in the mean compensatory ability of hybrids relative to their wild progenitors, or any notable costs to compensation in terms of body morphology, could affect the ability of hybrids to persist in changing environments. We compared CG of farmed, wild and hybrid (F1, F2, wild backcross) juvenile Atlantic salmon (*Salmo salar*). Wild salmon experienced both lower routine and CG rates relative to farmed salmon, while hybrids were intermediate. However, the compensatory responses (slopes of the reaction norms) for each cross were parallel, indicating that hybridization did not affect the CG response itself. Morphological costs to compensation were not detected. In addition to contributing to risk assessments of the consequences of interbreeding between wild and escaped domesticated organisms, we conclude that plasticity studies on domesticated–wild hybrids and their progenitors are useful for testing basic predictions about the evolution of phenotypic plasticity, as well as understanding the evolutionary significance of hybrids.

Introduction

Adaptive phenotypic plasticity is one means by which organisms respond to environmental change. Plasticity consists of two components: the trait in a particular environment and the trait's across-environment reaction norm (DeWitt and Scheiner 2004; Brommer et al. 2005). Empirical evidence suggests that selection can act on both the trait and the slope(s) of the reaction norm (Schlichting and Levin 1986; DeWitt and Scheiner 2004), as both can be heritable and exhibit individual- and population-level variability (Ellers et al. 2008). Although variability in population-level plasticity has received much attention, comparatively few studies have examined the effect of hybridization on reaction norms (Weber and D'Antonio 1999; Parris 2000), particularly in fishes (Fraser et al. 2007; Piché et al. 2008; Darwish and Hutchings 2009). This is especially true in the context of escaped domesticated or captive-reared organisms, whose phenotypes are partly a result of generations of artificial selection and plasticity to the domestic environment. Will domesticated–wild hybrids express intermediate traits and reaction norm slopes relative to their parents? Or will hybridization disrupt, or enhance, the ability of hybrids to respond to environmental change?

Growth is plastic. Organisms, in the absence of restraints, grow at 'routine' growth rates. After a period of growth depression, they can exhibit compensatory growth (CG), defined as an increase in the growth rate of an organism after a period of growth depression, such that the organism grows faster than it would under conditions of routine growth (Bohman 1955). The CG

trajectory usually converges with that of a routinely growing individual upon reaching the routine state (Ali et al. 2003). CG can be an adaptive response by which organisms buffer environmental variability (Ali et al. 2003), and it may have co-evolved with a suite of phenotypic traits under divergent selective regimes (Fraser et al. 2007). Selection can act on both the trait [herein referred to as the compensatory and routine growth rates, calculated and collectively referred to as specific growth rates (SGR)] and the slope of the reaction norm (herein referred to as the CG response), resulting in a shift in the elevation of the reaction norm and/or a change in its degree of plasticity. It is an open question how hybridization between populations under different selection regimes will affect CG.

Hybridization between domesticated and wild organisms can result in outbreeding depression wherein, through a number of mechanisms (such as the introduction of maladaptive domestically selected traits), hybrids exhibit reduced fitness relative to the midpoint fitness value of parents (McGinnity et al. 2003; Fraser et al. 2008). Alternatively, hybridization can lead to elevated fitness in hybrids relative to parents, known as heterosis (Mercer et al. 2006). This can arise in hybrids via increased heterozygosity, which could mask deleterious alleles (dominance model) or through the interaction of novel allele combinations, which produce a superior phenotype (overdominance model) (Birchler et al. 2006). Both outbreeding depression and heterosis have been reported in domesticated–wild hybrid fishes (McClelland et al. 2005; Fraser et al. 2008), but neither have been investigated from the perspective of CG. Plasticity studies are essential in this context as hybrid fitness relative to the parents may vary depending on the environment (Mercer et al. 2006; Darwish and Hutchings 2009).

Although plasticity in growth rates can be adaptive, rapid growth as exhibited during compensation may come with costs (Arendt 1997; Gotthard 2000; but see Hutchings 2006). These costs must be less than the cost of not compensating (Metcalfe and Monaghan 2001). Costs may be behavioral, physiological, developmental or morphological (Arendt and Wilson 2000; Arendt et al. 2001; Robinson and Wardrop 2002). Morphological costs remain poorly studied (Ali et al. 2003). During compensation, the growth of various tissues (skeletal, muscular, nervous, etc.) occurs at above-routine rates; this could result in deviations from the adaptive morphology of routinely growing individuals. For example, some transgenic fishes modified for faster growth have been shown to have altered opercula and caudal peduncles, deeper heads and shallower bodies than nontransgenic fishes (Farrell et al. 1997; Ostenfeld et al. 1998; Li et al. 2009). In migratory fishes such as salmonids, such deviations could reduce oxygen uptake in the gills, increase drag and limit thrust, resulting in lowered critical swimming speeds, reduced swimming efficiency and increased migratory mortality (Farrell et al. 1997; Ostenfeld et al. 1998; Fraser et al. 2007). In the context of the present work, the existence of potential costs underscores the importance of examining potential changes in the costs of compensation in hybrids relative to parents. The degree to which costs (should they exist) differ between hybrids and their parental populations is not known.

Although CG has been studied in salmonid fishes, it has not been examined in domesticated–wild hybrids. This is of concern because of the low abundance of many wild populations into which farmed salmon are escaping (Morris et al. 2008), the role that CG can play in migration survival and maturity (Maclean and Metcalfe 2001), and the rapid evolution that can be exhibited by domesticated salmon (Roberge et al. 2006). Selection within the farm environment could alter CG and its costs. In the food-saturated farm environment, poor compensators could potentially thrive, while selection for faster growth could concomitantly increase the CG rate (Schultz et al. 2002; Fraser et al. 2007), leading to a positive shift in the elevation of the reaction norm and a decline in its slope. Furthermore, the ancestral wild population of the farmed salmon and the wild populations into which farmed salmon escape could have evolved divergent CG rates and responses. Farming might also relax selection against the costs of compensation, which could exacerbate the impact of farmed-wild salmon hybridization.

Farmed Atlantic salmon (*Salmo salar*) in eastern North America escape into wild salmon rivers recurrently and in large numbers (Morris et al. 2008). Successful farmed-wild salmon hybridization has been reported (Carr et al. 1997; Lage and Kornfield 2006). In this study, farmed salmon from Saint John River (New Brunswick) (the only population currently used in eastern North American salmon aquaculture) and wild salmon from Tusket River (southern Nova Scotia) were used. Farmed salmon have been observed very infrequently in Tusket River (Morris et al. 2008), making this a useful model salmon population as the likelihood of past introgression is low, but the threat of future introgression does exist.

The objectives of this study were to determine whether: (i) wild salmon exhibited lower CG rates and steeper CG responses than their farmed counterparts; (ii) farmed-wild hybrids exhibited intermediate CG rates and responses relative to their parents; (iii) costs to compensation could be measured as deviances from the morphology of routinely growing fish; and (iv) potential costs were higher in farmed salmon and/or farmed-wild hybrids. In addition, we examined potential differences in the following: (i) body morphology among five crosses of salmon,

and (ii) the incidence of parr maturation between crosses and treatments.

Materials and methods

Salmon populations

In 2001, wild salmon adults were collected from Tusket River (43°53′1″N 65°59′2″W), and farmed salmon gametes were collected from fourth-generation farmed salmon that had originated from Saint John River. In the Aquatron at Dalhousie University (Halifax, NS), two generations of crosses (generated in 2001 and 2005) were raised, such that in 2006 there were populations of genotypically wild Tusket River (TT) salmon, farmed (FF) salmon, F1 (FT) and F2 (FT × FT) farmed-wild hybrids, and a wild backcross (BC = TT × FT) (the crosses were generated as follows: TT: $n = 4$ females, 9 males, 12 families; FF: $n = 8$ females, 8 males, 11 families; F1: $n = 8$ FF females, 9 TT males, 11 families; F2: $n = 7$ females, 8 males, 14 families; BC: $n = 10$ females, 12 males, 12 families, with the same individuals as used to generate the TT and F2 families). Prior to the experiment, the juvenile salmon were raised under equal densities in 100-L tanks and then pooled together in 1800-L tanks at densities resembling that of the farmed environment (see Fraser et al. 2010 for details). The growth experiment was carried out in the laboratory, because of the difficulties of controlling for the food environment in a natural setting.

