Compensatory response ‘defends’ energy levels but not growth trajectories in brown trout, *Salmo trutta* L.

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Compensatory growth is an organism’s reaction to buffer deviations from targeted trajectories. We explored the compensatory patterns of juvenile brown trout under field and laboratory conditions. Divergence of size and condition trajectories was induced by manipulating food levels in the laboratory and then releasing the trout into a river. In the stream, the length trajectories of food-restricted and control fish were parallel, but food-restricted fish exhibited partial compensation for mass and rapid recovery of condition. A laboratory experiment on similar sized fish did not provide evidence for compensatory growth in length or mass. In contrast, data matched the compensatory patterns shown in the stream: length trajectories were parallel and the convergence of mass trajectories ceased as soon as food-restricted fish recovered condition to the level of controls. These results show that (i) brown trout did not compensate for depression in structural growth and (ii) mass recovery was targeted to reinstate condition or energy reserves, but not size at a given age. This does not support the common view that compensatory growth can be a general response to growth depression. Rather, compensation in other salmonids could be related to size thresholds associated with developmental switches at the onset of sexual maturation and migration.

Keywords: compensatory growth; life-history; nutritional deficit; structural growth; *Salmo trutta*; storage

1. INTRODUCTION

It is often assumed that the growth patterns of animals are largely preprogrammed and relatively fixed (Roff 1992; Stearns 1992). However, there is sound evidence that some organisms are capable of reacting after periods of food deprivation by increasing their growth rates compared to those of non-deprived individuals (Jobling 1994). These compensatory responses tend to buffer the individual’s deviation from an assumed optimal size at a given age and restore the growth trajectories that would have been exhibited in the absence of nutritional stress. The observation of compensatory growth shows that animals often grow at a rate below that physiologically possible, which suggests that there is a trade-off between rapid growth and survival or developmental performance (Ricklefs *et al.* 1994; Metcalfe & Monaghan 2001).

Salmonid fish are well suited for studies of compensatory growth. They have indeterminate growth and body size can exert a strong influence on juvenile survival (Hutchings 1994), timing of seaward migration (Nicieza *et al.* 1991) and reproductive success (Fleming & Gross 1994). Many life-history traits show high levels of both plasticity and genetic variation, which results in a huge diversity of life cycles between and within species. That diversity provides an exceptional background to test hypotheses about the evolutionary significance of compensatory growth. Despite many populations having

economic or social value, we have information about compensatory growth for relatively few species and evolutionary scenarios (Ali *et al.* 2003).

The narrow taxonomic scope of compensatory growth studies has two important implications. One is the lack of potentially useful information for the management of particular species. The second is the failure to synthesize a comprehensive body of knowledge that allows inferences about the evolutionary significance of compensatory growth from the existing diversity of ecological and evolutionary scenarios. In this sense, it can be crucial to compile as much information as possible on the occurrence and magnitude of compensatory responses in species (or populations) with marked differences in life-cycle strategies or environmental pressures (see Schultz *et al.* 2002; Sogard & Olla 2002).

This study was designed to assess compensatory responses in the brown trout (*Salmo trutta* L.), a species for which research on compensatory growth has seldom been conducted (Ali *et al.* 2003; but see Pirhonen & Forsman 1998, 1999). We looked at the compensation dynamics of juvenile brown trout in two different situations. First, we conducted a mixed laboratory–field experiment to look for potential compensatory response under natural conditions. Most of the strong evidence for compensatory growth stems from laboratory or hatchery experiments. In consequence, there are reasonable doubts about the relevance of this phenomenon for wild populations. Second, we carried out a laboratory experiment in order to obtain a data set roughly comparable to the majority of previously published studies. In these experiments, we manipulated food levels to produce a

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divergence between the growth trajectories of experimental and control individuals.

