

Divergent compensatory growth responses within species: linked to contrasting migrations in salmon?

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Abstract Animals often exhibit accelerated or “compensatory” growth (CG) after periods of environmentally induced growth depression, raising important questions about how they cope with environmental variability. We tested an underexplored hypothesis regarding the evolutionary consequences of CG; namely, that natural populations differ in CG responses. Common-garden experiments were used to compare subadult growth following food restriction between groups (control, treatment) of two Atlantic salmon (*Salmo salar*) populations and their first-generation (F_1) hybrids. The populations are found at similar latitudes but characterized by differences in migration distance. We predicted that long-distance migrants would better maintain growth trajectories following food restriction than short-distance migrants because they: (1) require larger body sizes to offset energetic costs of migration and (2) face greater time constraints for growth as they must leave non-breeding areas earlier to return to breeding areas. Long-distance migrants grew faster, achieved quicker CG (relative to controls), and their overall body morphology was more streamlined (a trait known to improve swimming efficiency) than slower growing short-distance migrants. F_1 hybrids were generally intermediate in “normal” growth, CG, and body morphology. We concluded that CG responses may differ

considerably among populations and that the conditions generating them are likely interconnected with selection on a suite of other traits.

Keywords Growth compensation · Adaptive divergence · Natural selection · Long-distance migration · Life history

Introduction

Animals show remarkable abilities to respond to environmental variability. Among these is the ability to grow faster than “normal” following periods of environmentally induced growth depression (Wilson and Osbourne 1960; Metcalfe and Monaghan 2001). Such compensatory growth (CG) implies that animals can regulate their growth rates and trajectories to cushion departures from an optimal growth trajectory (Ali et al. 2003). Compensatory growth also illustrates that animals often grow at submaximal rates and, accordingly, several recent experimental studies have examined tradeoffs between maximal growth and survival or developmental stability (Billerbeck et al. 2001; Carlson et al. 2004; Johnsson and Bohlin 2006).

Theory predicts that CG might be adaptive in populations where predictable changes in resource availability occur seasonally, where individuals of reduced size experience greater risks, or where the costs of CG can be delayed (Sibly and Calow 1986; Yearsley et al. 2004; Mangel and Munch 2005). Despite this, and the fact that remarkable differences in life histories and environmental pressures exist within many species, few studies have addressed whether populations differ in CG, the conditions under which it might occur, and the evolutionary mechanisms that might drive such differences (but see Schultz et al. 2002).

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Salmonid fish populations are ideal for studying the evolutionary consequences of CG. There is evidence that several species exhibit CG [e.g. rainbow trout (*Oncorhynchus mykiss*) Quinton and Blake 1990; Atlantic salmon (*Salmo salar*) Nicieza and Metcalfe 1997; brown trout (*Salmo trutta*) Johnson and Bohlin 2006], and that populations exhibit genetic differences in growth rates and digestion rates (Nilsson 1992; Nicieza et al. 1994). These differences are typically associated with environmental heterogeneity, implying that selective pressures could also lead to population differences in CG.

One potential means by which this might occur relates to the importance of reaching size thresholds at different life history stages. Rapid growth evolves when there is a need to reach a minimum body size in a limited time (Arendt 1997). In migratory salmonids, migration to marine habitats in the spring requires a juvenile threshold size and physiological changes (“smolting”) (Nicieza and Metcalfe 1997; Alvarez and Nicieza 2005). Accordingly, juvenile body size tends to be positively correlated with early marine survival (Bilton et al. 1982; Holtby et al. 1990), and, within populations, individuals about to migrate show greater CG than individuals delaying migration because they are too small (Nicieza and Metcalfe 1997).

Whether maintaining growth trajectories after periods of lower food availability is also important at later stages in salmonids (e.g. subadult, adult) is unknown, but this might be especially critical for populations with long-distance migrations. Such migrations typically incur greater energetic costs (Kinnison et al. 2001), so to offset these, long-distance migrants often need larger body sizes than short-distance migrants (Taylor and Foote 1991; Crespi and Teo 2002; Fraser and Bernatchez 2005; Jonsson and Jonsson 2006). Long-distance migrants also have greater time constraints for growth imposed on them as they must leave marine feeding areas earlier to return to breeding areas in rivers (see Both and Visser 2001; Drent et al. 2006). Consequently, following food restriction, long-distance migrants could also gain more from returning faster to a suitable body size than short-distance migrants.

