

Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon

Neil B. Metcalfe,¹ Colin D. Bull¹‡ and Marc Mangel^{2*}

¹*Fish Biology Group, Division of Environmental and Evolutionary Biology, Graham Kerr Building, Institute of Biomedical and Life Sciences, University of Glasgow, Glasgow G12 8QQ, UK and*

²*Department of Applied Mathematics and Statistics, Jack Baskin School of Engineering, University of California, Santa Cruz, CA 95064, USA*

ABSTRACT

The trade-off in the allocation of resources between skeletal growth and the storage of reserves has received little attention, despite relevance to all growing organisms. We explored this trade-off by manipulating food availability for juvenile Atlantic salmon, *Salmo salar*, so as to create the same reduction in growth and loss of energy reserves at different times of the year. The fish showed seasonal differences in their responses to the nutritional deficit when food was restored. In winter, fish restored lipid reserves, but their growth in length over the recovery period was negligible. In summer, fish allocated resources to growth in length as well as the restoration of lipid reserves; moreover, this skeletal growth was significantly faster than that of control fish that had received food *ad libitum* throughout. We demonstrate that current physiological and energetic models of animal growth cannot account for such seasonal variation in compensatory growth and allocation patterns, and the regulation of growth and energy reserves is a dynamic and state-dependent process. We then predict – on the basis of expected effects on fitness – how somatic allocation and catch-up growth should vary over time and in contrasting environments.

Keywords: Atlantic salmon, body size, fat reserves, growth, *Salmo salar*.

INTRODUCTION

Resource allocation is most often studied as the trade-off between gonads and soma. Observed patterns in this case are complex and depend on factors such as the effect of body size on mortality and reproductive success (Vance, 1992; Perrin and Sibly, 1993; Gurney and Middleton, 1996). A more neglected allocation process, but one that is equally important, is the partitioning of resources between somatic growth, in terms of increase in skeletal size, and the deposition of easily mobilized nutritional reserves. Investment in growth may lead

* Author to whom all correspondence should be addressed. e-mail: msmangel@cats.ucsc.edu

‡ Present address: Forth Fisheries Foundation, Institute of Aquaculture, University of Stirling, Stirling FK9 4LA, UK.

Consult the copyright statement on the inside front cover for non-commercial copying policies.

to benefits of increased future reproductive success and survival, but organisms generally maintain a minimum investment in reserves to prevent starvation and survive periods of adversity (Tveiten *et al.*, 1996) or for production of gonads at a later date (Reznick and Yang, 1993; Doughty and Shine, 1998). Therefore, there is a trade-off between growth and energetic reserves that may vary with the harshness of the environmental conditions (Lesage *et al.*, 2001; Post and Parkinson, 2001).

Many species experience natural fluctuations in rates of food intake, and periods of food shortage or interrupted foraging lead to decreases in growth rate and depletion of energy stores. When food availability subsequently improves, animals usually respond by displaying increased consumption and growth rates, typically referred to as compensatory or catch-up growth (Weatherley and Gill, 1981; Ashworth, 1986; Schew and Ricklefs, 1998). The pattern of compensation is variable, with catch-up growth sometimes being restricted to restoration of lost reserves (Miglav and Jobling, 1989), whereas in other circumstances growth rates are elevated to the extent that the animal recovers body size in terms of length and/or mass (Hayward *et al.*, 1997; Nieceza and Metcalfe, 1997). There are at least three alternative hypotheses to explain this diversity in compensatory response:

1. *Nutritional state hypothesis*: there is a fixed response to a given nutritional deficit, independent of season (Broekhuizen *et al.*, 1994).
2. *Physiological constraint hypothesis*: the environment imposes physiological constraints on performance so that contrasting compensatory responses occur in different seasons or under different environmental conditions. For instance, the extent to which growth rate can be enhanced may be temperature-dependent (P. Abrams, personal communication).
3. *Facultative response hypothesis*: animals have evolved compensatory responses that maximize their long-term fitness, and the response therefore varies according to the life stage and nutritional state of the organism and the time of year, in a facultative manner (*sensu* Clark and Mangel, 2000).