The manipulation of growth trajectories can have implications for other life-history variables that are size related, thus raising the possibility of multiple targets for compensation. In addition to a reduction in growth rates, energy reserves shrink during periods of food shortage (Bull *et al.* 1996; Nicieza & Metcalfe 1997). Both body size and energy reserves can exert a strong influence on fitness (Calow 1977). Hence, the triggering of hyperphagic responses can be a primary response to either restoring minimum energy reserves (the *reserve minimum hypothesis*), or recovering of the growth trajectory (the *growth trajectory hypothesis*). To discriminate between these two hypotheses, and to examine a possible trade-off between allocation to energy reserves and skeletal growth, we examined the growth trajectories for length and mass, and the changes in size-independent body mass, a measure of condition. A convergence of length trajectories would support the growth trajectory hypothesis, whereas no convergence for both mass and length would suggest absence of compensation. A pattern of growth trajectories converging for mass, but parallel for length, would support the reserve minimum hypothesis. Specifically, we address three questions. (i) Do juvenile brown trout restore growth trajectories after a period of growth depression? (ii) During the recovery phase, is there a readjustment of body condition? And (iii) to what extent do the compensatory responses observed under laboratory conditions reflect the potential for compensation in natural situations? We present empirical work demonstrating that a period of nutritional stress can cause an increase in mass growth unconnected to the recovery of structural growth trajectories.

2. MATERIAL AND METHODS

(a) *Field experiment*

The materials for the field experiment were 1500 brown trout eggs obtained by single crosses of five females and five males caught by electrofishing in the River Porcia (43°27' N, 06°55' W). This is a small coastal stream (drainage area 132 km², main channel length ~22 km) draining to the Cantabrian Sea. The eggs were incubated at the laboratory at 9.0 ± 0.1 °C. One month after hatching, fish were reared in 10 L cages placed inside 120 L containers filled with dechlorinated water at 15.9 ± 0.1 °C. Fish were fed *ad libitum* on frozen chironomid larvae (MBF Bvba, Essen, Belgium) and dry pellets (Trouvit, Trouw España SA; energy content according to manufacturer: 17.66 kJ g⁻¹).

On 11 December 2001 (day 0), 142 one year old brown trout were randomly allocated to two 80 L tanks (71 fish per tank). The temperature was set at 15.9 ± 0.1 °C. Fish were anaesthetized (benzocaine, 60 mg L⁻¹), measured for length (±0.01 mm) and wet mass (±0.01 g), and individually marked by using spots of Alcian blue in 1–4 fin locations (see Herbing *et al.* 1990). In one tank, the amount of food (Trouvit) provided was restricted according to Elliott's (1976) equations to maintain growth at 10% of the maximum rate. The second group was used as control and fed *ad libitum*. At day 38, control and food-restricted fish were starved for 48 h, and then measured for length and mass prior to release into the River Porcia. On 23 January 2002 (day 43), the fish

were released in a 200 m section of the river with an average width of 1.2–1.5 m and maximum depth of 40 cm. Electro-fishing was done on 15 March 2002 (day 94), and the recaptured fish were measured and weighed. Over the study period (23 January–15 March), water temperatures in the River Porcia fluctuated between 7.8 and 11.2 °C (mean ± 1 s.d.: 9.43 ± 0.57).

(b) *Laboratory experiment*

The experimental animals were the offspring of six pairs of second-generation hatchery brown trout collected in the Celadilla del Río hatchery. This strain originated from wild trout caught in the upper River Carrión (42°56' N, 04°39' W). We collected a sample of 300 fertilized eggs from each of six single male–female crosses. Experimental conditions during incubation and rearing were the same as for the field experiment.

On 18 June 2003 (day 0), we held 60 fish (age 0+) individually in flasks of 9.7 cm diameter and 14.5 cm height fitted with mesh windows. The fish were anaesthetized and measured for length (±0.01 mm) and wet mass (±0.01 g). Thirty fish were assigned to the restricted-food treatment and 30 to the control group. The flasks were randomly allocated inside a 240 L recirculating system with continuous biological filtration. Every week, a water amount equivalent to one-third of the total water volume was removed and replaced with dechlorinated tap water. Water temperature was set at 15.9 ± 0.1 °C. Air pumps were used to ensure oxygen saturation and thermal homogeneity. In addition, the position of each flask was randomly reassigned every week to minimize the risk of spatial effects. Maintenance rations were calculated as in the former experiment. Controls were fed *ad libitum* three times a day. Every 2 days, the flasks were cleaned and faeces removed. Growth manipulation was imposed for 16 days, and during this period the fish were measured and weighed on two occasions (days 9 and 16). Thereafter, all the fish were fed *ad libitum* three times a day. Growth was monitored on days 23 and 36. All measurements were done following a 24 h starvation period.