Our study's main objective was to examine whether contrasting migrations favor interpopulation differences in CG. We employed common-garden experiments to test the hypothesis that differences exist in CG with differing migration distances. We specifically compared CG between two Atlantic salmon populations (Nova Scotia, Canada) known to have different marine migrations, and their F_1 hybrids. These populations are found at similar latitudes and exhibit a similar size at the onset of marine migration. However, available tagging studies suggest that a considerable proportion of Stewiacke river individuals undergo shorter distance marine migrations to the Gulf of Maine (on the order of 500–1,500 km), whereas long-dis-

tance migrants from the LaHave river population travel to feeding areas off the coast of Greenland (2,500–3,000 km, Jessop 1986; Mills 1989; LaCroix et al. 2005; COSEWIC 2006). These populations also differ in other migratory traits, including adult breeding migration timing (earlier in LaHave), and incidence of iteroparity (lower in LaHave) (DFO 2002; COSEWIC 2006). Similar trait differences are known to have a genetic basis in other salmon populations, and presumably reflect adaptation to divergent environments (Taylor 1991).

As long-distance migrants, we predicted that LaHave salmon would show a greater capacity to maintain growth trajectories following periods of food restriction than Stewiacke salmon. Intermediate CG in F_1 hybrids would also indicate that CG has an additive genetic basis. By testing whether CG differences exist between intraspecific populations with contrasting migrations, we hoped to explore the potential evolutionary consequences of CG in natural populations. In utilizing juvenile salmon that had reached the age of migration to sea in both populations, we also aimed to consider how other facets of migration beyond juvenile stages might favour CG in salmonid populations.

Materials and methods

History of experimental fish

Parental fish gametes were obtained at the Coldbrook Biodiversity Facility, Coldbrook, Nova Scotia, Canada, from adult salmon collected in the Lahave (LA) and Stewiacke (ST) rivers. The LA adults originated from the wild. The ST adults were comprised of fish captured from the wild as juveniles in 1998 and raised to sexual maturity in captivity as part of an endangered salmon rehabilitation program (COSEWIC 2006). Crosses were performed at the Dalhousie University Aquatron Facility in November 2002 at which time three different populations were created: pure LA, pure ST, and their F_1 hybrids (LA \times ST). Pure populations consisted of five full-sibling families, with F_1 hybrid families comprising a mixture of the same males and females used to generate pure LA and ST (the ratios of LA:ST females and males were 3:2 and 2:3, respectively). Initially 250 eggs from each family were randomly allocated to each of four replicate tanks (total of 60, 100 L circular tanks, diameter = 0.66 m, height = 0.43 m). Eggs were kept in the dark at temperatures of 4–6 °C and dead eggs were removed daily. The photoperiod cycle was adjusted to a 12 h light:12 h dark cycle once hatching occurred in February–March 2003. Exogenous feeding began in May 2003, at which time densities were adjusted in each tank to equal one another and fish in each tank were fed the

same amount of commercial dry feed daily. Tanks were cleaned periodically; constant air, water flow (replacement every 5 h) were maintained in all tanks. Fish were maintained in this fashion at ambient water temperature (1 standard deviation ± 0.1 °C between all tanks) until the start of the CG experiment in August 2005.

Compensatory growth

We selected and pooled fish from the tanks of each family that were 167–180 mm in length. This length range corresponded to the approximate size at which the fish would migrate to sea in the wild, at an average age of 2+ years; this is also the age in the wild populations when most fish would have smolted and migrated from the study's rivers (Amiro 2003; COSEWIC 2006). To reduce any potential confounding density-dependent factors prior to the attainment of 167–180 mm, we only selected fish from similar density tanks (100–115 individuals), similar mortality schedules, and with no significant differences in within-tank length variation (based on an analysis of variance ANOVA; data not shown). Because of these requirements, however, replicates of ten fish per randomly allocated tank were uneven between populations for the study (total tanks: $n = 42$; replicates, LA $n = 11$, ST $n = 9$, F₁ hybrids $n = 22$, total $n = 420$ fish). All fish were held under a 12 h light:12 h dark photoperiod at ambient water temperature that decreased steadily from 12 to 5 °C over the course of the experiment (August 10, 2005 until January 31, 2006). The same air, water flow (replacement every 5 h) and temperatures (1 standard deviation ± 0.1 °C) were maintained between all tanks at a given time throughout the experiment.

All tanks were fed the same regime of commercial dry feed (15 ml, twice daily/tank) for the first 27 days to allow fish time to adjust to their assigned tanks. This regime was found to be enough such that food was never exhausted within tanks (results not shown, see also Elliott 1975). Between days 27 and 65 (a total of 38 days), the food restriction period, “treatment” tanks (half of each population's replicates: LA $n = 5$, ST $n = 4$, F₁ $n = 11$) were placed on a maintenance regime (1.25 ml, twice daily/tank), whereas “control” fish were maintained on the same regime as above. After day 65, the start of the compensatory period, treatment fish were returned to the control fish regime and all fish were fed this unrestricted regime (15 ml, twice daily/tank) to the end of the experiment (day 174). Length (to the nearest mm) and weight (to the nearest 0.5 g) of all fish was measured a total of ten times throughout the experiment, on days 27, 49, 65, 75, 85, 96, 106, 128, 153, and 174. Minimal mortality (1.9%) occurred during the experiment and eight of 42 tanks contained nine instead of ten fish; in such cases, the daily food amount

given was reduced by 10%. Note that the control food regime was greater than what all fish were fed before the experiment (2–3 \times) to increase growth performance over the course of the experiment. It is therefore possible that all fish would be exhibiting some degree of growth compensation to day 27 (i.e., before treatment fish were starved).