The CG experiment

From May 3–11, 2007, the five crosses (FF, TT, FT, F2, BC) of one-plus year-old juvenile salmon (parr) were matched for length and, if possible, mass and assigned to one of two treatments (food limited or routinely growing, $n = 45$ tanks). Despite our efforts, FF were on average 1.1 g lighter than the heaviest crosses (BC and TT) (Tables 1 and S1), but during the food limitation period, these differences between crosses disappeared (Table S1). Each of the forty-five 100-L tanks contained ten salmon ($n = 450$ fish in total, with four replicates each of TT routinely growing, TT food limited, F2 routinely growing, F2 food limited, FF routinely growing; five replicates each of FF food limited, FT routinely growing, FT food limited, BC routinely growing, BC food limited). All fish were held under a seasonal photoperiod cycle. The ambient water temperature was initially 9°C, but rose through the first half of the experiment to 20°C and then declined by December to 7°C. Each tank experienced the same water temperature (within 0.1°C) and air and water flow throughout the course of the experiment. Tanks were drained of excess food daily.

From day 0 (introduction to experimental tanks) to 18, the fish were allowed to acclimate to their new tanks and new densities. All fish were fed Corey Feeds Hi-Pro Hatchery Feed (2 and 3 mm pellets, containing 18.3–18.6 MJ/kg of digestible energy) to satiation twice daily. Beginning on May 28, half of each cross was subjected to a period of food limitation (fed ∼1% body weight daily). Routinely growing (fully fed) fish were fed twice a day to satiation (fed ∼5–10% body weight daily). The food limitation period lasted 50 days, which was long enough to ensure that food limited fish were significantly smaller, both in length and mass, than the routinely growing fish. From June 16 to December 15, 2007, routinely growing and compensating (previously food limited) fish were fed to satiation twice daily (the % body weight consumed declined over time in response to seasonal declines in metabolic rate; excess food was always observed in the tanks). Fork length (to the nearest mm) and mass (to the nearest 0.1 g) were measured on days 0 and 18 (the acclimation period), days 34 and 68 (the food limitation period), and days 80, 91, 102, 114, 125, 153, 192 and 217 (the compensatory period). Fish were not fed during the 24 h immediately preceding the measurements and were nonlethally anesthetized for the procedure (total experimental mortality = 2.4%, $n = 11$). Mortalities were replaced with fin-clipped salmon of the same cross and of approximately the same size; these replacement fish allowed for potential density effects to be controlled, but they were excluded from analyses. All salmon were lethally sampled at the end of the experiment, and their sex and maturity status were recorded.

The morphology experiment

Photographs of all experimental salmon were taken three times for morphological analyses: at the beginning (day 18) and end (day 68) of the food limitation period and at the end of the compensatory period (day 217). This allowed us to control for any initial morphological differences between crosses and treatments, and any morphological differences caused by the food limitation period. Left-side, whole body photographs were taken of anesthetized fish from a mounted digital camera and uploaded into the program TPSDIG2 (Rohlf 2006). Twenty-one morphological landmarks were plotted on each photograph (Fig. S1); the coordinates of those landmarks were imported into the software TPSRELW (Rohlf 2006), which was used to identify diversity of shape variation within and between the crosses and treatments, independent of body size. (TPSRELW does this by computing a consensus body shape by way of a generalized orthogonal least-square Procrustes average; all specimens are aligned with respect to this consensus shape by way of thin-plate

Table 1. Summary of mean length (mm), mass (g), condition, and specific growth rate (SGR) (length and mass) measurements for routinely growing and food limited/compensating wild (TT), backcrossed (BC = wild × hybrid), second-generation hybrid (F2), first-generation hybrid (FT) and farmed (FF) Atlantic salmon, with least-squares standard errors in (), for key measurement days/periods throughout the experiment.

		TT		BC		F2		FT		FF	
Metric	Day	Routinely growing	Food limited	Routinely growing	Food limited	Routinely growing	Food limited	Routinely growing	Food limited	Routinely growing	Food limited
Length	18	100.2 (1.0)	102.4 (1.0)	102.2 (0.9)	103.4 (0.9)	101.9 (1.0)	101.5 (1.0)	100.9 (0.9)	101.0 (0.9)	100.1 (1.0)	100.4 (0.9)
	68	136.2 (1.2)	114.5 (1.2)	140.5 (1.1)	115.8 (1.1)	139.3 (1.2)	115.4 (1.3)	141.0 (1.1)	116.5 (1.1)	140.2 (1.2)	115.0 (1.1)
	217	174.7 (3.2)	172.1 (3.3)	183.5 (2.9)	175.8 (2.9)	190.5 (3.3)	183.2 (3.5)	198.4 (2.9)	193.3 (2.9)	198.1 (3.2)	195.1 (2.9)
Mass	18	12.3 (0.4)	12.9 (0.4)	12.4 (0.3)	12.9 (0.3)	12.5 (0.4)	12.4 (0.4)	12.1 (0.3)	11.9 (0.3)	11.5 (0.4)	11.6 (0.3)
	68	35.0 (1.0)	18.1 (1.0)	37.2 (0.9)	18.0 (0.9)	35.2 (1.0)	17.8 (1.0)	37.0 (0.9)	17.8 (0.9)	35.7 (1.0)	17.1 (0.9)
	217	64.9 (3.8)	62.8 (3.9)	74.3 (3.4)	66.7 (3.4)	81.4 (3.9)	75.6 (4.1)	93.6 (3.4)	87.0 (3.4)	89.7 (3.8)	85.1 (3.4)
Condition	18	0.081 (0.001)	0.080 (0.001)	0.077 (0.001)	0.078 (0.001)	0.078 (0.001)	0.079 (0.001)	0.079 (0.001)	0.077 (0.001)	0.077 (0.001)	0.076 (0.001)
	68	0.089 (0.001)	0.079 (0.001)	0.086 (0.001)	0.076 (0.001)	0.084 (0.001)	0.076 (0.001)	0.084 (0.001)	0.074 (0.001)	0.084 (0.001)	0.074 (0.001)
	217	0.076 (0.001)	0.075 (0.001)	0.075 (0.001)	0.076 (0.001)	0.073 (0.001)	0.076 (0.001)	0.075 (0.001)	0.074 (0.001)	0.072 (0.001)	0.072 (0.001)
SGR-L	0–18	0.42 (0.08)	0.46 (0.08)	0.54 (0.07)	0.56 (0.07)	0.47 (0.08)	0.50 (0.08)	0.55 (0.07)	0.58 (0.07)	0.47 (0.08)	0.42 (0.07)
	19–68	0.61 (0.02)	0.22 (0.02)	0.64 (0.01)	0.23 (0.01)	0.62 (0.02)	0.26 (0.02)	0.67 (0.01)	0.28 (0.01)	0.67 (0.02)	0.27 (0.01)
	69–217	0.17 (0.01)	0.27 (0.01)	0.18 (0.01)	0.28 (0.01)	0.21 (0.01)	0.31 (0.01)	0.23 (0.01)	0.34 (0.01)	0.23 (0.01)	0.35 (0.01)
SGR-M	0–18	1.49 (0.27)	1.43 (0.27)	1.84 (0.24)	2.05 (0.24)	1.64 (0.27)	1.71 (0.27)	1.99 (0.24)	2.01 (0.24)	1.40 (0.27)	1.30 (0.24)
	19–68	2.09 (0.06)	0.68 (0.06)	2.20 (0.06)	0.66 (0.06)	2.06 (0.06)	0.73 (0.06)	2.23 (0.06)	0.80 (0.06)	2.26 (0.06)	0.78 (0.06)
	69–217	0.42 (0.04)	0.82 (0.04)	0.46 (0.04)	0.88 (0.04)	0.56 (0.04)	0.97 (0.04)	0.62 (0.04)	1.06 (0.04)	0.62 (0.04)	1.08 (0.04)

spline analysis, Bookstein 1991). Partial warps, which correspond to deformations in shape from the consensus, were calculated and displayed as two-dimensional relative warps (RWs) for interpretation. To detect differences between treatments, consensus shapes were calculated for each cross; to detect differences between crosses, all crosses were pooled together and the consensus shape calculated.