At the end of the experiment, the fish were starved for 72 h and then killed by an overdose of benzocaine (225 mg L⁻¹). Total non-polar lipids were determined by Soxhlet extraction of dried samples using petroleum ether. After six washing cycles, the samples were dried, and the lipid content was calculated as the difference between total dry mass and lean dry mass.

(c) *Statistical analysis*

We used MANOVA to test for overall differences in body length and mass at each sampling time. Differences in growth rates during the 'compensation' phase (after introduction to the river, or resumption of *ad libitum* rations) were evaluated by ANCOVA of the size-increments (mass or length) during a given interval, using size (mass or length) at the start of that interval as a covariate. In addition, the growth trajectories of control and food-restricted fish were compared by repeated-measures ANOVA. Ration level was a between-subjects factor, and the repeated measures of length or mass at different times was a within-subjects factor. This approach has the advantage of the simultaneous testing of three hypotheses; a significant interaction between ration and time would indicate differences in the slopes of the growth trajectories, whereas in the absence of an interaction,

significant effects of ration and time would reveal consistent size differences and growth, respectively.

Next we wanted to evaluate the differences in physiological condition between deprived and control fish. We used ANCOVA of body mass adjusted for body length to check for changes in the relative values of mass and length. This circumvents the statistical problems associated with the use of ratios (Packard & Boardman 1987). Finally, we compared size-adjusted lipid content at the end of the experiment using dry lean mass as a covariate.

All the analyses of covariance were conducted after verification of the assumption of homogeneity of regression slopes. The assumptions of homogeneity of variances (ANOVA), and homogeneity of deviations from individual regressions (ANCOVA) were checked with the Cochran C-test (Underwood 1997). Box's *M* statistic was used to test for the homogeneity of dispersion matrices (MANOVA). Length and mass data were transformed to their natural logarithms in order to meet the assumptions of parametric analysis. Analyses were performed using SPSS v. 11.5 (SPSS, Inc., Chicago, IL).

3. RESULTS

(a) *Growth compensation in the wild*

Juvenile brown trout allocated to the control and treatment groups were similar in size (MANOVA; Wilk's $\lambda = 0.98$, $F_{2,110} = 0.76$, $p = 0.47$). There was no association between food levels and mortality rates (control: 15.7%; restricted-food: 22.5%; $\chi^2 = 1.06$, d.f. = 1, $p = 0.303$). Ration size had an important effect on juvenile size at the end of the manipulation period in laboratory tanks. On average, food-restricted brown trout had growth rates close to zero (figure 1). As expected, growth manipulation had a clear effect on body condition. Differences in mass adjusted for length were negligible at day 0, but clear after 38 days of food restriction (figure 1c).

On 15 March (51 days after release into the river), we recaptured 16 (27.1%) and 19 (34.5%) fish from the control and the food-restricted groups, respectively. Recapture rates were not significantly different ($\chi^2 = 0.74$, d.f. = 1, $p = 0.39$). We found no evidence of differences in growth. Size differences were clear at release (MANOVA; Wilk's $\lambda = 0.44$, $F_{2,32} = 20.26$, $p < 0.0001$) and persisted at recapture (Wilk's $\lambda = 0.81$, $F_{2,32} = 3.79$, $p = 0.033$). Separate ANOVAs indicated that these differences were retained for both length ($F_{1,33} = 7.66$, $p = 0.0092$) and mass ($F_{1,33} = 7.76$, $p = 0.0088$). In fact, length increments adjusted for mean initial length did not differ between control and food-restricted individuals (ANCOVA; $F_{1,32} = 0.27$, $p = 0.61$). However, food-restricted animals gained mass at a faster rate than controls (ANCOVA; $F_{1,32} = 4.51$, $p = 0.041$). The analysis of growth trajectories confirmed these results: a repeated-measures ANOVA showed significant effects of ration and time of sampling (release versus recapture) on length, but the length trajectories were statistically parallel (figure 1a; table 1). Likewise, food level and time had an effect on mass, but in this case there was a significant interaction (table 1) indicating convergence of the mass trajectories (figure 1b).