We allow these hypotheses to compete by presenting novel data on the contrasting resource allocation patterns of juvenile Atlantic salmon, *Salmo salar*, subjected to the same experimental reduction in nutritional reserves in summer and in winter. The nutritional state hypothesis would predict a similar response in both seasons, whereas the other two hypotheses would predict seasonally dependent responses. However, in the case of the physiological constraint hypothesis, this seasonal effect would arise because the fish were incapable of exhibiting the same resource allocation in the two seasons, while the facultative response hypothesis would predict that this allocation was flexible. The data are inconsistent with the first two hypotheses, thus demonstrating that somatic allocation is a dynamic, state-dependent process. This allows novel general predictions of the patterns of allocation and growth compensation to be expected in contrasting environments.

METHODS

Experiments were conducted in summer (July to September 1995) and winter (October 1994 to January 1995). Fish were underyearling full-sib offspring of sea-run adults caught in the River Almond, Perthshire, UK. They were reared on commercial pelleted salmon food provided to excess by automatic feeders dispensing a trickle of food every 20 min, and were

kept in conditions of ambient photoperiod and temperature at the University Field Station, Loch Lomond, both before and during the experiments.

We used a non-destructive method of estimating the lipid content of experimental fish from morphometric measurements, as has been used successfully in other studies (Simpson *et al.*, 1992; Adams *et al.*, 1995; Bull *et al.*, 1996), since it was essential to monitor changes in lipid content over time in individual fish. This method is based on relationships between morphometric measurements and body fat content, as determined in separate samples of fish that are subjected to a range of morphometric measurements before being killed to allow determination of whole body lipid content using solvent extraction (Simpson *et al.*, 1992). Fat content is reported as either the percentage of body mass (%*F*) or the mass of fat (*F*) per fish, depending on the analysis (e.g. percentages are used when comparing fish of different sizes, whereas mass of fat is used when calculating the changes in fat reserves within the same fish over time). For the summer experiment, the calibration equation to predict fat was based on 28 fish sampled on 20 July from the same stock population and selected to cover a broad size distribution. Half of these fish had been deprived of food over the preceding 2 weeks to generate a wide range of lipid levels. The range of body sizes and fat (as a percentage of body wet weight) was similar between these calibration fish (33–58 mm fork length, 0.4–5.4% fat) and the experimental fish in the summer experiment (30–70 mm, estimated 0–5.6% fat). Percentage fat in the calibration fish was best predicted by a combination of fork length (*l*), body mass (*m*) and body widths at the leading edges of the dorsal (*w_d*), pelvic (*w_p*) and anal fins (*w_a*) (all body widths being measured to the nearest 0.1 mm and standardized for body length; Simpson *et al.*, 1992):

$$\%F = 0.455l - 5.34m + 1.791w_d + 3.589w_p - 4.699w_a - 16.422 \quad (1)$$

$$(r^2 = 0.726, n = 28, P < 0.001)$$

A separate sample of 55 fish from the stock population was used to produce a calibration equation for the winter experiment, since there appear to be seasonal changes in body proportions (Simpson *et al.*, 1992). These fish were sampled on 27 November (*n* = 35) and 17 January (*n* = 20), with approximately half of the fish having previously been subjected to 3 weeks of food deprivation to broaden the distribution of fat levels. Again there was a good overlap between the size and fat ranges of these calibration fish and the corresponding ranges for fish subsequently used in the winter experiment (calibration fish: length = 49–74 mm, fat = 1.6–7.2%; experimental fish: length = 55–71 mm, estimated fat = 0–7.6%). The equation that best predicted total body fat in winter was:

$$F = 0.09776m - 0.00413l + 6.11w_d + 10.9w_p - 7.93w_a - 0.125 \quad (2)$$

$$(r^2 = 0.637, n = 55, P < 0.001)$$

At the start of each experiment (summer: 3 July; winter: 19 October), fish (*n* = 40 in summer, 34 in winter) were taken at random from the holding tank and given a unique combination of alcian blue dyemarks to allow individual identification. They were weighed to the nearest 0.1 g and the appropriate morphometric measurements were taken to enable their total lipid content to be estimated. These experimental fish were maintained in a 1 m diameter holding tank and fed to excess. At the start of each manipulation (summer: 12 July; winter: 24 October), half of the fish were randomly allocated to the deprived group and moved to a separate tank where they were deprived of food for a period of time (summer: 30 days; winter: 42 days) that was sufficient to produce a temporary reduction

in body fat (Weatherley and Gill, 1981; Metcalfé and Thorpe, 1992). The duration of the deprivation period differed between seasons so as to achieve approximately the same reduction in percentage body fat (%F) despite different water temperatures (summer: mean = 18.2°C, range 16.4–21.6°C; winter: mean = 8.4°C, range 6.0–9.1°C).