Statistical analyses for compensatory growth

Factorial ANOVAs were first used to compare mean body size at the first measurement (day 27) and up to the end of the food restriction period (day 65). Three metrics of mean body size were analyzed: length, weight, condition ($k = g/cm^3 \times 10,000$), as well as changes in variability within these (coefficient of variation = CV = SD/mean). During the compensatory period (days 65–106; see below for days 106–174), we used analyses of covariance (ANCOVAs), with day as a covariate, to investigate changes in body size over time. As we compared three metrics of mean body size (or variability in body size) in the above analyses, critical α values were taken to be $0.05/3 = 0.0167$. During the compensatory period, we also investigated specific growth rate changes (in length and weight, e.g. for length:

$$\% \text{ length day}^{-1} = \frac{\ln L_{t_2} - \ln L_{t_1}}{t_2 - t_1} \times 100,$$

where L is length in mm and t_1 and t_2 represent subsequent measurement days) using factorial ANOVA incorporating population, food regime (control vs. treatment) and time period (days 65–75, 75–85, 85–96, 96–106; $\alpha = 0.05/2$). ANCOVA/ANOVA assumptions of normality and equal variances were met.

Due to space limitations, on day 106 it was necessary to combine replicate tanks, by population and by control/treatment, each into one large, randomly assigned tank (1,182 L; length = 240 cm, width = 82 cm, height = 60 cm), except for F₁ hybrids which were combined into two tanks each for controls/treatments. All tanks received equal numbers of individuals. At this time ration amounts were adjusted proportionately, with each tank receiving approximately 15 ml for every ten fish in the tank. Statistical analyses were conducted only on data collected prior to the transfer of fish to larger tanks due to inadequate tank replicates following transfer. Growth data collected following day 106 are presented for discussion only.

Morphological analyses

We complemented CG analyses by comparing body morphology between populations (LA, ST, F₁ hybrid), as interpopulation morphological differences in salmonids can be linked to migration distance (Taylor and Foote 1991;

Fraser and Bernatchez 2005). Individuals were sampled with an overdose of the anaesthetic MS-222 on day 174 (controls/treatments: LA $n = 40/40$, ST $n = 40/37$, F₁ $n = 46/46$, half from each tank in both cases). Each fish was placed on its right side on a measuring board with the caudal fin extended and subsequently photographed (whole body) using a digital camera mounted overhead. Photos were imported into the program TPSDIG (Rohlf 2003), from which coordinates of 17 landmarks were obtained (Fig. 1).

We conducted geometric morphometric analyses using our digitized landmarks. This approach retains information on spatial covariation among landmarks while considering where a given measurement is taken relative to others (Rohlf 2003). We used the software TPSRELW (Rohlf 2003) to center, scale and align coordinates for our specimens for determining a consensus configuration, and then to compare each set of individual coordinates to the consensus using thin-spline analysis (Bookstein 1991). Individual specimen coordinates were then deformed towards the consensus configuration in TPSRELW based on a set of bending energy values called partial warps. Principal components of these partial warps, termed relative warps (RWs), summarize the major trends in body shape variation among specimens (Rohlf 2003). We considered only the first four RWs as dependent variables for shape variation analyses below because these explained much of the variation among individuals (28.4, 15.7, 11.1 and 8.5%, respectively) and could be readily interpreted. Potential allometric effects of body size on RWs were removed by including centroid size (square root of the sum of squared distances from each landmark to the location on a specimen that minimizes that sum) as a covariate in body shape analyses, a common procedure in geometric morphometrics (Bookstein 1991). In our study, for instance, centroid

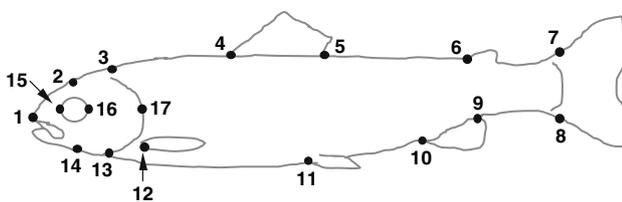


Fig. 1 Landmarks used for geomorphometric analyses on *Salmo salar* populations: 1, anterior lip of the upper jaw; 2, head at the midpoint of the eye; 3, supraoccipital notch; 4, anterior dorsal fin insertion; 5, posterior dorsal fin insertion; 6, adipose fin insertion; 7, dorsal terminus of the caudal flexure; 8, ventral terminus of the caudal flexure; 9, posterior insertion of the anal fin; 10, anterior insertion of the anal fin; 11, insertion of the pelvic fin; 12, insertion of the pectoral fin; 13, meeting point of the gill plate on the ventral midline; 14, midpoint of the gill plate on the ventral midline; 15, most anterior point of the eye; 16, most posterior point of the eye; 17, posterior edge of the operculum

size was highly correlated with standard length ($r > 0.98$, $P < 0.001$ for each population).