The unequal effect of previous food restriction on the growth trajectories for mass and length was related to

Figure 1. Growth trajectories for (a) length, (b) mass and (c) changes in length-adjusted masses of food-restricted (open circles) and control (filled circles) trout recaptured 51 days after introduction into the River Porcía. 'Manipulation' and 'recovery' periods correspond to the time of growth manipulation in the laboratory and the time of growth in the river, respectively. Data are least-squares means ($\pm$ s.e.m.) obtained from ANCOVA.

changes in body condition. At the time of release, controls had length-adjusted masses significantly higher than those of food-restricted fish (ANCOVA for recaptured individuals; $F_{1,32} = 23.83$, $p < 0.0001$), but after 51 days these differences were negligible ($F_{1,32} = 0.13$, $p = 0.73$; figure 1c).

(b) *Growth compensation under laboratory conditions*

At the start of the experiment, there were no differences in overall size between controls and food-restricted fish (MANOVA; Wilk's $\lambda = 0.97$; $F_{2,53} = 0.92$, $p = 0.40$). After 9 days, controls were larger than food-restricted fish (Wilk's $\lambda = 0.82$; $F_{2,53} = 5.88$, $p = 0.0049$). By the end of the manipulation (day 16), there was a significant divergence between controls and food-deprived fish (Wilk's $\lambda = 0.50$; $F_{2,53} = 27.02$, $p < 0.0001$; figure 2), the effect of ration size being significant for both length ($F_{1,54} = 9.59$, $p = 0.0031$) and mass ($F_{1,54} = 21.83$, $p < 0.0001$). Food restriction had a rapid effect on condition. The length-adjusted masses of the two groups, indistinguishable at day 0 (ANCOVA; $F_{1,53} = 1.58$, $p = 2.14$), were markedly different by day 9 ($F_{1,53} = 10.18$, $p = 0.0024$). This divergence continued up to

Table 1. Results of repeated-measures ANOVA testing for effects of ration (days 1–38) and time (repeated measures on days 41 and 94) on the size of juvenile brown trout released in the River Porcía.

variable	sources	SS	d.f.	F-value	p
<i>between subjects</i>					
length	ration	0.252	1	8.91	0.0053
	error	0.935	33		
mass	ration	3.532	1	11.75	0.0016
	error	9.917	33		
<i>within subjects</i>					
length	time	0.089	1	139.30	<0.0001
	time × ration	0.001	1	1.22	0.2778
	error	0.021	33		
mass	time	1.351	1	170.09	<0.0001
	time × ration	0.100	1	12.55	0.0012
	error	0.262	33

Figure 2. Growth trajectories for (a) length, (b) mass and (c) changes in length-adjusted masses of age 0+ trout that were raised individually, and either exposed to a period of food-restriction (open circles) or maintained as a control group (filled circles). 'Manipulation' and 'recovery' periods correspond to the time of growth manipulation and growth after resumption of *ad libitum* rations, respectively. Apart from food supply, experimental conditions were kept constant over the 'manipulation' (days 1–16) and 'recovery' (days 17–36) periods. Data shown are least-squares means ($\pm$ s.e.m.).

the end of the manipulation ($F_{1,53}=37.89$, $p<0.0001$; figure 2).

Size differences persisted for 7 days after having switched the food-restricted group to *ad libitum* rations