TPSRELW allowed us to view deviations from the consensus fish shape for each RW. RWs representing nonbiological variation in body shape (openness of mouth or operculum, body alignment) were excluded from analyses, as were photographs that exhibited extreme instances of these.

Statistics and formulae

Compensation

Fork length (length from the tip of the jaw to the notch in the caudal fin) and mass were measured for all salmon throughout the course of the experiment. The regression coefficient of natural log-mass (g) on natural-log length (mm) was 3.086 (cross range: 2.987 for FF, to 3.114 for BC), so that our formula for estimating body condition was

Condition = [mass/(length^(3.086))] × 10 000.

For each measurement day, mixed effects ANOVAs (with tank as a random effect) were used to assess the significance of the cross, treatment and interaction terms for length, mass, and condition. Results for the compensatory period were analyzed with repeated measures ANOVAs, with cross, treatment, day and their four possible interactions as terms in the model and tank as a repeated measure. In this case, the level of replication was the individual fish.

Specific growth rate, defined as the % in length or mass that an individual/sample grew per day across a specified time period, was also calculated for each tank based on the formula:

$$\mathrm{SGR} = \%\,\mathrm{length/day} = \frac{\ln L_{t_2} - \ln L_{t_1}}{t_2 - t_1} \times 100$$

where L was the fork length (mm), t_1 was the beginning of the measurement period, and t_2 was the end of the measurement period. A similar equation was used for SGR for mass. Note that individuals were not marked, and tanks were thus the unit of replication. Each measurement period (days 0–18, 19–34, 92–217, etc.) was analyzed with ANOVAs, while the entire compensatory period (each measurement period between days 69–217) was analyzed with repeated measures ANOVA, with cross, treatment, period and their interactions as possible model terms and tank as a repeated measure.

The cross × treatment interaction term during the compensatory period for SGR was used to test the hypothesis that the CG response differed between crosses; a result of significance would lead to rejection of the null hypothesis that all crosses had identical reaction norm slopes. Furthermore, differences in mean SGR values between crosses would indicate differences in reaction norm elevation.

Coefficient of variation (CV) for length, mass and condition was calculated as CV = standard deviation/tank mean. Repeated measures ANOVAs, with tank as the repeated measure, were performed across the compensatory period to determine whether any crosses displayed greater variation in length and mass than others and to determine whether compensation reduced or increased CV relative to the routinely growing fish. Tanks were the unit of replication.

To avoid the problems of doing separate ANOVAs on dependent variables, alpha was set at 0.05/3 = 0.016 for length, mass, condition and CV tests, and 0.05/2 = 0.025 for all SGR tests. Assumptions of normality and equal variance were met. Degrees of freedom were estimated with the Kenward–Roger approximation.

Morphology

For the morphological analyses, differences between crosses were assessed by generating a consensus fish for all crosses pooled together. The resultant RW values were analyzed using mixed effects ANCOVAs with cross, treatment and cross × treatment interactions as the model terms, centroid size (a measure of allometric variation in body shape) as the covariate, and tank as a random effect. Differences between treatments were determined by generating a consensus fish for each cross with both treatments pooled together. The resultant RW values were analyzed using mixed effects ANOVAs, with treatment as the only model term and tank as a mixed effect. Alpha for both types of analyses was set at 0.05.

Genetic basis of trait differentiation

Line-cross analyses (Lynch and Walsh 1998) were performed on data for every stage of the experiment (initial conditions, food limitation period, compensatory period) to assess the genetic basis for length, mass, routine and CG rates, parr maturity and morphology. Briefly, the data (i.e. means and variances for each trait) were firstly fit with an additive model of genetic differentiation, with significance being assessed using a χ^2 goodness-of-fit test statistic. If this model was not adequate to fit the data, we then followed a similar procedure using a more complex model that incorporated additive-dominance. A

likelihood-ratio test was used to determine whether the additive-dominance model generated a significantly better fit than the simple additive model. Note that models incorporating epistatic effects could not be tested because of the low number of crosses generated ($n = 5$).

Results

CG variation

Temporal changes in length, weight and condition

Following the acclimation period (day 18), there were no significant differences in length between any of the crosses or treatments, although the FF did have a significantly lower mass and condition than other crosses (Tables 1 and S1).

Following the food limitation period (day 68), each routinely growing cross was significantly larger both in length and mass and had a significantly higher body condition than its food limited counterpart (Figs 1, S2 and S3, Tables 1 and S1).

At the end of the compensatory period (day 217), there were no significant differences between treatments for mass and condition within each cross (Figs 1, S2 and S3, Tables 1 and S1). Nevertheless, mean mass was always lower in compensating fish, and complete compensation was not evident for length. Length and mass differed between crosses throughout the compensatory period, with the TT and BC being, on average, smaller than the FF and FT, and the F2 being intermediate (Fig. 1, Tables 1 and S2). All crosses fully compensated for body condition within the first twelve days of the compensatory period (Fig. 1, Table S1), after which the compensating fish took on higher conditions than the routinely growing fish until at least day 192.

Specific growth rate

During the acclimation period (days 0–18), there were no significant differences in the SGR for length (SGR-L) or mass (SGR-M) for the different crosses/treatments. During the food limitation period (days 19–68), the food limited

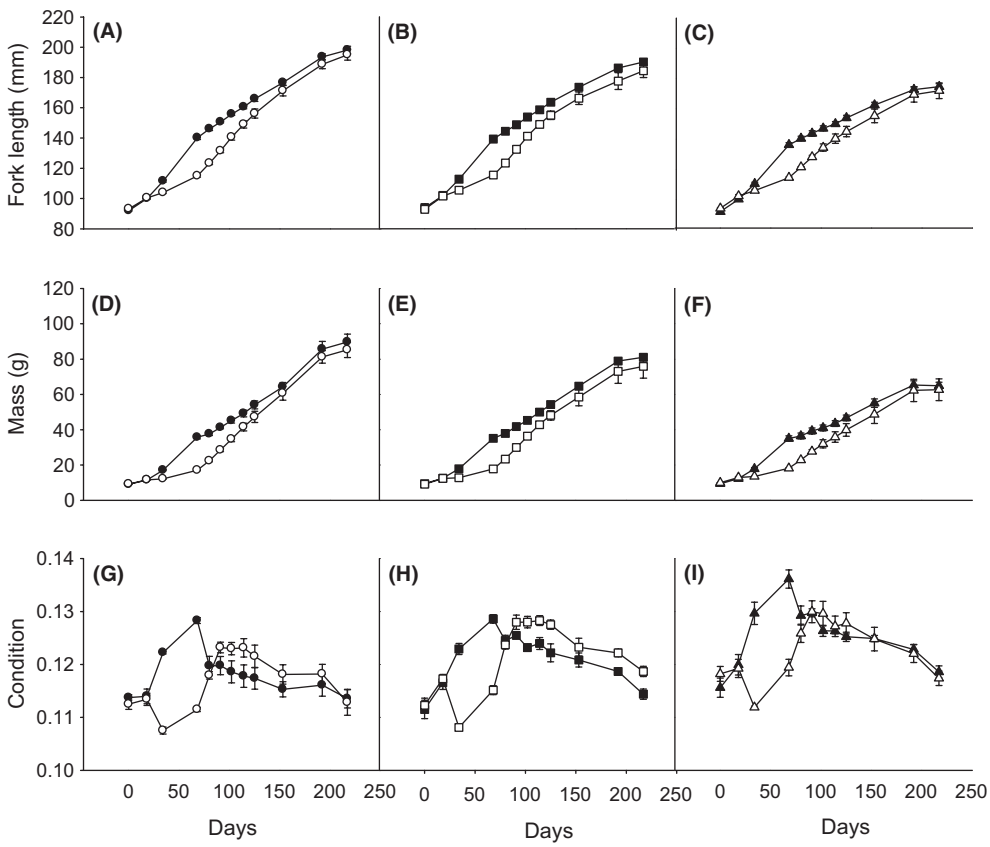

Figure 1 Growth metrics for farmed salmon (first column), second-generation hybrids (second column) and wild salmon (third column) through the entire experiment. Days 19–68 correspond to the deprivation period, days 69–217 to the compensatory period. Open symbols represent food limited/compensating treatment, and closed symbols represent the routinely growing fish. (A–C) Fork length (mm), (D–F) mass (g) and (G–I) condition measurements. Standard errors are included.