Body shape data were tested for effects attributable to centroid size (covariate), population (LA, ST, F₁), food regime before the compensatory period (control, treatment) and the interaction between population and food regime, using a MANCOVA. Note that because morphology photos were taken on day 174, fish were kept in treatment-specific tanks from days 106 to 174, such that tank effects on morphology were possible. Encouragingly, we found no differences in within-tank mean RW1–RW4 scores between the two tanks harboring either F₁ hybrid control or treatment fish (student t -tests, all P values > 0.05), so they were pooled for the MANCOVA. Nevertheless, as a result of potential tank effects, we focused chiefly on the overall effect of population and whether these effects reflected biologically important differences between populations.

Results

Body size at the onset of food restriction

On day 27, we found no evidence for differences in any body size variables between populations, food regimes, or for the interaction between population and food regime, with only two exceptions (Table 1). Weight CV and condition CV were different between populations, with LA salmon showing the most variability (Fig. 2e,f).

Body size at the end of the food restriction period

On day 65 we found, as expected, considerable differences between fish experiencing different food regimes for most body size variables (Table 1). Control fish were longer, heavier and in better condition than treatment fish (Fig. 2a–c); they were also more variable in condition than treatment fish (Fig. 2f). Populations also differed in all body size variables except condition (Table 1). Stewiacke salmon tended to be the shortest, lightest, but the most variable in body size, while LA salmon were the longest and heaviest (Fig. 2a–f). The interaction between population and food regime was only significant for length (Table 1). Here, the magnitude of length difference between control and treatment fish was greatest in LA salmon and least in ST salmon (Fig. 2a).

Body size changes and specific growth during the compensatory period

During the compensatory period, we were mainly interested in the interaction between population and food regime in our models, as this allowed us to test whether

Table 1 Results of ANOVA examining body size variable responses of salmon at: (1) the onset of the food restriction period (day 27), and (2) the end of the food restriction period (day 65)

Day 27							
Factor	<i>df</i>	Length		Weight		Condition	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Population	2, 36	3.17		4.37		4.57	
Food regime	1, 36	0.42		0.16		0.04	
Population × food regime	2, 36	2.86		0.78		0.07	
	<i>df</i>	Length (CV)		Weight (CV)		Condition (CV)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Population	2, 36	2.72		5.37	*	7.17	**
Food regime	1, 36	0.69		2.11		0.75	
Population × food regime	2, 36	1.34		1.83		0.83	
Day 65							
Factor	<i>df</i>	Length		Weight		Condition	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Population	2, 36	11.85	***	5.49	*	0.27	
Food regime	1, 36	290.11	***	383.05	***	260.24	***
Population × food regime	2, 36	5.93	*	4.57		0.23	
	<i>df</i>	Length (CV)		Weight (CV)		Condition (CV)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Population	2, 36	5.84	*	6.53	**	5.65	*
Food regime	1, 36	2.14		1.61		12.82	***
Population × food regime	2, 36	2.83		3.16		4.38	

Degrees of freedom (*df*) and *F* values (*F*) are presented for each factor in the model