(MANOVA; Wilk's $\lambda=0.86$; $F_{2,53}=4.36$, $p=0.018$); controls were larger ($F_{1,54}=8.81$, $p=0.0044$) and heavier ($F_{1,54}=8.78$, $p=0.0045$) than food-restricted fish (figure 2). During this period (days 17–23), adjusted length increments of controls and food-restricted fish were similar (ANCOVA; $F_{1,53}=0.04$, $p=0.83$). By day 16, the size of food-restricted fish was similar to the size of controls on day 9 (figure 2). An ANOVA on the absolute growth rates in length of controls during days 9–16 and food-restricted fish during days 16–23 confirmed the lack of compensatory growth ($F_{1,54}=0.93$, $p=0.34$). In contrast, food restriction had a delayed effect on mass increases adjusted for initial mass ($F_{1,53}=16.39$, $p<0.0002$). Differential growth allocation by the food-restricted fish achieved a recovery to the condition shown by controls; length-adjusted masses of both groups were indistinguishable after 7 days of *ad libitum* rations (ANCOVA; $F_{1,53}=0.07$, $p=0.80$; figure 2c). Moreover, a comparison of the mass increments of controls during days 9–16 and food-restricted fish during days 16–23 indicated that, for fish of similar size, there was no compensation in mass (ANOVA; $F_{1,54}=0.02$, $p=0.88$).

By day 36, food-restricted brown trout were still smaller than controls (length: $F_{1,54}=4.32$, $p=0.042$; mass: $F_{1,54}=4.73$, $p=0.034$; lean dry mass: $F_{1,54}=4.99$, $p=0.003$). During the last period (days 24–36), we found no significant differences between control and food-restricted trout in growth in length (ANCOVA; $F_{1,53}=2.16$, $p=0.15$) or growth in mass (ANCOVA; $F_{1,53}=1.32$, $p=0.25$). Nor did we find differences in body condition between the two groups of fish (ANCOVA; $F_{1,53}=0.41$, $p=0.52$). At the end of the experiment, size-adjusted lipid content did not differ between food-restricted and control fish (ANCOVA; $F_{1,53}=0.79$, $p=0.38$). The slopes of the regressions of lipid content on lean dry mass were not significantly different (ANCOVA; $F_{1,52}=2.45$, $p=0.12$). Lean dry mass adjusted for length did not differ between groups (ANCOVA; $F_{1,53}=0.75$, $p=0.39$). There were no differences in the regressions of lean dry mass on length for control and food-restricted fish (ANCOVA for slopes; $F_{1,52}=0.02$, $p=0.89$; figure 3).

These results were confirmed by the analysis of growth trajectories. During the compensatory phase (days 17–36), there were significant effects of ration and time on length, but not a significant ration × time interaction

Figure 3. Relationship between lean dry mass and length at the end of the 'recovery' phase for food-restricted and control trout that were raised individually.

(table 2), indicating that there was no convergence of the length trajectories (figure 2a). In contrast, there was a significant interaction between ration and time for mass (table 2). Separate analyses conducted on each period revealed a strong interaction between ration and time for the first period (days 17–23; $F_{1,54} = 26.07$, $p < 0.0001$) but not for the second (days 24–36; $F_{1,54} = 0.30$, $p = 0.59$). Thus, the convergence of mass trajectories ceased as soon as food-restricted fish achieved the mass-at-size of controls (figure 2b,c), thus indicating that there was no true compensatory growth but rather the regulation of allocation between overall mass and structural growth.

4. DISCUSSION

The analysis of body condition and growth trajectories, and the comparison of lipid levels and lean dry mass, provided support for the reserve minimum hypothesis. Our data showed unequivocally that (i) juvenile brown trout do not compensate for lost structural growth, (ii) food-restricted fish are able to reinstate their body condition rapidly after the resumption of *ad libitum* food, and (iii) partial recovery for body mass was associated with the readjustment of an energetic state. The last point was corroborated by the observation that size-adjusted dry mass did not differ between experimental groups at the end of the recovery phase. This allows us to discard the possibility that the rapid recovery of mass-at-length in the compensating group could be due to a rapid influx of body water rather than storage. Stream and laboratory fish produced an identical outcome, suggesting that laboratory studies can provide a reliable approximation of the potential for compensation in natural situations. The failure to demonstrate a compensation of structural (length) growth in the river fish might be interpreted as an indication of food shortages. In that case, the fish would not be able to grow at the high rates required to produce a compensatory response. However, there are several indications that the conditions experienced by the fish in the River Porcia were not so restrictive as to preclude compensatory growth. First, despite the relatively slow growth of the fish in the river compared to the laboratory,

highly significant effects of time of sampling (release versus recapture) on length and mass evidenced substantial growth in the wild. Second, juvenile brown trout were able to readjust their length-corrected masses, which indicates that environmental conditions were not harsh enough to prevent growth compensation. Third, in the laboratory, fish did not compensate for growth in length despite being fed *ad libitum* rations. Finally, the lowering of growth rates after release into the river might be unrelated to food shortage, but caused by the lower temperatures in the river during the recovery period. In fact, during the electrofishing operations, we observed large numbers of macroinvertebrates emerging from the river substratum.