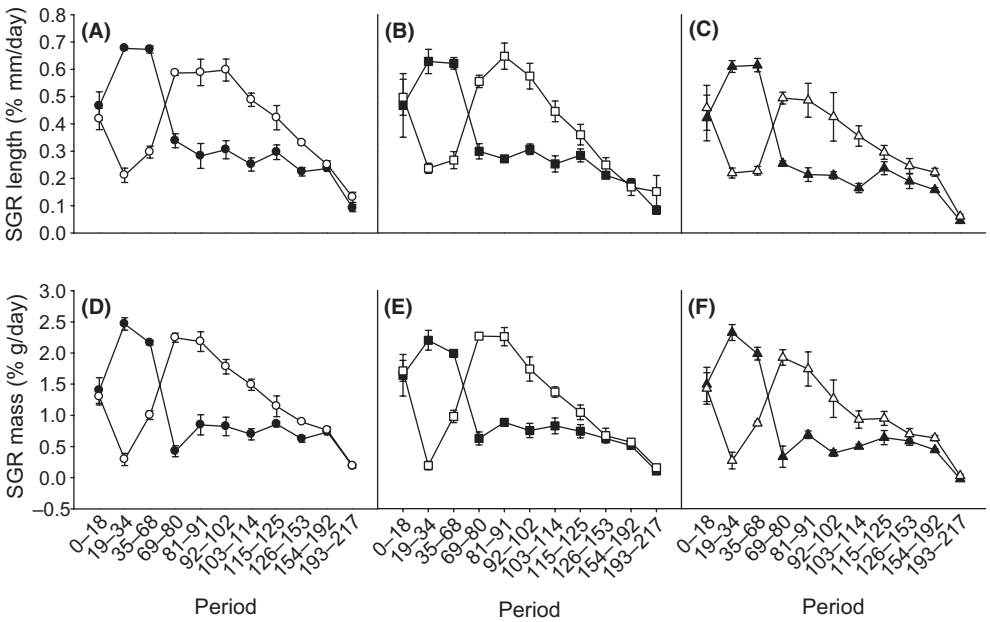

Figure 2 Specific growth rate for (A–C) length (%mm/day) and (D–F) mass (%g/day) throughout the experiment for farmed salmon (first column), second-generation hybrids (second column) and wild salmon (third column). Days 19–68 correspond to the deprivation period, days 69–217 to the compensatory period. Open symbols represent food limited/compensating treatment, and closed symbols represent the routinely growing fish. Standard errors are included.

fish had significantly lower SGR-L and SGR-M than their routinely growing counterparts (Fig. 2, Table S3).

During the compensatory period, two aspects of compensation were analyzed: the CG response (indicated by the slope of the reaction norm), in which differences between crosses could be evidenced as significant cross × treatment interactions, and the compensatory and routine growth rates (indicated by the elevation of the slopes), in which the mean growth rates themselves could be compared. No significant cross × treatment interaction was found for either SGR-L or SGR-M, when the entire compensatory period was considered (Fig. 3, Table 2) or when each period was analyzed separately (Table S3). There was also no significant cross × period interaction term, indicating that all crosses behaved in a similar manner at each stage of the compensatory period. Period × treatment was significant, because of the convergence of the routinely growing and compensating SGR sometime between days 154 and 192, signalling the completion of CG for both length and mass. Despite parallel reaction norm slopes, the CG rates did differ between crosses. TT salmon, with their lower routine growth rate, also had the lowest CG rate, followed by the BC, F2 and FT, while the fast-growing FF salmon had the fastest CG rate. The lack of a significant interaction term shows that the TT and FF salmon and their hybrids were similarly plastic, shifting their CG rate above their routine rate by the same amount (Fig. 3).

The greatest difference between compensating and routinely growing SGR-L occurred from days 81–91, indicating that there was a slight delay (i.e. days 69–80) before CG reached its maximum (Fig. 2). For SGR-M, the greatest difference between the compensating and routinely growing treatments occurred immediately after the food limitation period, from days 69–80. This was consistent for all crosses.

Coefficient of variation

Only by day 68 were significant differences detected in CV for mass and length between treatments (Fig. S4, Table S4), but these differences disappeared during the compensatory period (days 69–217). In general, CV for mass and length increased throughout the compensatory period, being highest for TT and FT, lowest for FF, and higher overall for compensating fish than routinely growing fish, although these differences were not significant (Fig. S4, Table S2). FF had a significantly higher CV for condition than the FT and F2.

Incidence of male parr maturity

In February of 2008, all fish were lethally sampled and their sex and maturity assessed. By chance, there were differences between treatments in the numbers of females and males (range: 48% female for compensating FT, 22% compensating F2) and mature males (range: 53% mature

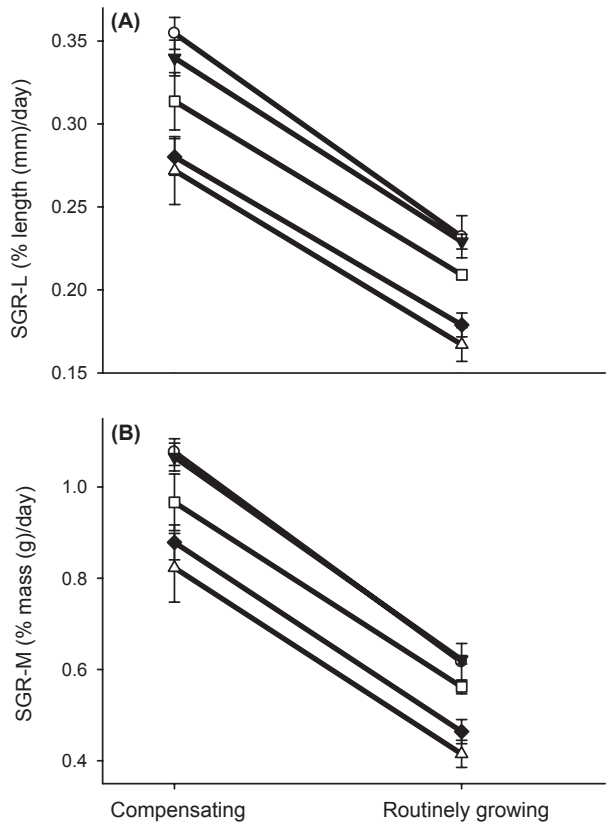

Figure 3 Reaction norms for specific growth rate, averaged across the compensatory period for the routinely growing and compensating fish, for (A) length and (B) mass. Circles represent farmed salmon, inverted triangles represent first generation hybrids, squares represent second-generation hybrids, diamonds represent wild backcross and triangles represent wild salmon. Open/closed symbols are for clarity only. Standard errors are included.

males for routinely growing BC, 23% compensating FF). Proportionally, there were no patterns between treatments – neither the routinely growing nor compensating fish had consistently higher or lower incidences of male maturity. However, among crosses, FF had the lowest incidence of male maturity (44% mature parr, calculated as number mature parr/total number males × 100%), followed by the FT (52%), F2 (65%), TT (75%) and BC (84%).

Body morphology among crosses

Morphological differences among crosses were observed throughout the course of the experiment (Fig. S5, Table S5). At the end of the acclimation period (day 18), TT had a significantly deeper body, smaller head, shorter ventral caudal peduncle and a longer dorsal fin than the FF and FT (RW2, RW3, RW6). Hybrids were often, but not always, intermediate: BC and F2 had significantly reduced lengths between the head and dorsal fin, larger heads, and less rounded bodies than the other crosses (RW4).