CV Coefficient of variation

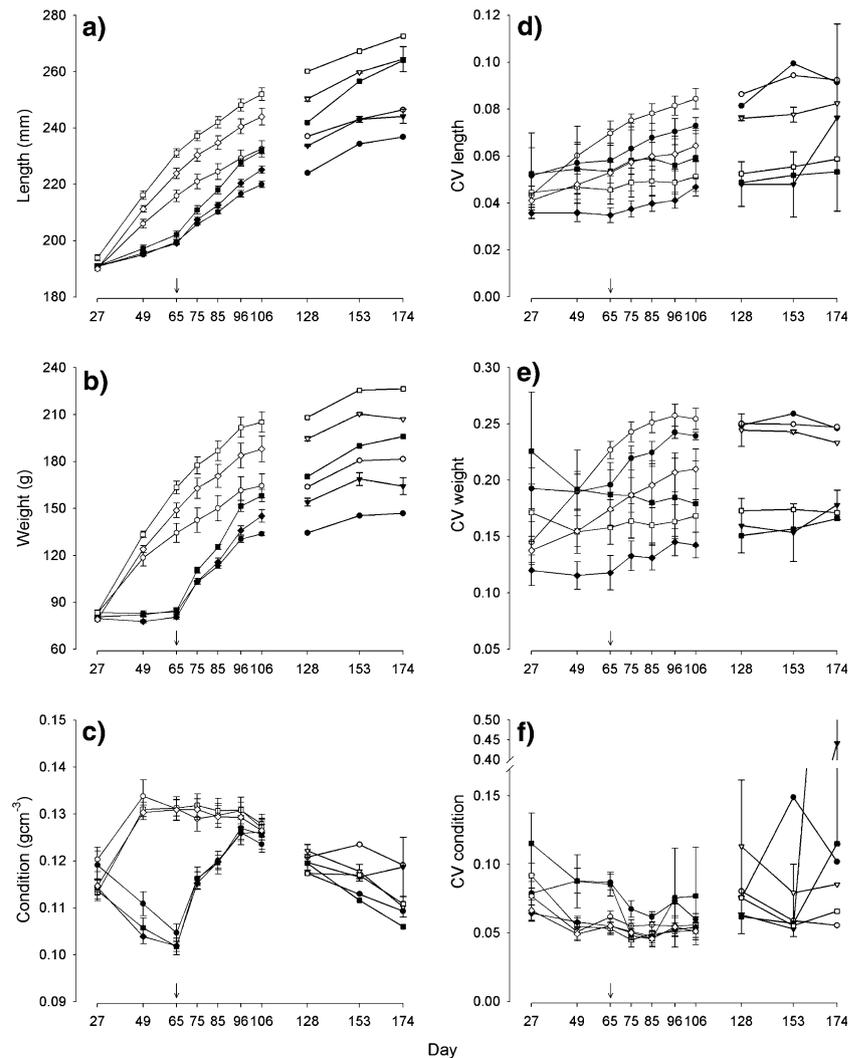
P* ≤ 0.0167 ($\alpha = 0.05/3$; see “Materials and methods”); *P* ≤ 0.005; ****P* ≤ 0.001

populations differed in their compensatory growth responses following food restriction. This interaction was significant for length and weight, regardless of how growth analyses were approached (i.e., changes in body size over time vs. specific growth rate, Tables 2, 3). Considering population changes in body size over time, LA salmon grew the fastest, ST salmon grew the slowest, and F₁ hybrids were intermediate in growth (Fig. 2a,b). However, treatment fish grew faster than control fish, especially immediately following the food increase (up to day 96), with treatment LA growing faster relative to their control than treatment ST (Fig. 2a,b). Similarly, when considering specific growth rate, treatment fish exhibited higher specific growth rates than control fish until day 106, but the magnitude of these differences was greatest in LA salmon, followed by F₁ hybrids, and lowest in ST salmon (Fig. 3). These results indicated, collectively, that treatment LA

salmon compensated in growth more quickly relative to their control following food restriction than ST salmon. By day 106, the body condition of treatment fish had also been restored to similar levels of control fish (Fig. 2c). By the end of the experiment (day 174), full compensation in body size due to faster growth rate in treatment fish had almost occurred, as treatment fish were between 92 and 97% of the length of controls, and between 79 and 86% of the weight (Fig. 2a,b).

Length and weight variation within tanks increased over time in most populations during the compensatory period, with ST salmon exhibiting a greater amount of variability in body size than LA salmon or F₁ hybrids (Table 2; Fig. 2d,e). However, there were no consistent trends in within-tank variation between food regimes of populations to account for the significant population × food regime interaction for length and weight CV (Table 2; Fig. 2d,e).

Fig. 2a–f **a** Length, **b** weight, **c** condition, **d** CV length, **e** CV weight, **f** CV condition throughout the experimental period for LaHave (*squares*), F₁ hybrids (Stewiacke × LaHave: *diamonds*) and Stewiacke (*circles*) Atlantic salmon (*Salmo salar*) populations. *Open symbols* represent controls and *closed symbols* are food deprivation treatment groups. Growth data following transfer to larger tanks are indicated with *dashed lines*. *Arrows* indicate the day when treatment groups were switched back to the control food regime



Morphological divergence

For body shape analyses, we were mainly interested in the effect of population in our model and whether this effect could be interpreted biologically, as this would indicate that morphological differences existed between LA, ST and their F₁ hybrids. After controlling for body (centroid) size, the population effect was highly significant (Table 4), and examination of loadings for the first four RWs (Fig. 4) revealed four, readily identifiable trends: (1) ST had shorter caudal peduncles and posterior regions, as well as deeper bodies and heads than LA (positive values, RW1; negative values, RW3); (2) ST had longer, deeper heads than LA (negative values, RW2); (3) to a lesser degree, ST also had a more posterior placement of the dorsal fin than LA (positive values, RW4); (4) for most RWs, F₁ hybrids had mean RW values between those of ST and LA (either for controls or treatments), including along RW1, which explained as much of the variation in body shape as RW2 and RW3 combined (Fig. 4). These results indicated that F₁

hybrid body shape was largely intermediate between ST and LA. An example of the major morphological distinctions between ST and LA is also illustrated at the bottom of Fig. 4. Other significant effects (i.e., food regime, population × food regime) raised the possibility of an effect of CG on body shape (Table 4). However, due to the aforementioned potential for tank effects (see “Materials and methods”) and the lack of clear biological explanation for these differences (Fig. 4), they await further, more rigorous investigation.