The significance of these results is twofold. First, they provide strong evidence that previous studies reporting partial compensatory growth from mass data only could contribute to an overestimation of the occurrence of structural or skeletal compensatory growth (as opposed to a readjustment of the mass/size allometry). From this, it follows that structural compensatory growth could be less widespread than previously thought (Nicieza & Álvarez, unpublished manuscript). Second, our results point out that the evolutionary aspects of compensatory growth should not be set apart from the species life history. In fact, repeated failures to find evidence of compensatory growth in the brown trout contrast with a well-proven compensatory pattern in closely related species (Ali *et al.* 2003).

Food-restricted trout restored their body condition in less than 7 days, thus showing a potential for compensation. Rapid readjustments of mass-at-size and the replenishment of fat stores after a period of food restriction are not uncommon as a result of increased feeding rates (Metcalf & Thorpe 1992; Nicieza & Metcalfe 1997; Schultz *et al.* 2002). This reaction may reflect a generalized mechanism of energy 'insurance' against the risk of mortality associated with acute nutritional stress (Calow 1977; Bull *et al.* 1996; Schultz *et al.* 1998). In the Atlantic salmon, full readjustment of condition can take less than one week, but these changes can be accompanied by compensatory structural growth (Nicieza & Metcalfe 1997; Metcalfe *et al.* 2002). The cessation of the

Table 2. Results of repeated-measures ANOVA testing for effects of ration (days 1–16) and time (repeated measures on days 16, 23 and 36) on the size of trout raised individually in laboratory cages. (All the fish were fed *ad libitum* after day 16. Hence, the analysis is for the delayed effects of ration level.)

variable	sources	SS	d.f.	F-value	p
<i>between subjects</i>					
length	ration	0.146	1	7.68	0.0076
	error	1.030	54		
mass	ration	2.252	1	10.86	0.0017
	error	11.194	54		
variable	sources	Wilks' λ	d.f.	F-value	p
<i>within subjects</i>					
length	time	0.135	2, 53	169.27	<0.0001
	time $\times$ ration	0.979	2, 53	0.56	0.5737
mass	time	0.144	2, 53	156.96	<0.0001
	time $\times$ ration	0.641	2, 53	14.81	<0.0001

convergence of mass trajectories as soon as food-restricted fish recovered the control condition and the parallelism of the asynchronous mass trajectories (controls days 9–16 versus food-restricted days 16–23) indicate a clear-cut division of the processes of allocation to reserves and structural growth (Broekhuizen *et al.* 1994).

If growth depression can trigger a hyperphagic response causing a rapid recovery of body condition, why do juvenile brown trout not show compensation for lost structural growth? This point is especially puzzling because compensatory growth has been reported for several salmonids (see Ali *et al.* 2003). However, in most cases what has been shown was partial (but not full) compensation in mass growth (e.g. Miglavs & Jobling 1989; Jobling *et al.* 1993). Although mass compensation can reflect a higher rate of structural growth (Nicieza & Metcalfe 1997), here we have shown that mass may not be a reliable indicator of structural compensatory growth when the compensation is partial (see also Schultz *et al.* 2002). Unfortunately, only a few studies have examined the length dynamics of juvenile salmonids, and their results were diverse. While there is unequivocal evidence for the compensation of skeletal growth (Nicieza & Metcalfe 1997; Maclean & Metcalfe 2001), in some instances the hyperphagic response ceased as soon as lipid levels were restored (Morgan & Metcalfe 2001).