The other half of the fish, maintained on an excess feeding regime, were used as a control group. At the end of the deprivation period (summer: 11 August; winter: 5 December), fish in both treatment groups were weighed and measured for body length and estimation of percent fat. They were then fed to excess on bloodworms, *Chironomidae* spp., and pellets until the end of the experiment approximately 5 weeks later (summer: 13 September; winter: 10 January), when they were re-measured. This 5 week period was chosen, since previous work had indicated that most of the compensatory growth would have occurred by this point (Miglavš and Jobling, 1989; Metcalfé and Thorpe, 1992; Bull *et al.*, 1996).

Juvenile salmon show flexibility in the age at which they undergo the smolt transformation and migrate to sea (Metcalfé and Thorpe, 1990). Fish reared in favourable environments in the UK usually migrate at age 1 or 2 and by their first winter can be reliably classified into smolt groups on the basis of body length (Thorpe, 1977). Since fish in the different smolt age categories exhibit different patterns of growth (Metcalfé *et al.*, 1988), subsequent statistical analyses were restricted to fish that would migrate to sea aged 2 (and so would be resident in fresh water for at least a further year after the end of either experiment) by eliminating two fish that were identified as potential age 1 migrants at the end of the summer experiment. On average, 4 fish died in each deprived group and 3.5 in each control group over the course of the experiment.

Skeletal growth was defined as an increase in body length, and growth rates were calculated as specific growth rates (percent increase per day) in fork length:

$$(100[\ln(L_2) - \ln(L_1)]/(t_2 - t_1))$$

where L_x is the fork length at time t_x . Specific rates of change of body fat reserves (% change in grams of fat per day) were calculated in a similar manner; these were approximately normally distributed. All P -values reported are for two-tailed tests.

RESULTS

There was no difference in the condition, measured as either fork length or estimated fat reserves (expressed as percent of body weight), of the control and deprived fish at the start of the experiments (summer fork length: $t_{23} = 1.46$, n.s.; fat: $t_{23} = 0.11$, n.s.; winter fork length: $t_{24} = 1.16$, n.s.; fat: $t_{29} = 0.52$, n.s.). The period of food deprivation had the desired effect of reducing the fat of the fish used in both experiments to a similar extent (Fig. 1): a two-way analysis of variance (ANOVA) of percent fat at the end of the deprivation period in relation to experiment (winter *vs* summer) and treatment (control *vs* deprived) showed that the effect of treatment was highly significant ($F_{1,50} = 97.20$, $P < 0.001$), but there was no difference between the experiments ($F_{1,50} = 0.32$, $P = 0.57$) and there was no significant experiment by treatment interaction ($F_{1,50} = 0.13$, $P = 0.72$).

The deprived fish were therefore assumed to have similar nutritional reserves at the end of the period of food deprivation in both seasons. They responded by increasing their fat stores over the following 5 weeks, whereas control fish showed a tendency to lose fat over the same period (Fig. 2a). A two-way ANOVA showed that the specific rate of change of fat reserves during the post-deprivation period was influenced by treatment (deprived *vs*

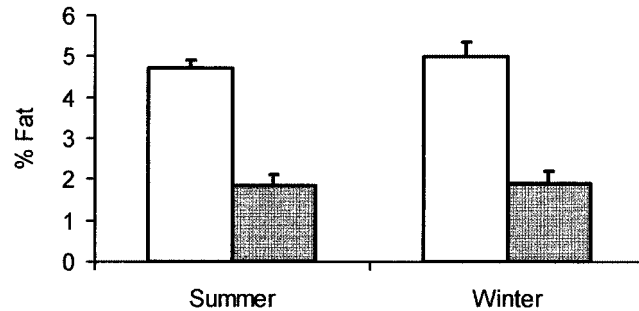


Fig. 1. Fat content of juvenile Atlantic salmon at the end of the period of food manipulation in the summer and winter experiments (mean \pm standard error). White bars = control fish, shaded bars = deprived fish; $n = 11$ – 15 fish per group.

control: $F_{1,50} = 57.30$, $P < 0.001$), but not by season (summer *vs* winter: $F_{1,50} = 0.02$, $P = 0.90$) and there was no interaction between treatment and season ($F_{1,50} = 1.66$, $P = 0.20$). Fish thus appeared to show a similar compensatory response to fat depletion in winter as in summer.