Discussion

Genetically-based population differences in growth rates and body morphology

Our study’s objective was to examine whether contrasting migrations favor interpopulation differences in CG. Before carrying this out, we were firstly able to confirm that

Table 2 Body size variable responses of salmon over the compensatory growth period (days 65–106)

Factor	df	Length		Weight		Condition	
		F	P	F	P	F	P
Population	2, 203	66.61	***	30.78	***	0.11	
Food regime	1, 203	614.02	***	473.85	***	110.05	***
Day	1, 203	463.16	***	275.35	***	36.43	***
Population × food regime	2, 203	10.98	***	7.08	***	0.04	

Factor	df	Length (CV)		Weight (CV)		Condition (CV)	
		F	P	F	P	F	P
Population	2, 203	34.55	***	40.36	***	4.24	*
Food regime	1, 203	9.97	***	9.39	**	8.35	**
Day	1, 203	10.58	***	7.26	**	0.18	
Population × food regime	2, 203	14.55	***	15.09	***	2.48	

Results of full factorial ANCOVA incorporating day as a covariate are shown

Degrees of freedom (df) and F values (F) are presented for relevant factors in the model

CV Coefficient of variation

*P ≤ 0.0167 (α = 0.05/3; see ‘‘Materials and methods’’); **P ≤ 0.005; ***P ≤ 0.001

Table 3 Specific growth (SG) responses of salmon over the compensatory growth period (days 65–106) based on ANOVA

Factor	df	SG Length		SG Weight	
		F	P	F	P
Population	2, 144	12.06	***	9.35	***
Food regime	1, 144	84.32	***	419.63	***
Time period	3, 144	47.85	***	168.64	***
Population × food regime	2, 144	3.37	*	4.45	*
Population × time period	6, 144	1.31		2.01	
Food regime × time period	3, 144	4.38	**	52.69	***
Population × food regime × time period	6, 144	0.85		0.57	

Degrees of freedom (df) and F values (F) are presented for each factor in the model

*P ≤ 0.025 (α = 0.05/2; see ‘‘Materials and methods’’);

P ≤ 0.005; *P ≤ 0.001

genetically based growth rate differences (regardless of CG) existed beyond juvenile stages between our populations of Atlantic salmon. Control LA salmon grew faster than ST salmon, and their F₁ hybrids showed an intermediate pattern of growth over the entire experiment. In addition, genetically-based morphological differences existed between the populations, and these differences correspond with the contrasting migration distances of the two populations in nature. Long-distance LA migrants were more streamlined in body shape and had longer posterior regions than short-distance ST migrants, traits known to improve swimming and presumably energetic efficiency for longer migrations in other salmonids (Taylor and Foote 1991; Hawkins and Quinn 1996; Fraser and Bernatchez 2005). F₁ hybrids were again largely intermediate in these morphological traits. We then compared interpopulation growth of control fish with that of treatment fish experiencing a 38-day period of restricted food.

Genetically-based population differences in compensatory growth responses

The results of this experiment supported our hypothesis that genetically based differences in CG responses exist between salmon populations. LA treatment fish compensated more rapidly relative to their controls than ST treatment fish in specific growth rate changes for length and weight. Thus, faster growing LA salmon also achieved quicker CG than slower growing ST salmon beyond juvenile stages. This was observed continuously up to 31–41 days (days 96–106 of the experiment) after the food restriction period of 38 days (days 27–65). The CG response of F₁ hybrids was intermediate to that of pure populations for most measurement days, but it was much closer to that of LA salmon (in length and weight) at the earliest stage of compensation (days 65–75). This raises the possibility that a degree of dominance underlies the initial