Interspecific variation in the capacity for compensatory growth can be related to differences in selection pressures associated with characteristics of the life cycle (Sogard & Olla 2002). Rapid growth evolves when there is a need to achieve a minimum size in a limited time (Ludwig & Rowe 1990; Arendt 1997). In the Atlantic salmon, seaward migration is preceded by physiological and morphological changes restricted to a narrow time-window in spring. The transformation occurs only if a threshold size is reached, and fish failing to achieve this threshold prior to the time-window defer migration until the next spring (Thorpe 1977; Nicieza *et al.* 1991). Time constraints must be much weaker for the brown trout because of the greater diversity of life histories and flexibility in migration time (Klemetsen *et al.* 2003). Therefore, priority of allocation to mass-at-size recovery instead of skeletal

growth may be related to the relaxation of time constraints. Strikingly, salmon data support this idea. Studies based on deferred migrants found no compensation of structural growth (Morgan & Metcalfe 2001), weak compensation (Nicieza & Metcalfe 1997), or delayed compensation (Maclean & Metcalfe 2001; Metcalfe *et al.* 2002). In contrast, early migrants showed a clear pattern of full compensation during the autumn and winter preceding the first time-window (Nicieza & Metcalfe 1997). In the brown trout, compensatory growth (in mass) was observed in an anadromous strain (Pirhonen & Forsman 1999), which provides additional support for a link between growth compensation and the existence of size-thresholds for seaward migration.

In conclusion, the results of this study demonstrate a compensatory response in juvenile brown trout following nutritional stress. However, this response was associated with the restoration of a particular mass: length allometry and energy reserves, but unrelated to the recovery of 'lost' skeletal growth. The recovery of condition in both experiments indicates that in brown trout, the priority following a period of resource shortage is allocation to condition as opposed to compensation for lost growth opportunities. These findings suggest a clear-cut division of the allocation to reserves and skeletal growth, and hence provide empirical support for growth models based on the maintenance of an ideal reserve/structure allometry (e.g. Broekhuizen *et al.* 1994; Jones *et al.* 2002). Therefore, present data support the idea of a lipostatic regulation of allocation between investments in overall mass and structural growth, but not a lipostatic regulation of compensatory growth. The absence of compensation for structural growth cannot be attributed to an interference effect of the readjustment of body condition: this finished within one week and thereafter there was no compensation at all. Hence, it seems that in brown trout the fitness costs of rapid growth outweigh those of lost structural growth, presumably because of the relaxation of temporal constraints. This stresses the importance of selecting the right dimension to evaluate growth; mass can provide an unreliable estimate of skeletal growth

because, after nutritional stress, reserve and structural tissues contribute to growth in mass.