After the food limitation period (day 68), the greatest amount of morphological variation (45%) was explained by body depth (RW1, RW2) (Table S5), with the TT and BC having significantly deeper bodies than the FT and FF. After the compensatory period (day 217), TT and BC still had significantly deeper bodies (RW1), while F2 and TT had significantly broader caudal fins (RW6) than FF, with BC and FT as intermediates.

Body morphology between treatments

After the acclimation period, there were no biologically relevant morphological differences between routinely growing and food limited treatments within each cross, for RW1 through RW10 (Fig. 4, Table S6), with two exceptions. For BC, the routinely growing treatment had a significantly longer caudal fin than the food limited treatment (RW5) (although this RW also included variation in the openness of the mouth); and for TT, the

Table 2. Repeated measures ANOVA examining SGR for length and mass during the compensatory period (days 68–217), with growth period as a factor.

	SGR length			SGR mass		
Factor	d.f.	*F*	*P*	d.f.	*F*	*P*
Cross	4,340	31.72	****	4,340	23.83	****
Treatment	1,340	624.64	****	1,340	827.14	****
Period	7,340	180.93	****	7,340	194.13	****
Period × Treatment	7,340	40.48	****	7,340	97.16	****
Cross × Treatment	4,308	1.00	0.41	4,308	0.75	0.56

Tank was treated as a repeated measure. Cross × Treatment, Cross × Period and Cross × Treatment × Period were nonsignificant and removed from the model; because of the interest in Cross × Treatment, the results of the model with that term are shown for that term.
SGR, specific growth rate.
****$P \leq 0.0001$

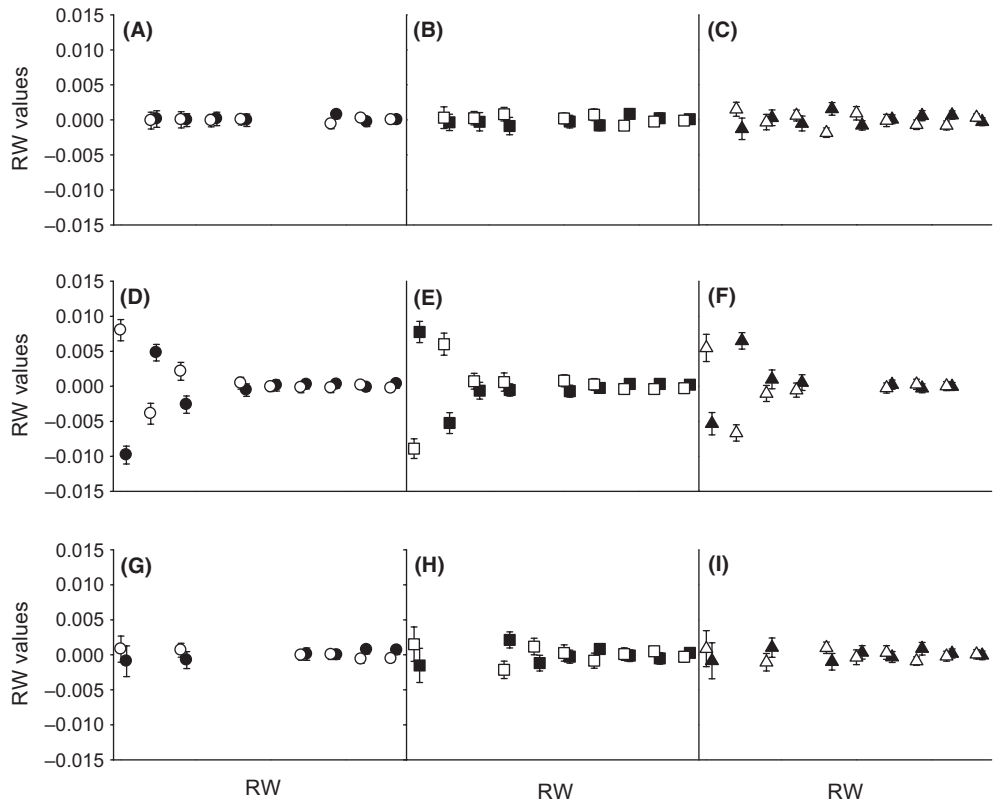

Figure 4 Morphological variation between treatments for each cross, for relative warps 1 through 10, on (A–C) day 18 (prior to the food limitation period), (D–F) day 68 (after food limitation period) and (G–I) day 217 (end of compensatory period), for farmed salmon (first column), second-generation hybrids (second column) and wild salmon (third column). Open symbols represent food limited/compensatory treatment, and closed symbols represent routinely growing fish. Standard errors are included.

routinely growing treatment had a significantly deeper body than the food limited treatment (RW5).

After the food limitation period, morphological differences between the treatments were explained primarily by a loss of fat reserves, with the food limited fish being significantly thinner than the routinely growing fish for every cross (Fig. 4, Table S7). There were no other significant, biologically relevant differences between treatments.

Having analyzed initial morphological differences between treatments before and after the food limitation period, we could interpret additional postcompensatory morphological differences as deviations in morphology because of compensation (Fig. 4, Table S8). Such deviations could then be interpreted as potential fitness costs. Only two morphological differences were found. Routinely growing BC had significantly rounder bodies than compensating BC. Additionally, all compensating hybrids (BC, F2 and FT) had significantly longer caudal fins than their routinely growing counterparts (although this was significant only at alpha = 0.05 for F2). This pattern was not observed for the FF or TT, even after examining eighteen additional RWs that explained <1% of the overall variation (data not shown).

Genetic basis of trait differentiation

Line-cross analyses showed that a simple additive genetic model was sufficient to explain the length, mass, routine growth rates, CG rates, initial and final morphologies and incidence of parr maturity values for each cross for every measurement period (Fig. 5, Table S9). Although trait expression in FT hybrids appeared to be nonadditive in some cases, the variation around the means was too high to reject the additive model.

Discussion

How do domesticated–wild hybrids respond to a changing environment? Does hybridization enhance or disrupt the ability to be plastic, or do hybrids simply take on the intermediate plastic phenotype of either parent, with

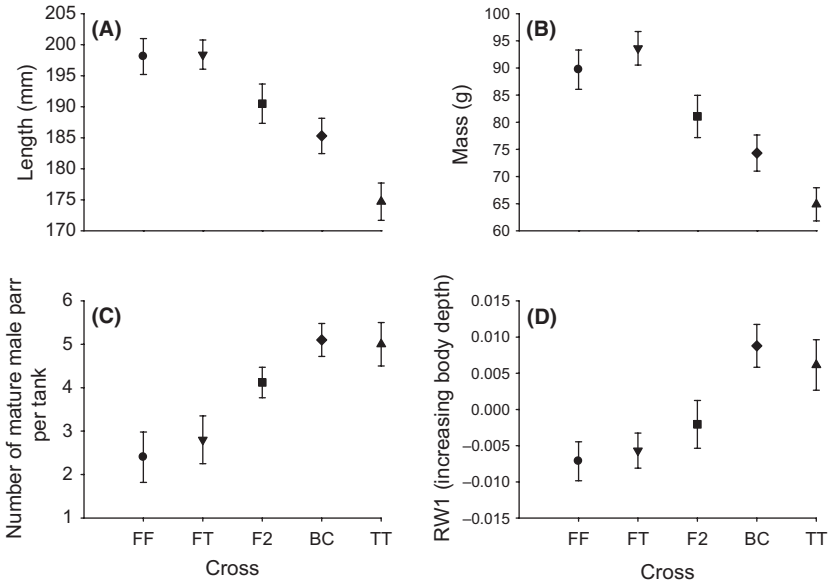

Figure 5 Examples of traits that did not differ from additivity, using the line-cross analysis of Lynch and Walsh (1998). (A) Length (mm) of the routinely growing crosses on day 217. (B) Mass (g) of the routinely growing crosses on day 217. (C) The number of mature male parr found per tank, for each cross. (D) Relative warp 1 values for each cross on day 217, with higher values denoting greater body depth. Standard errors are included.

the resulting fitness consequences of that phenotype? This study is the first to address these questions from the perspective of CG. To summarize the results within the context of our objectives: (i) wild salmon juveniles (parr) exhibited lower routine and CG rates than their farmed counterparts, but the slopes of the reaction norms were the same for both; (ii) the three multigenerational hybrid crosses exhibited intermediate routine and CG rates (keeping in mind that BC are ¾ TT), but hybridization did not affect the slope of their reaction norms; and (iii and iv) morphological costs to compensation were not evident in any of the crosses, as defined by the landmarks used. Beyond these main objectives, consistent, genetically based differences between the crosses were detected for the following: (i) body morphology and (ii) the incidence of male parr maturity. Thus, the present study suggests that farmed-wild hybridization can alter CG in hybrids by, at the very least, producing intermediate routine and CG rates; farming does not appear to relax selection for CG; and CG after a period of food limitation may not compromise juvenile salmon body morphology.