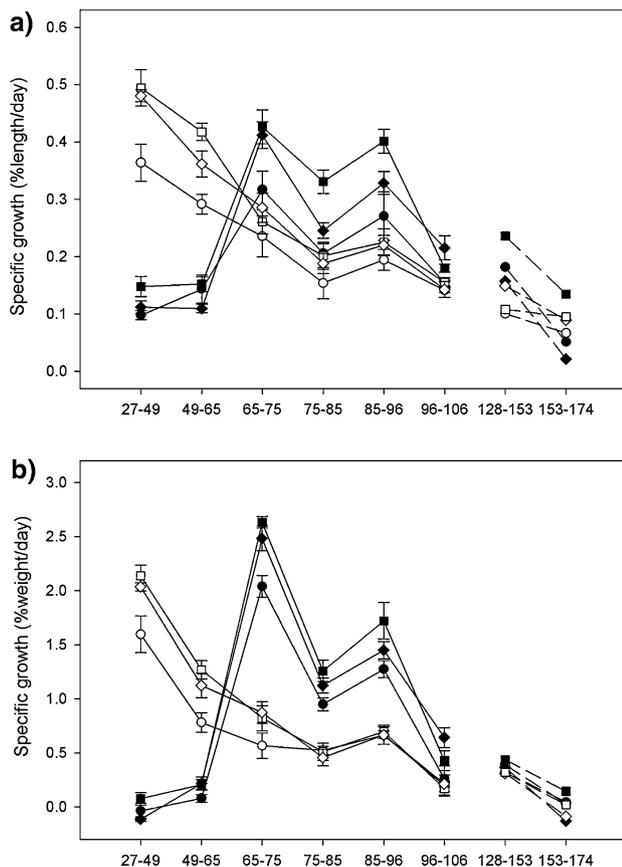


Fig. 3a–b Specific growth rates of *Salmo salar* over the experimental period for **a** length and **b** weight. Symbols and lines are the same as for Fig. 2

Table 4 Results of MANCOVA examining body shape variation between populations and food regimes (control vs. treatment) at the end of the experiment (day 174)

Factor	df	Wilk's λ	Approximate F	P
Centroid size	4, 239	0.747	20.20	***
Population	8, 478	0.673	13.11	***
Food regime	4, 239	0.933	4.31	**
Population \times food regime	8, 478	0.728	10.23	***

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

genetic expression of CG in salmon. Other explanations, however, such as a sex ratio skew between our pure populations, could explain the pattern if the sexes have different CG responses. Overall, the mechanisms underlying the observed CG differences likely reflect differences in growth efficiencies and/or consumption rates (Bradley et al. 1991; Jobling and Koskela 1996; Nicieza and Metcalfe 1997; Ali et al. 2003).

Social status and condition can lead to variation in CG between individuals (Jobling and Koskela 1996). Some studies have documented greater interindividual size

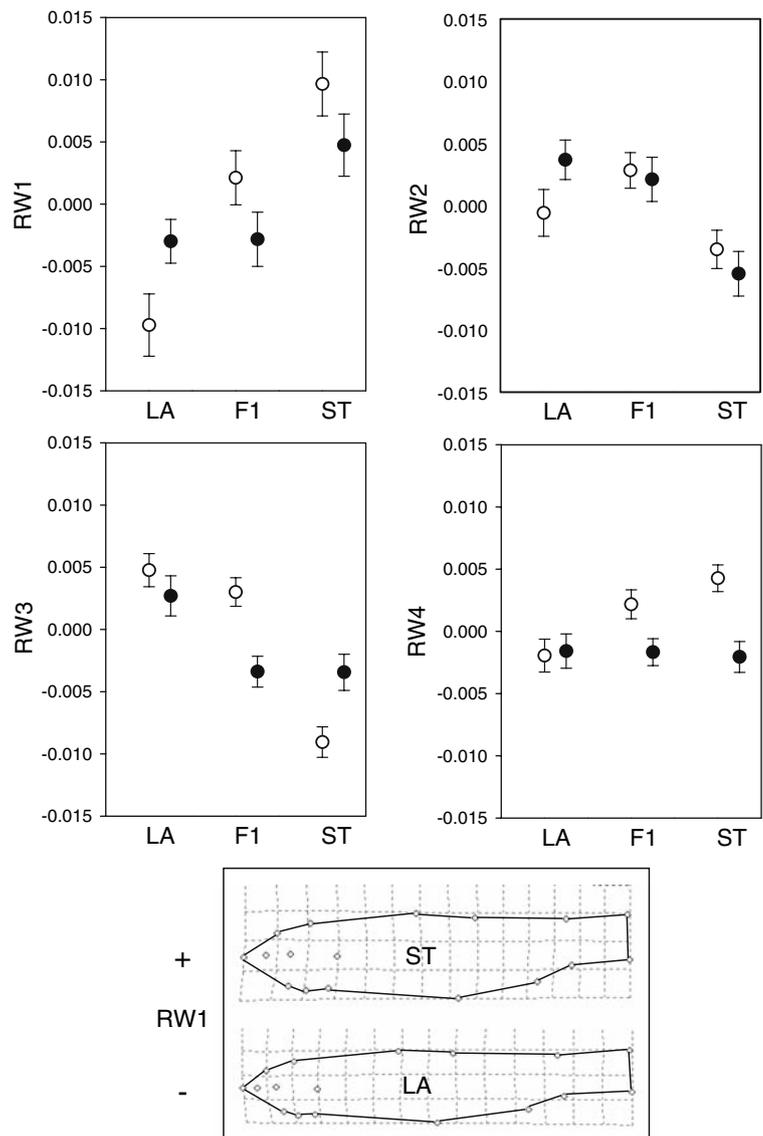
differences when food is restricted versus when it is unrestricted, implying that aggressive interactions increase and dominance hierarchies are more prominent when food is restricted (Dill et al. 1981; Jobling and Koskela 1996; Nicieza and Metcalfe 1997). In contrast, we generally observed greater CV for body size (length and weight) in all populations during the compensatory period. We also observed consistently greater CV for body size in ST salmon. These results raise three points. First, CG differences were mainly attributable to differing responses to unlimited rations (i.e. following deprivation) rather than to a differential response to food restriction (i.e. during deprivation). Second, aggressive interactions might have been too energetically costly in our study during the food deprivation period. Third, behavioral interactions might affect individual CG differently among populations.