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REFERENCES

- Ali, M., Nicieza, A. & Wootton, R. J. 2003 Compensatory growth in fishes: a response to growth depression. *Fish Fish.* **4**, 147–190.
- Arendt, J. D. 1997 Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.* **72**, 149–177.
- Broekhuizen, N., Gurney, W. S. C., Jones, A. & Bryant, A. D. 1994 Modelling compensatory growth. *Funct. Ecol.* **8**, 770–782.
- Bull, C. D., Metcalfe, N. B. & Mangel, M. 1996 Seasonal matching of foraging effort to anticipated energy requirements in anorexic juvenile salmon. *Proc. R. Soc. B* **263**, 13–18.
- Calow, P. 1977 Ecology, evolution and energetics: a study in metabolic adaptation. *Adv. Ecol. Res.* **10**, 1–62.
- Elliott, J. M. 1976 Energy losses in the waste products of brown trout (*Salmo trutta* L.). *J. Anim. Ecol.* **45**, 561–580.
- Fleming, I. A. & Gross, M. R. 1994 Breeding competition in a Pacific salmon (Coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* **48**, 637–657.
- Herbinger, C. M., Newkirk, G. F. & Lanes, S. T. 1990 Individual marking of Atlantic salmon: evaluation of cold branding and jet injection of Alcian Blue in several fin locations. *J. Fish Biol.* **36**, 99–101.
- Hutchings, J. A. 1994 Age- and size-specific costs of reproduction within populations of brook trout, *Salvelinus fontinalis*. *Oikos* **70**, 12–20.
- Jobling, M. 1994 *Fish bioenergetics*. London: Chapman & Hall.
- Jobling, M., Jørgensen, E. H. & Siikavuopio, S. I. 1993 The influence of previous feeding regime on the compensatory growth response of maturing and immature Arctic charr, *Salvelinus alpinus*. *J. Fish Biol.* **43**, 409–419.
- Jones, W., Gurney, W. S. C., Speirs, D. C., Bacon, P. J. & Youngson, A. F. 2002 Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon. *J. Anim. Ecol.* **71**, 916–924.
- Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F. & Mortensen, E. 2003 Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol. Freshw. Fish* **12**, 1–59.
- Ludwig, D. & Rowe, L. 1990 Life-history strategies for energy gain and predator avoidance under time constraints. *Am. Nat.* **135**, 686–707.
- Maclean, A. & Metcalfe, N. B. 2001 Social status, access to food and compensatory growth in juvenile Atlantic salmon. *J. Fish Biol.* **58**, 1331–1346.
- Metcalfe, N. B. & Monaghan, P. 2001 Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**, 254–260.
- Metcalfe, N. B. & Thorpe, J. E. 1992 Anorexia and defended energy levels in over-wintering juvenile salmon. *J. Anim. Ecol.* **61**, 175–181.
- Metcalfe, N. B., Bull, C. D. & Mangel, M. 2002 Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon. *Evol. Ecol. Res.* **4**, 871–881.
- Miglav, I. & Jobling, M. 1989 The effect of feeding regime on proximate body composition and patterns of energy deposition in juvenile Arctic charr, *Salvelinus alpinus*. *J. Fish Biol.* **35**, 1–11.
- Morgan, I. J. & Metcalfe, N. B. 2001 Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. *Proc. R. Soc. B* **268**, 295–301.
- Nicieza, A. G. & Metcalfe, N. B. 1997 Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. *Ecology* **78**, 2385–2400.
- Nicieza, A. G., Braña, F. & Toledo, M. M. 1991 Development of length-bimodality and smolting in wild stocks of Atlantic salmon, *Salmo salar* L., under different growth conditions. *J. Fish Biol.* **38**, 509–523.
- Packard, G. C. & Boardman, T. J. 1987 The misuse of ratios to scale physiological data that vary allometrically with body size. In *New directions in ecological physiology* (ed. M. E. Feder, A. F. Bennett, W. W. Burggren & R. B. Huey), pp. 216–239. Cambridge University Press.
- Pirhonen, J. & Forsman, L. 1998 Effect of prolonged feed restriction on size variation, feed consumption, body composition, growth and smolting of brown trout, *Salmo trutta*. *Aquaculture* **162**, 203–217.
- Pirhonen, J. & Forsman, L. 1999 Can smolting and maturation of hatchery-reared brown trout *Salmo trutta* L. be affected by food deprivation during the first and second years of rearing? *Aquac. Res.* **30**, 611–620.
- Ricklefs, R. E., Shea, R. E. & Choi, I. 1994 Inverse relationship between functional maturity and exponential growth rate of avian skeletal muscle: a constraint on evolutionary response. *Evolution* **48**, 1080–1088.
- Roff, D. A. 1992 *The evolution of life histories: theory and analysis*. New York: Chapman & Hall.
- Schultz, E. T., Conover, D. O. & Ehtisham, A. 1998 The dead of winter: size-dependent variation and genetic differences in seasonal mortality among Atlantic silverside (Atherinidae: *Menidia menidia*) from different latitudes. *Can. J. Fish. Aquat. Sci.* **55**, 1149–1157.
- Schultz, E. T., Lankford, T. E. & Conover, D. O. 2002 The covariance of routine and compensatory juvenile growth rates over a seasonality gradient in a coastal fish. *Oecologia* **133**, 501–509.
- Sogard, S. M. & Olla, B. L. 2002 Contrasts in the capacity and underlying mechanisms for compensatory growth in two pelagic marine fishes. *Mar. Ecol. Progr. Ser.* **243**, 165–177.
- Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.
- Thorpe, J. E. 1977 Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *J. Fish Biol.* **11**, 175–184.
- Underwood, A. J. 1997 *Experiments in ecology—their logical design and interpretation using analysis of variance*. Cambridge University Press.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.