However, their compensatory response in skeletal (length) growth was quite different. In summer, the specific growth rate in fork length of the deprived fish was on average 68% higher than that of controls, indicating a pronounced compensatory response, whereas in winter deprived fish grew no faster than controls (Fig. 2b). An ANOVA of specific growth rates in fork length showed highly significant effects of both season ($F_{1,52} = 568.02$, $P < 0.001$) and treatment ($F_{1,52} = 49.43$, $P < 0.001$). More importantly, the response to the treatment differed between seasons (interaction between season and treatment: $F_{1,52} = 43.92$, $P < 0.001$).

DISCUSSION

The period of food deprivation created the same decline in fat reserves in summer or winter. The nutritional state hypothesis of compensation, exemplified by the model of Broekhuizen *et al.* (1994), would therefore predict that, on being given free access to food again, the fish would make the same relative allocation of resources to reserves and body growth in both seasons. However, while the pattern of fat restoration was almost identical, fish showed completely different responses in terms of skeletal growth, with previously deprived fish in summer exhibiting marked acceleration of length growth rates, whereas in winter they grew in length no faster than controls.

The physiological constraint hypothesis would interpret this as being due to a change in the constraints acting on the animal, the fish being physiologically incapable of increasing their skeletal growth rate in winter, perhaps because of lower temperatures. The low growth rate of both control and experimental fish in winter might initially seem to support this hypothesis. However, this low growth rate is partly a consequence of the life-history strategy that they are adopting (i.e. deferred seaward migration), since fish adopting this strategy have a much suppressed appetite over winter (Metcalf *et al.*, 1986; Metcalf and Thorpe, 1992). In contrast, their siblings that are adopting the alternative strategy of early migration show no appetite suppression in winter (apart from that imposed by decreased temperature) and so grow some 3–5 times faster than deferred migrants under exactly the same environmental conditions (Higgins and Talbot, 1985; Kristinsson *et al.*, 1985; Nicieza *et al.*, 1994).

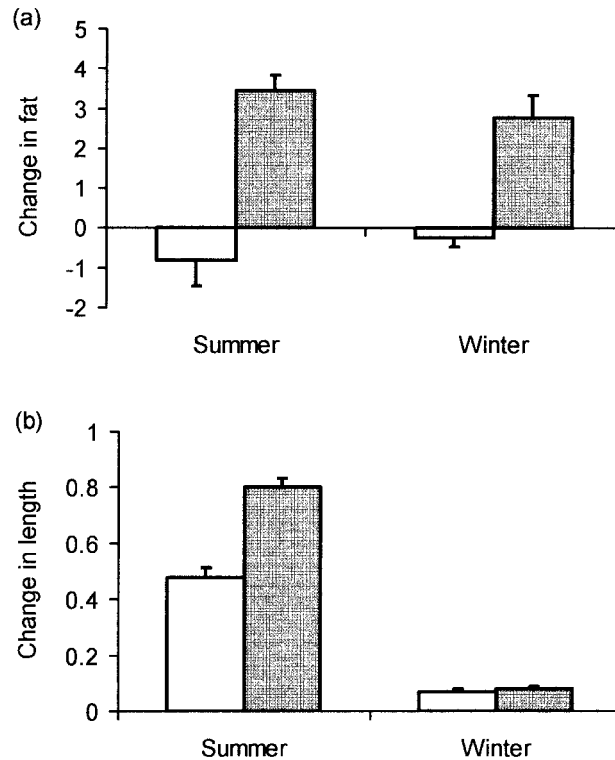


Fig. 2. Daily percentage changes in (a) percent fat and (b) fork length in juvenile Atlantic salmon in the 5 weeks after the period of food manipulation in the summer and winter experiments (mean \pm standard error). White bars = control fish, shaded bars = deprived fish; $n = 11-15$ fish per group.