Until further investigations examine the potential for CG differences to occur among intraspecific populations, the generality of our findings is unknown. Our evidence for faster CG associated with faster routine growth in migratory salmon populations parallels recent work by Schultz et al. (2002). In a common environment, they found more rapid routine growth and CG in a higher-latitude population of juvenile Atlantic silverside (*Menidia menidia*) than a lower-latitude population. The greater CG of higher-latitude fish was hypothesized to be an adaptation to the more seasonal environments of northern latitudes where growing seasons are shorter (Schultz et al. 2002). Conversely, no CG differences were detected between Atlantic cod populations (*Gadus morhua*), but these populations also did not exhibit routine growth differences (Purchase and Brown 2001).

Alternative explanations for the observed population differences in compensatory growth

One of our study populations is endangered (ST) so CG differences between ST and LA could relate to reduced adaptive potential in ST, resulting from a smaller population size and associated lower genetic variation relative to LA. For example, when the LA gametes were collected (2002), the returning adult population had ranged annually from 500 to 1,000 individuals over the previous five years (DFO 2002), whereas Herbingier et al. (2006) recently estimated the effective population size (N_e) of the last wild juvenile collection in ST (1998; from which our ST gametes were generated) to be 69. This N_e estimate is below general guidelines for maintaining long-term evolutionary potential in natural populations ($N_e = 500$; Frankham et al. 2002). On the other hand, salmonid fish populations can exhibit remarkable adaptive potential despite low N_e (Koskinen et al. 2002), ST exhibits similar levels of genetic variation (e.g. at microsatellite DNA loci) relative to other,

Fig. 4 Mean (± 1 SE) for relative warp (RW) scores between cross types and food regimes (*open circles* = control, *filled circles* = treatment). The percentage of variation explained by each RW was: 28.4% (RW1), 15.7% (RW2), 11.1% (RW3) and 8.5% (RW4). Below is an example of body shape variation from the RW explaining the most variation (RW1) between *Salmo salar* from LaHave (LA) and Stewiacke (ST) populations. Extremes of observed morphological divergence based on thin-plate spline transformations from the TPSRELW software are illustrated (Rohlf 2003)



larger eastern North American populations (King et al. 2001; Fraser et al. 2007), and $N_e = 69$ exceeds the minimum N_e required to avoid short-term problems relating to adaptive potential and inbreeding in salmon (Waples 1990).

Additional selective pressures could also contribute to CG differences between our study populations. First, while the age at migration is most often 2+ years in LA and ST, it is less variable in LA than in ST (Amiro 2003; COSEWIC 2006), implying that there may be greater pressures to reach juvenile size-thresholds in LA than in ST. Second, though a lack of data on each river precludes a comparison, juvenile food availability and population density conditions in LA and ST might differentially affect CG. Third, in traveling farther to principal marine feeding areas, LA salmon might experience more extended periods of unpredictable food availability in transit than ST salmon.

This implies that selective advantages of CG could alternatively arise if feeding areas fluctuate differently in food availability within seasons. Fourth, achieving faster CG likely requires greater risk-taking during foraging (Ali et al. 2003), and the extent to which LA and ST salmon experience differing predation pressures is unknown. More generally, functional differences in population CG might also relate to selective pressures acting on post-reproductive survival, as this differs among salmonid populations and can vary with body size (Hutchings 1994; Bull et al. 1996; Letcher et al. 1996; Crespi and Teo 2002).

Study implications

Overall, our results suggest that selective pressures that favor faster growth also favor more rapid CG in salmon. Beyond juvenile stages, there is apparently a stronger

association between body size and fitness in long-distance (LA) than short-distance (ST) migrants. We have hypothesized that this is because long-distance migration should favor individuals that can maintain faster growth trajectories in spite of variable environmental conditions and the need to leave nonbreeding areas earlier to return to breeding areas. Nevertheless, the proceeding discussion illustrates that different tradeoffs exist between growth and the maintenance of other functions at various life history stages in salmon. As a result, we believe that the conditions generating inter-population differences in CG are likely diverse and interconnected with selection on a multitude of other phenotypic and life history traits. Further investigation of these phenomena should provide invaluable insights into the ecological and evolutionary significance of compensatory growth.

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