Tusket River and farmed salmon express varying levels of genetic differentiation across a variety of quantitative traits (Fraser et al. 2008, 2010; Lawlor et al. 2009). Although our results are most pertinent in the context of farmed–wild interactions in southern Nova Scotia and wild populations located there, the CG rate differences we found could be exacerbated in other, more diverged, salmon populations.

CG and hybridization

Compensatory growth occurred during the compensatory period, as evidenced by an increase in the SGR of the food limited fish over that of the routinely growing fed fish. Full compensation was evident for mass, but only partial compensation was evident for length. This is consistent with the results of previous food limitation experiments on Atlantic salmon (Nicieza and Metcalfe 1997; Maclean and Metcalfe 2001; Fraser et al. 2007).

Farmed salmon, which grow in a stable food environment and are bred for fast growth (Glebe 1998), had the same CG response (the same reaction norm slope) as the wild salmon. Based on the present study, it would seem that artificial selection has only altered the mean across-environment trait and not the reaction norm itself, although a study of backcrossed farmed and wild Atlantic salmon from the same region did yield significant differences in reaction norms for traits in early life (Darwish and Hutchings 2009). Differences in the CG responses of divergent wild populations of both Atlantic salmon and Atlantic silverside (*Menidia menidia*) have been documented (Schultz et al. 2002; Fraser et al. 2007). It is possible that the similar CG responses of wild Tusket River and farmed Saint John River salmon might be attributable

to the relatively few generations of selected breeding in the farmed salmon, the selection of similar CG responses in both the Saint John and Tusket Rivers, and/or selection for CG in farmed salmon because of increased competition associated with increased densities.

Hybrids exhibited CG responses that did not differ significantly from those of their parents. A similar pattern has been documented in the plasticity of *Carpobrotus* spp. and their hybrids (Weber and D'Antonio 1999). Had the parents differed in their response, we might have expected an intermediate slope in the hybrids (Fraser et al. 2007) or potentially a very different slope indicative of hybrid vigor (Repka et al. 1999) or outbreeding depression (Parris 2000). Intermediate slopes have the potential to increase hybrid fitness if the parental reaction norms cross and the trait is correlated with fitness; under these circumstances, the hybrids would have a maximized fitness across environments (Silim et al. 2001).

The elevation of the reaction norm slope (that is, the traits themselves) did differ between crosses, with farmed salmon, which are selected for faster growth, having both faster routine and CG rates relative to TT salmon. The hybrids were intermediate, and their trait expression was consistent with that predicted by an additive genetic model, a result similar to that reported in other hybrid plasticity studies (Weber and D'Antonio 1999; Fraser et al. 2007). If the elevation of the slope is correlated with fitness, then hybrids should perform consistently better than one parent but worse than the other in either parental environment. In the context of domesticated–wild hybridization, any deviation from the wild phenotype, even if additive, could be to the detriment of the hybrids. Indeed, reduced fitness of farmed salmon in wild salmon rivers has been noted in other studies (e.g. McGinnity et al. 2003).

Caveats regarding compensation

While the compensatory responses were the same but the compensatory and routine growth rates were different between crosses, there are some caveats to this interpretation that must be noted. First, differences in tank sex ratios were observed at the end of the experiment. If the sexes allocate energy during compensation in different ways, this may have affected our results. Second, FF salmon expressed a lower incidence of male parr maturity than the TT; this could account for the rapid mean growth rate of FF. However, many of the mature parr were as large as immature fish by the end of the experiment, a result consistent with the observation that the fastest growing males in these populations are those that mature as parr (Piché et al. 2008). When the lengths and masses of the mature parr were removed from the final measurements, the results were still consistent with our earlier observations. Third, the Tusket River has an average pH of 4.6–5.2 (Fraser et al. 2008), but the TT salmon were raised at a neutral pH typical of the farmed environment. As parr are less sensitive to pH than their earlier life stages (Lacroix 1989; Fraser et al. 2008), any influence of this neutral acidity on growth may have been minimal.

Finally, the observation that the SGR of the routinely growing fish during the food limitation period was higher than the SGR ever achieved by the compensating fish could be explained by seasonal changes in temperature (high during the food limitation period, declining through the compensatory period). Compensation could thus be attributed to a delay in seasonal anorexia in the food limited fish. Additionally, all fish had been raised at high densities prior to the experiment; the acclimation period may have triggered CG as a result of lowered experimental densities, and this may not have been completed by the beginning of the experiment. Thus, the routinely growing fish may have experienced a short period of CG during the food limitation period that was suppressed in the food limited fish until the compensatory period. This explanation is supported by the low but increasing body condition of fish in both treatments during the acclimation period and by the decline in the routine SGR during the food limitation period. However, it should be noted that this caveat does not affect the cost component of our study, as any morphological cost should still have been higher in the compensating fish because of both high pre-experimental densities and the food limitation period.

Costs to compensation

We were able to compare the morphologies of each food limited/compensating cross with the morphologies of their respective routinely growing crosses at three crucial stages during the experiment: before the food limitation period, after the food limitation period but before the compensatory period, and after the compensatory period. This enabled us to determine whether any differences observed between treatments at the end of the experiment could be attributed to chance differences caused by the experimental design, the lack of nutrients during the food limitation period, or increased growth rates during the compensatory period. Compensatory-related deviations in morphology from that of routinely growing fish could then be interpreted as a potential cost of compensation, although, without undertaking any assessments of survival and fecundity in the wild, these, if found, could only be considered presumed costs.

At the beginning of the experiment, there were no important differences between treatments within each

cross. After the food limitation period, the only morphological differences observed were in terms of lost body mass in the food limited fish. After the compensatory period, it was expected that, if there were morphological costs to compensation, the compensating and routinely growing fish would be morphologically distinct in ways not explicable by the food limitation period. This was not the case: both treatments were morphologically similar in all biologically relevant RWs with the exception of the length of the caudal fin. All of the compensating hybrid salmon had significantly longer caudal fins than their routinely growing counterparts. This difference was not seen in the pure wild or pure farmed crosses, possibly suggesting a breakdown in the mechanics of tissue deposition in the hybrids. However, the total amount of variation explained by these differences was small; and so overall, although suggestive, we conclude that there were no obvious CG-related deviations in morphology as defined by the landmarks we used. This is contrary to the findings of studies on growth hormone–transgenic fishes modified for faster growth (Ostenfeld et al. 1998; Li et al. 2009). Our work does not rule out the possibility that other morphological costs to compensation might exist, such as increased fluctuating asymmetry.

Farmed-wild hybridization and conservation

Escaped farmed salmon have been detected in 54 wild salmon rivers in eastern North America, and some of these rivers have contained farmed salmon over multiple years and at proportions exceeding 20% (Morris et al. 2008). At these proportions, models predict that farmed salmon pose a genetic threat to wild populations (Hutchings 1991; Hindar et al. 2006). Farmed salmon are known to successfully mate in these rivers, both with other farmed salmon and with wild salmon (Carr et al. 1997; Lage and Kornfield 2006), but the extent to which this occurs remains unknown. Given the depressed abundance of many of the populations into which farmed salmon are escaping (Morris et al. 2008), the effects of hybridization are of concern (e.g. Wolf et al. 2001).