These differences in appetite and growth are linked to different selection pressures: deferred migrants minimize the risk of predation by reducing foraging activity (Bull *et al.*, 1996), while survival rates in migrants are positively correlated with body size at the time of migration (Lundqvist *et al.*, 1994). Since fish that switch from the deferred to the early migration strategy in mid-winter also change their length growth rate accordingly (Duston and Saunders, 1997), it is unlikely that there is any physiological constraint that would have prevented the previously deprived early migrant fish in the winter experiment from increasing their skeletal growth rate.

This lack of fit between the data and the first two hypotheses suggests that we need to explore the implications of the facultative response hypothesis. Skeletal growth rates are generally maintained at sub-maximal levels (Arendt, 1997), and levels of nutritional reserves are regulated at fixed (Kennedy, 1953; Weigle, 1994) or sliding set-points (Mrosovsky, 1990; Bull *et al.*, 1996). However, previous theories of growth or resource allocation have not considered the relationship between these two processes, leading to mismatches between data and theory. For instance, conventional growth models based on bioenergetics are poor at predicting patterns of compensatory growth (Whitledge *et al.*, 1998). Conversely, the only mathematical model of compensatory growth (Broekhuizen *et al.*, 1994) assumes that compensation is based on the restoration of a target ratio of

energetic reserves to structural tissues, and so cannot explain either why skeletal growth rates may be accelerated in compensating fish, or why such 'catch-up' skeletal growth should continue after depleted energetic reserves have been restored (Xie *et al.*, 2001). Jobling and Johansen (1999) suggested that a feedback system in which appetite was regulated by the ratio of lipid to lean body mass (the lipostat, *sensu* Kennedy, 1953) could still generate differences in skeletal growth rates if the rate of lipid restoration was variable (leading to over- or undershooting compensation). However, this model still cannot explain why animals that are experimentally manipulated, so that they are small for their age or time of year but otherwise well nourished (and hence with normal energy to structural tissue ratios), subsequently show elevated 'catch-up' skeletal growth rates (Mortensen and Damsgård, 1993; Leimar, 1996; Nicieza and Metcalfe, 1997; Gotthard, 1998). Nor can any of the models explain the seasonal variation in response observed in the present study.

The view that allocation is both dynamic and state dependent overcomes these limitations by considering the long-term consequences of both different rates of resource acquisition and patterns of allocation (Clark and Mangel, 2000). A strong qualitative prediction, supported by the experimental results, is that fish experiencing a temporary food shortage in summer should subsequently compensate for 'lost' skeletal growth as well as restore depleted reserves. This relates to the effects of body size on fitness later in the year. In small well-nourished salmonids, the mean and maximum recorded percentage fat values are higher in larger fish (Elliott, 1976; Simpson *et al.*, 1992; Post and Parkinson, 2001), indicating that they are able to store proportionally more reserves. As a result, they tolerate starvation better (Ludsin and DeVries, 1997) and generally end the winter in better condition (Ludsin and DeVries, 1997; Berg and Bremset, 1998). This is probably the most important reason for the widespread finding of body length-dependent overwinter survival of juvenile fish (Smith and Griffith, 1994; Meyer and Griffith, 1997). Therefore, there may be a strong selection pressure for fish to attain a large skeletal size before the onset of winter (so that they can carry more fat; Post and Parkinson, 2001), leading to catch-up growth in individuals that have fallen behind the expected growth trajectory.

Although compensatory growth usually involves an increase in food intake rate, an elevation in skeletal growth rates may still result in reduced resources allocated to other needs. For instance, fast-growing animals have been shown to reduce their rate of protein degradation and, therefore, their investment in body maintenance (Samuels and Baracos, 1995; Morgan *et al.*, 2000). Compensatory growth is also associated with a variety of longer-term costs (Metcalfe and Monaghan, 2001), and salmonids with elevated growth rates have been shown to be more prone to muscle damage (Christiansen *et al.*, 1992), coronary arterial lesions (Saunders *et al.*, 1992) and subsequent reduction in fat deposition and sexual maturation rates (Morgan and Metcalfe, 2001). Compensatory responses can, therefore, be costly and we should only expect to see them when the costs of not compensating are still higher. For example, in the present study, the fish compensated for lost length only in summer. This is likely to be a consequence of two factors. First, food deprivation does not result in as much 'lost growth' in winter as in summer, because delayed migrant salmon are not normally growing much at this time anyway. Second, the predation risk associated with attempting to increase food acquisition rates (Martel and Dill, 1995; Damsgård and Dill, 1998) is higher in winter than summer, due to lower temperatures and levels of food availability. In effect, the fish's pattern of feeding and resource allocation after a period of food shortage is thus likely to be adapted to take account of both (1) the

discrepancy between its current state and that expected for the time of year and (2) the relative cost of restoring any deficit.

Several general predictions emerge from this framework. First, individuals that are skeletally larger or in better nutritional condition should compensate less for any period of poor food availability, regardless of time of year, due to the smaller discrepancy between actual and expected state. Second, the strength of compensatory responses should vary with latitude and altitude (i.e. degree of seasonality). Animals living at high latitudes or altitudes should respond most strongly and rapidly to any temporary periods of food shortage during their brief season of growth, because the relative extent of lost growth and the costs of not having restored lost reserves or body growth by the onset of winter will be higher.

A third prediction is that animals should show a stronger compensatory response the closer they appear to be (as judged by seasonal cues such as photoperiod) to the end of the favourable period for growth. In the case of animals growing in a temperate environment, a period of food shortage in late summer should induce a stronger and more rapid compensation than the equivalent shortage in spring, due to the reduced time available to restore lost reserves and body size before the onset of poorer feeding conditions. This situation is analogous to that faced by animals undergoing a period of growth prior to a seasonally dependent life-history event such as metamorphosis, sexual reproduction or migration, when they must trade off the costs of growth with the subsequent advantages of having attained a greater final body size or nutrient store. Animals born later in the season should grow faster (Abrams *et al.*, 1996), a prediction upheld by work on insect larval growth rates (Leimar, 1996; Gotthard, 1998). However, the model of Abrams *et al.* (1996) does not investigate the potential effects of variation in food supply during the period of growth.

Smith-Gill (1983) distinguished between adaptive phenotypic responses by animals to changes in their environment ('developmental conversion') and environmentally imposed phenotypic variation that did not involve any adaptive flexible response ('phenotypic modulation'). Schew and Ricklefs (1998) noted that it is often difficult to tell which process is at work when changes in food availability affect growth rates – are the observed patterns of growth simply fixed by physiological constraints, or are they an adaptive and flexible response? There is a clear need for an experimental approach such as the one described here to disentangle these explanations.

ACKNOWLEDGEMENTS

The work of N.B.M. was part-funded by a NERC grant, that of C.D.B. by a NERC PhD Studentship and that of M.M. in part by cooperative agreement NA77FL0433 from the National Oceanic and Atmospheric Administration. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. The US Government is authorized to reproduce and distribute for governmental purposes. The work was carried out under a licence from the UK Home Office. We thank V. Cameron for fish maintenance, BOCM Pauls for provision of fish food, and P. Abrams and M. Jobling for helpful comments.

REFERENCES

- Abrams, P.A., Leimar, O., Nylin, S. and Wiklund, C. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *Am. Nat.*, **147**: 381–395.