The three crosses of farmed-wild hybrid Atlantic salmon expressed numerous phenotypes that were intermediate to and significantly distinct from those of either parental cross, including length, mass, growth rates, parr maturity and body morphology (although in many cases, the first-generation hybrids were similar to the FF). Without proper field experiments, however, it is impossible to say whether these intermediate phenotypes will help, hinder, or not alter already depressed wild salmon populations. Nevertheless, given the wealth of circumstantial evidence in support of the hypothesis of local adaptation in wild Atlantic salmon, particularly with respect to growth and life history metrics (Garcia de Leaniz et al. 2007), and the evidence from river experiments that hybrids have lower fitness than their wild counterparts (McGinnity et al. 2003), it is not unreasonable to suppose that the hybridization of farmed and wild Tusket River salmon could be detrimental to wild salmon populations.

Faster growth of hybrids relative to that of wild salmon could be of benefit for long-distance migration (Metcalfe and Monaghan 2003; Fraser et al. 2010) or overwintering survival (Garvey et al. 1998), but could be selected against in the acid-impacted Tusket River, in which food levels may be comparatively low (Fraser et al. 2008). Morphology is important for migration and critical swimming speed (e.g. Hawkins and Quinn 1996); intermediate morphologies in the hybrids could affect swimming performance and thus fitness. The lower incidence of mature male parr in the farmed salmon and their hybrids (see also Fleming and Einum 1997; McGinnity et al. 2003) can likely be attributed to the sole use of mature anadromous males in the breeding design. If this lower incidence reflects a loss of plasticity in maturation, this could have significant effects on hybrid reproductive success. Although speculative, the differences between farmed and Tusket River salmon documented here and in other studies (Fraser et al. 2010; Houde et al. 2010) provide cause for concern in light of the magnitude of farmed salmon escapes (Morris et al. 2008), the conservation status of wild populations, and the potential for hybridization between farmed and wild salmon.

General implications

Studies on phenotypic plasticity in domesticated–wild hybrids and their progenitors yield important insights in a number of areas. For conservation purposes, plasticity cannot be ignored. Although in this study there were no differences in the reaction norm slopes of the parental and hybrid populations (as documented by Darwish and Hutchings (2009) in their comparison of wild and farmed backcrossed salmon), the differences in reaction norm elevation highlight the importance of across-environment studies. Single-environment experiments run the risk of missing important complexities that are only discovered by taking plasticity into account (e.g. Mercer et al. 2006).

There are several means by which studies on domesticated and wild organisms can contribute to our knowledge of the evolution of phenotypic plasticity. First, domestication can provide a unique opportunity to study the relative time frame over which evolutionary changes to reaction norms are possible. For Atlantic salmon, in which artificial selection is strong but the number of generations of domestication is still few, the robustness of plasticity to evolutionary change can be readily assessed.

In this case, the farmed salmon were as plastic as their wild counterparts. By studying plasticity in other organisms which have undergone longer, but still known, generations of domestication, relatively rapid evolutionary changes (or a lack thereof) in plasticity may be found. It may also be possible to test a key prediction of plasticity evolution through domestic and wild populations: that plasticity will be favoured in populations that live in predictably variable environments, but will be selected against in stable environments because of the costs of plasticity (DeWitt and Scheiner 2004). Domesticated organisms live in relatively stable food, and potentially diurnal and thermal, environments compared to their wild progenitors. In our experiment, farmed Atlantic salmon were still as plastic in their growth rates as wild Atlantic salmon, possibly because the costs of plasticity in this case were low, four generations of domestication were not enough to select against plasticity, plasticity was favoured for another reason in the farmed salmon, or the prediction itself was incorrect.

Domesticated–wild hybridization can also provide insights into plasticity as a mechanism for evolutionary change, albeit indirectly and without uncoupling it from natural selection. The literature abounds with the consequences of hybridization on speciation, ranging from the persistence of species pairs when hybrid fitness falls below the adaptive peaks of the parents (Hatfield and Schluter 1999) to the collapse of species pairs (Taylor et al. 2005) and to the formation of novel populations with their own peculiar life histories (Schartl et al. 1995). Hybrids can outperform parental species in certain environments through the interactions of novel allelic arrangements (Birchler et al. 2006) or have less genetic variation than parental populations (Norris et al. 1999). By comparing the plasticity of hybrids to their parental populations, we gain that much more insight into how hybrids can persist and thereby affect speciation.

In sum, studies on the plasticity of domesticated–wild hybrids and their progenitors are important for both conservation and plasticity theory. Despite the near-ubiquitous occurrence of escaped domesticated organisms, few of these studies have been carried out. Our findings, that farmed salmon and their hybrids were just as plastic as wild salmon but had higher reaction norm elevations for CG, contribute to what will hopefully become a growing body of literature on the interactions between plasticity, domestication, conservation and hybridization.

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Literature cited

Ali, M., A. Nicieza, and R. J. Wootton. 2003. Compensatory growth in fishes: a response to growth depression. Fish and Fisheries **4**:147–190.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. The Quarterly Review of Biology **72**:149–177.

Arendt, J. D., and D. S. Wilson. 2000. Population differences in the onset of cranial ossification in pumpkinseed (*Lepomis gibbosus*), a potential cost of rapid growth. Canadian Journal of Fisheries and Aquatic Sciences **57**:351–356.

Arendt, J., D. S. Wilson, and E. Stark. 2001. Scale strength as a cost of rapid growth in sunfish. Oikos **93**:95–100.

Birchler, J. A., H. Yao, and S. Chudalayandi. 2006. Unraveling the genetic basis of hybrid vigor. Proceedings of the National Academy of Sciences **103**:12957–12958.

Bohman, V. R. 1955. Compensatory growth of beef cattle: the effect of hay maturity. Journal of Animal Science **14**:249–255.

Bookstein, F. L. 1991. Morphometric Tools for Landmark Data. Cambridge University Press, New York, USA.

Brommer, J. E., J. Merilä, B. C. Sheldon, and L. Gustafsson. 2005. Natural selection and genetic variation for reproductive reaction norms in a wild bird population. Evolution **59**:1362–1371.

Carr, J. W., J. M. Anderson, F. G. Whoriskey, and T. Dilworth. 1997. The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. ICES Journal of Marine Science **54**:1064–1073.

Darwish, T. L., and J. A. Hutchings. 2009. Genetic variability in reaction norms between farmed and wild backcrosses of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences **66**:83–90.

DeWitt, T. J., and S. M. Scheiner. 2004. Phenotypic Plasticity: Functional and Conceptual Approaches. Oxford University Press, New York, New York.

Ellers, J., J. Mariën, G. Driessen, and N. M. van Straalen. 2008. Temperature-induced gene expression associated with different thermal reaction norms for growth rate. Journal of Experimental Zoology **310B**:137–147.

Farrell, A. P., W. Bennett, and R. H. Devlin. 1997. Growth-enhanced transgenic salmon can be inferior swimmers. Canadian Journal of Zoology **75**:335–337.

Fleming, I. A., and S. Einum. 1997. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. ICES Journal of Marine Science **54**:1051–1063.

Fraser, D. J., L. K. Weir, T. L. Darwish, J. D. Eddington, and J. A. Hutchings. 2007. Divergent compensatory growth responses within species: linked to contrasting migrations in salmon? Oecologia **153**:543–553.

Fraser, D. J., A. M. Cook, J. D. Eddington, P. Bentzen, and J. A. Hutchings. 2008. Mixed evidence for reduced local adaptation in

wild salmon resulting from interbreeding with escaped farmed salmon: complexities in hybrid fitness. Evolutionary Applications **1**:501–512.

Fraser, D. J., A. L. S. Houde, P. V. Debes, P. O'Reilly, J. D. Eddington, and J. A. Hutchings. 2010. Consequences of farmed-wild hybridization across divergent wild populations and multiple traits in salmon. Ecological Applications **20**(4): 935–953.