- Adams, C.E., Huntingford, F.A. and Jobling, M. 1995. A non-destructive morphometric technique for estimation of body and mesenteric lipid in Arctic charr: a case study of its application. *J. Fish Biol.*, **47**: 82–90.
- Arendt, J.D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Q. Rev. Biol.*, **72**: 149–177.
- Ashworth, A. 1986. Catch-up growth in children. *Nutr. Rev.*, **44**: 157–163.
- Berg, O.K. and Bremset, G. 1998. Seasonal changes in the body composition of young riverine Atlantic salmon and brown trout. *J. Fish Biol.*, **52**: 1272–1288.
- Broekhuizen, N., Gurney, W.S.C., Jones, D.E. and Bryant, A.D. 1994. Modelling compensatory growth. *Funct. Ecol.*, **8**: 770–782.
- Bull, C.D., Metcalfe, N.B. and Mangel, M. 1996. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. *Proc. R. Soc. Lond. B*, **263**: 13–18.
- Christiansen, J.S., Martínez, I., Jobling, M. and Amin, A.B. 1992. Rapid somatic growth and muscle damage in a salmonid fish. *BAM*, **2**: 235–239.
- Clark, C.W. and Mangel, M. 2000. *Dynamic State Variable Models in Ecology: Methods and Applications*. New York: Oxford University Press.
- Damsgård, B. and Dill, L.M. 1998. Risk-taking behavior in weight-compensating coho salmon, *Oncorhynchus kisutch*. *Behav. Ecol.*, **9**: 26–32.
- Doughty, P. and Shine, R. 1998. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology*, **79**: 1073–1083.
- Duston, J. and Saunders, R.L. 1997. Life histories of Atlantic salmon altered by winter temperature and summer rearing in fresh- or sea-water. *Env. Biol. Fishes*, **50**: 149–166.
- Elliott, J.M. 1976. Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. *J. Anim. Ecol.*, **45**: 273–289.
- Gotthard, K. 1998. Life history plasticity in the satyrine butterfly *Lasiommata petropolitana*: investigating an adaptive reaction norm. *J. Evol. Biol.*, **11**: 21–39.
- Gurney, W.S.C. and Middleton, D.A.J. 1996. Optimal resource allocation in a randomly varying environment. *Funct. Ecol.*, **10**: 602–612.
- Hayward, R.S., Noltie, D.B. and Wang, N. 1997. Use of compensatory growth to double hybrid sunfish growth rates. *Trans. Am. Fish. Soc.*, **126**: 316–322.
- Higgins, P.J. and Talbot, C. 1985. Growth and feeding in juvenile Atlantic salmon. In *Nutrition and Feeding in Fish* (C.B. Cowey, A.M. Mackie and J.G. Bell, eds), pp. 243–263. London: Academic Press.
- Jobling, M. and Johansen, S.J.S. 1999. The lipostat, hyperphagia and catch-up growth. *Aquacult. Res.*, **30**: 473–478.
- Kennedy, G.C. 1953. The role of depot fat in hypothalamic control of food intake in the rat. *Proc. R. Soc. Lond. B*, **140**: 578–592.
- Kristinsson, J.B., Saunders, R.L. and Wiggs, A.J. 1985. Growth dynamics during the development of bimodal length-frequency distribution in the juvenile Atlantic salmon (*Salmo salar* L.). *Aquaculture*, **45**: 1–20.
- Leimar, O. 1996. Life history plasticity: influence of photoperiod on growth and development in the common blue butterfly. *Oikos*, **76**: 228–234.
- Lesage, L., Crête, M., Huot, J. and Ouellet, J.-P. 2001. Evidence for a trade-off between growth and body reserves in northern white-tailed deer. *Oecologia*, **126**: 30–41.
- Ludsin, S.A. and DeVries, D.R. 1997. First year recruitment of largemouth bass: the interdependency of early life stages. *Ecol. Appl.*, **7**: 1024–1038.
- Lundqvist, H., McKinnell, S., Fångstam, H. and Berglund, I. 1994. The effect of time, size and sex on recapture rates and yield after river releases of *Salmo salar* smolts. *Aquaculture*, **121**: 245–257.
- Martel, G. and Dill, L.M. 1995. Influence of movement by coho salmon (*Oncorhynchus kisutch*) parr on their detection by common mergansers (*Mergus merganser*). *Ethology*, **99**: 139–149.