Garcia de Leaniz, C., I. A. Fleming, S. Einum, E. Verspoor, W. C. Jordan, S. Consuegra, N. Aubin-Horth *et al.* 2007. A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biological Reviews **82**:173–211.

Garvey, J. E., R. A. Wright, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size. Canadian Journal of Fisheries and Aquatic Sciences **55**:2414–2424.

Glebe, B. D. 1998. East Coast salmon aquaculture breeding programs: history and future. Canadian Stock Assessment Secretariat. Research document 1998/157.

Gotthard, K. 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. Journal of Animal Ecology **69**:896–902.

Hatfield, T., and D. Schluter. 1999. Ecological speciation in sticklebacks: environment-dependent hybrid fitness. Evolution **53**:866–873.

Hawkins, D. K., and T. P. Quinn. 1996. Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences **53**:1487–1496.

Hindar, K., I. A. Fleming, P. McGinnity, and O. Diserud. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. ICES Journal of Marine Science **63**:1234–1247.

Houde, A. S., D. J. Fraser, and J. A. Hutchings. 2010. Reduced anti-predator responses in multi-generational hybrids of farmed and wild Atlantic salmon (*Salmo salar* L.). Conservation Genetics **11**(3): 785–794.

Hutchings, J. A. 1991. The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. Aquaculture **98**:119–132.

Hutchings, J. A. 2006. Survival consequences of sex-biased growth and the absence of a growth-mortality trade-off. Functional Ecology **20**:347–353.

Lacroix, G. L. 1989. Ecological and physiological responses of Atlantic salmon in acidic organic rivers of Nova Scotia, Canada. Water, Air, and Soil Pollution **46**:375–386.

Lage, C., and I. Kornfield. 2006. Reduced genetic diversity and effective population size in an endangered Atlantic salmon (*Salmo salar*) population from Maine, USA. Conservation Genetics **7**:91–104.

Lawlor, J. L., A. Dacanay, J. A. Hutchings, L. L. Brown, and S. A. Sperker. 2009. Differences in pathogen resistance within and among cultured, conservation-dependent, and endangered populations of Atlantic salmon, *Salmo salar* L. Environmental Biology of Fishes **84**:69–78.

Li, D., W. Hu, Y. Wang, Z. Zhu, and C. Fu. 2009. Reduced swimming abilities in fast-growing transgenic common carp *Cyprinus carpio* associated with their morphological variations. Journal of Fish Biology **74**:186–197.

Lynch, M., and B. Walsh. 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates Inc., Massachusetts, USA.

Maclean, A., and N. B. Metcalfe. 2001. Social status, access to food, and compensatory growth in juvenile Atlantic salmon. Journal of Fish Biology **58**:1331–1346.

McClelland, E., J. Myers, J. Hard, L. Park, and K. Naish. 2005. Two generations of outbreeding in coho salmon (*Oncorhynchus kisutch*): effects on size and growth. Canadian Journal of Fisheries and Aquatic Sciences **62**:2538–2547.

McGinnity, P., P. Prodöhl, A. Ferguson, R. Hynes, N. ó Maoiléidigh, N. Baker, D. Cotter *et al.* 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London B **270**:2443–2450.

Mercer, K. L., D. L. Wyse, and R. G. Shaw. 2006. Effects of competition on the fitness of wild and crop-wild hybrid sunflower from a diversity of wild populations and crop lines. Evolution **60**:2044–2055.

Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology and Evolution **16**:254–260.

Metcalfe, N. B., and P. Monaghan. 2003. Growth versus lifespan: perspectives from evolutionary ecology. Experimental Gerontology **38**:935–940.

Morris, M. R. J., D. J. Fraser, A. Heggelin, F. G. Whoriskey, J. W. Carr, S. F. O'Neil, and J. A. Hutchings. 2008. The prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. Canadian Journal of Fisheries and Aquatic Sciences **65**:2807–2826.

Nicieza, A. G., and N. B. Metcalfe. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. Ecology **78**:2385–2400.

Norris, A. T., D. G. Bradley, and E. P. Cunningham. 1999. Microsatellite genetic variation between and within farmed and wild Atlantic salmon (Salmo salar) populations. Aquaculture **180**:247–264.

Ostenfeld, T. H., E. McLean, and R. H. Devlin. 1998. Transgenesis changes body and head shape in Pacific salmon. Journal of Fish Biology **52**:850–854.

Parris, M. J. 2000. Experimental analysis of hybridization in leopard frogs (Anura: Ranidae): larval performance in desiccating environments. Copeia **2000**:11–19.

Piché, J., J. A. Hutchings, and W. Blanchard. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. Proceedings of the Royal Society B **275**:1571–1575.

Repka, S., S. Veselá, A. Weber, and K. Schwenk. 1999. Plasticity in filtering screens of *Daphnia cucullata* × *galeata* hybrids and parental species at two food concentrations. Oecologia **120**:485–491.

Roberge, C., S. Einum, H. Guderley, and L. Bernatchez. 2006. Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. Marine Ecology **15**:9–20.

Robinson, B. W., and S. L. Wardrop. 2002. Experimentally manipulated growth rate in threespine sticklebacks: assessing trade offs with developmental stability. Experimental Biology of Fishes **63**:67–78.

Rohlf, F. J. 2006. tpsRelw, Relative Warp Analysis, version 1.44. Department of Ecology and Evolution, State University of New York at Stony Brook.

Schartl, M., B. Wilde, I. Schlupp, and J. Parzefall. 1995. Evolutionary origin of a parthenoform, the Amazon molly *Poecilia formosa*, on the basis of a molecular genealogy. Evolution **49**:827–835.

Schlichting, C. D., and D. A. Levin. 1986. Phenotypic plasticity: an evolving plant character. Biological Journal of the Linnean Society **29**:37–47.

Schultz, E. T., T. E. Lankford, and D. O. Conover. 2002. The covariance of routine and compensatory juvenile growth rates over a seasonality gradient in a coastal fish. Oecologia **133**:501–509.

Silim, S. N., R. D. Guy, T. B. Patterson, and N. J. Livingston. 2001. Plasticity in water-use efficiency of *Picea sitchensis*, *P. glauca* and their natural hybrids. Oecologia **128**:317–325.

Taylor, E. B., J. W. Boughman, M. Groenenboom, M. Sniatynski, D. Schluter, and J. L. Gow. 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. Molecular Ecology **15**:343–355.

Weber, E., and C. M. D'Antonio. 1999. Phenotypic plasticity in hybridizing *Carpobrotus* spp. (Aizoaceae) from coastal California and its role in plant invasion. Canadian Journal of Botany **77**:1411–1418.

Wolf, D. E., N. Takebayashi, and L. H. Rieseberg. 2001. Predicting the risk of extinction through hybridization. Conservation Biology **15**:1039–1053.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Landmarks used for morphological analyses.

Figure S2. Length for all crosses throughout the experiment.

Figure S3. Mass for all crosses throughout the experiment.

Figure S4. Coefficient of variation for length, mass and condition, for all crosses, throughout the experiment.

Figure S5. Morphological variation between crosses on day 18.

Table S1. Results of mixed effects ANOVAs examining length, mass and body condition.

Table S2. Results of repeated measures ANOVAs examining length, mass and condition.

Table S3. Results of ANOVAs examining SGR for length and mass.

Table S4. Results of ANOVAs examining the coefficient of variation (CV) for length, mass and body condition.

Table S5. Results of mixed effects ANCOVAs, with tank as a random effect, examining morphological variation between crosses using Relative Warps (RW).

Table S6. Results of mixed effects ANOVAs examining morphological differences between treatments within each cross, with tank as a random effect, at the beginning of the experiment.

Table S7. Results of mixed effects ANOVAs examining morphological differences between treatments within each cross, with tanks as a random effect, at the end of the food limitation period.

Table S8. Results of mixed effects ANOVAs examining morphological differences between treatments within each cross, with tank as a random effect, at the end of the compensatory period.

Table S9. Results of line-cross analyses for hybrid traits.

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