- Metcalfé, N.B. and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.*, **16**: 254–260.
- Metcalfé, N.B. and Thorpe, J.E. 1990. Determinants of geographical variation in the age of seaward-migrating salmon, *Salmo salar*. *J. Anim. Ecol.*, **59**: 135–145.
- Metcalfé, N.B. and Thorpe, J.E. 1992. Anorexia and defended energy levels in over-wintering juvenile salmon. *J. Anim. Ecol.*, **61**: 175–181.
- Metcalfé, N.B., Huntingford, F.A. and Thorpe, J.E. 1986. Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.*, **64**: 2439–2446.
- Metcalfé, N.B., Huntingford, F.A. and Thorpe, J.E. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. *J. Anim. Ecol.*, **57**: 463–474.
- Meyer, K.A. and Griffith, J.S. 1997. First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. *Can. J. Zool.*, **75**: 59–63.
- Miglav, I. and Jobling, M. 1989. The effects of feeding regime on food consumption, growth rates and tissue nucleic acids in juvenile Arctic charr, *Salvelinus alpinus*, with particular respect to compensatory growth. *J. Fish Biol.*, **34**: 947–957.
- Morgan, I.J. and Metcalfé, N.B. 2001. Deferred costs of catch-up growth after autumnal food shortage in juvenile salmon. *Proc. R. Soc. Lond. B*, **268**: 295–301.
- Morgan, I.J., McCarthy, I.D. and Metcalfé, N.B. 2000. Life-history strategies and protein metabolism in overwintering juvenile Atlantic salmon: growth is enhanced in early migrants through lower protein turnover. *J. Fish Biol.*, **56**: 637–647.
- Mortensen, A. and Damsgård, B. 1993. Compensatory growth and weight segregation following light and temperature manipulation of juvenile Atlantic salmon (*Salmo salar* L.) and Arctic charr (*Salvelinus alpinus* L.). *Aquaculture*, **114**: 261–272.
- Mrosovsky, N. 1990. *Rheostasis: The Physiology of Change*. Oxford: Oxford University Press.
- Nicieza, A.G. and Metcalfé, N.B. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. *Ecology*, **78**: 2385–2400.
- Nicieza, A.G., Reyes-Gavilán, F.G. and Braña, F. 1994. Differentiation in juvenile growth and bimodality patterns between northern and southern populations of Atlantic salmon (*Salmo salar* L.). *Can. J. Zool.*, **72**: 1603–1610.
- Perrin, N. and Sibly, R.M. 1993. Dynamic models of energy allocation and investment. *Annu. Rev. Ecol. Syst.*, **24**: 379–410.
- Post, J.R. and Parkinson, E.A. 2001. Energy allocation strategy in young fish: allometry and survival. *Ecology*, **82**: 1040–1051.
- Reznick, D. and Yang, A.P. 1993. The influence of fluctuating resources on life history: patterns of allocation and plasticity in female guppies. *Ecology*, **74**: 2011–2019.
- Samuels, S.E. and Baracos, V.E. 1995. Tissue protein turnover is altered during catch-up growth following *Escherichia coli* infection in weanling rats. *J. Nutr.*, **125**: 520–530.
- Saunders, R.L., Farrell, A.P. and Knox, D.E. 1992. Progression of coronary arterial lesions in Atlantic salmon (*Salmo salar*) as a function of growth rate. *Can. J. Fish. Aquat. Sci.*, **49**: 878–884.
- Schew, W.A. and Ricklefs, R.E. 1998. Developmental plasticity. In *Avian Growth and Development* (J.M. Starck and R.E. Ricklefs, eds), pp. 288–304. Oxford: Oxford University Press.
- Simpson, A.L., Metcalfé, N.B. and Thorpe, J.E. 1992. A simple non-destructive biometric method for estimating fat levels in Atlantic salmon, *Salmo salar* L., parr. *Aquacult. Fish. Manage.*, **23**: 23–29.
- Smith, R.W. and Griffith, J.S. 1994. Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. *Trans. Am. Fish. Soc.*, **123**: 747–756.
- Smith-Gill, S.J. 1983. Developmental plasticity: developmental conversion versus phenotypic modulation. *Am. Zool.*, **23**: 47–55.
- 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.

- Tveiten, H., Johnsen, H.K. and Jobling, M. 1996. Influence of maturity status on the annual cycles of feeding and growth in Arctic charr reared at constant temperature. *J. Fish Biol.*, **48**: 910–924.
- Vance, R.R. 1992. Optimal somatic growth and reproduction in a limited constant environment: the general case. *J. Theor. Biol.*, **157**: 51–70.
- Weatherley, A.H. and Gill, H.S. 1981. Recovery growth following periods of restricted rations and starvation in rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Biol.*, **18**: 195–208.
- Weigle, D.S. 1994. Appetite and the regulation of body composition. *FASEB J.*, **8**: 302–310.
- Whitledge, G.W., Hayward, R.S., Noltie, D.B. and Wang, N. 1998. Testing bioenergetics models under feeding regimes that elicit compensatory growth. *Trans. Am. Fish. Soc.*, **127**: 740–746.
- Xie, S., Zhu, X., Cui, Y., Wootton, R.J., Lei, W. and Yang, Y. 2001. Compensatory growth in the gibel carp following feed deprivation: temporal patterns in growth, nutrient deposition, feed intake and body composition. *J. Fish Biol.*, **58**: 999–1009.

