Seasonal patterns of growth, expenditure and assimilation in juvenile Atlantic salmon

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Summary

1. We report a modelling study of a data-set describing the growth of individual Atlantic salmon (*Salmo salar* L.) parr in the Girnock Burn (Scotland). A development of the compensatory growth model due to Broekhusien *et al.* (1994) was fitted to these data by numerical optimization.

2. The model uses carbon mass as a surrogate for an energy currency. This mass is divided into structure and reserve components, so as to describe decoupled changes in length and wet-weight.

3. Using the same parameters for all fish, our model explained 83% of the variability in length and weight at age. Adding a single additional parameter for each individual enabled the model to explain over 96% of length and weight variability.

4. Weak negative correlation between size at first capture and within-study growth argues against genetic causality of observed growth variability.

5. The energetic basis of our model enables us to infer time-series of net assimilation and basal maintenance rates for the observed individuals. Maximal growth occurs early in the season when high assimilation is accompanied by low temperatures and maintenance rates. In late season, continuing high assimilation is balanced by high maintenance rates consequent on summer temperatures.

Key-words: salmon, energetics, growth, individual, model.

Journal of Animal Ecology (2002) **71**, 916–924

Introduction

For several decades, staff at the Freshwater Laboratory of Fisheries Research Services (Pitlochry, Scotland) have carried out yearly electro-fishing surveys of Atlantic salmon (*Salmo salar* L.) parr at a number of locations in the catchment of the river Dee. A particularly complete dataset was collected between 1969 and 1978 in a tributary stream, the Girnock Burn, where temperature was also recorded. This dataset was the subject of a modelling study by Gani (2000), which indicated the desirability of describing the growth of identifiable individuals with higher (ideally monthly) temporal resolution.

Between October 1998 and December 1999, a programme of individual observations, very similar in concept to the study reported by Juanes *et al.* (2000), was carried out. A series of approximately monthly electro-

fishing sessions recaptured identified individuals from the 1997 hatch up to nine times, with the individual's weight and length measured at each recapture.

This paper reports a modelling study of this dataset, using a two-state-variable formulation developed from that used by Broekhusien *et al.* (1994) to describe compensatory growth in tank-reared salmonids. Our study is aimed at understanding both the systematic patterns of growth within the study period and the individual to individual variations in size-at-age.

We shall show that over 83% of the variability in observed length and weight at age is explicable on the basis of systematic growth from the observed length and weight at first capture. This implies that, although (unobserved) growth in the first year of life is highly variable, only about 17% of the variability we observe is due to variability in individual growth during the course of our study.

More than three-quarters of this additional variability can be explained by assigning one additional parameter to each fish. This parameter sets the scale

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of the individual's assimilation rate and thus defines how well that individual performs relative to the rest of the cohort. Surprisingly, we find that its value has a weak negative correlation with the individual's size at first capture (relative to the contemporaneous cohort average). We suggest that a genetic mechanism underlying individual variability would imply a strong positive correlation, and thus that our data argue against such causality.

Finally, our model allows us to infer the rates of net energy assimilation and (basal) maintenance expenditure which underly predicted changes in length and weight. We display time-series of these rates for several exemplary fish and show that they exhibit a consistent pattern in which early season growth is driven by high assimilation occurring at a time when temperatures, and hence maintenance expenditure, are low. By contrast, roughly similar assimilation rates after midseason produce little or no growth because they are counter-balanced by high maintenance rates concomitant upon high water temperatures.

The data

In 1998, F.R.S. Freshwater Laboratory began a programme of (approximately) monthly electro-fishing surveys on a short stretch of the Girnock above the smolt trap at Little Mill. The 140 m long study section, which is adjacent to Hampshire's bridge, was instrumented with temperature loggers from which daily (averaged) temperatures were obtained. A full description of the site, which is at Ordinance Survey G.R. 326959, can be found in Buck & Hay (1984).

In each survey, newly captured individuals longer than 7 cm were marked, initially using Alcian Blue dye marks applied by dental Panjet and latterly using injected Passively Induced Transponder (PIT) tags. A scale sample was taken from each newly marked individual before it was weighed, measured and released. Recaptured individuals were identified, weighed, measured and released.

The present work concerns 179 individuals whose ages, determined by examining scale samples, indicated that they came from the 1997 hatch. These individuals were observed between October 1998 and December 1999, during which time each was captured 2–9 times.

In Fig. 1 we show the daily temperatures in the study section together with the length and wet weight of each fish at each capture. To illustrate the nature of the individual growth histories we display three typical examples. Inspection of these data reveals that:

• During winter, individual length and weight change relatively little.
• There is a period of rapid growth covering (approximately) days 100 → 200, after which growth slows dramatically.
• The proportion of the total seasonal increment achieved during the early part of the rapid growth period is larger for length than for weight.

• Daily average temperatures mainly exceed 5 °C from day 100 until day 350.
• Individuals who are large or small relative to the cohort average at first capture tend to maintain this relationship through the period of observation.

From these observations, we infer that growth rates are determined by seasonal variations in food supply and/or appetite as well as temperature. Furthermore, we note that the changes in weight and length are sufficiently decoupled to suggest the need to model their dynamics separately, rather than assuming a fixed weight–length relation.

The model

In order to elucidate the implications of the data described above, we need a dynamic model capable of representing decoupled changes in length and weight. Although some of the parameters of such a model can be evaluated from information in the literature, a number will have to be determined by numerical optimization. This indicates that we need a structurally simple model with as small a parameter set as possible. We choose a simplified variant of the model used by Broekhusien *et al.* (1994) to explain compensatory growth in laboratory salmonid populations.

STATE VARIABLES AND OBSERVABLES

The Broekhusien model (Broekhusien *et al.* 1994) uses carbon mass as its currency. Given the strong relation between carbon mass and energy content (Carter *et al.* 1992), it is thus a dynamic energy budget model in the sense of Kooijman (1993). The model divides the total carbon mass of a reproductively inactive individual into two components: reserves (R) and structure (S). Reserves represent that part of the carbon mass which can be mobilized to meet basal metabolic costs under starvation conditions, while structure represents that part which cannot. Broekhuisen *et al.* identify reserves with fatty deposits and remobilisable parts of the musculature and equate structure with skeletal, circulatory and nervous tissues. They further argue that the reserve to structure ratio

$$\rho \equiv \frac{R}{S} \qquad \text{eqn 1}$$

is a direct measure of the individual's ability to withstand a bout of starvation, and hence of its 'condition'.

These definitions imply that structural carbon mass does not decrease during starvation-induced weight loss. Broekhuisen *et al.* argue that it is a surrogate for individual length (L), which likewise remains constant under starvation. They write the relation between the state variable S and the observable L as

$$L = L_0 S^\alpha \qquad \text{eqn 2}$$

where L_0 is the length–structure scale and α the length–structure power.
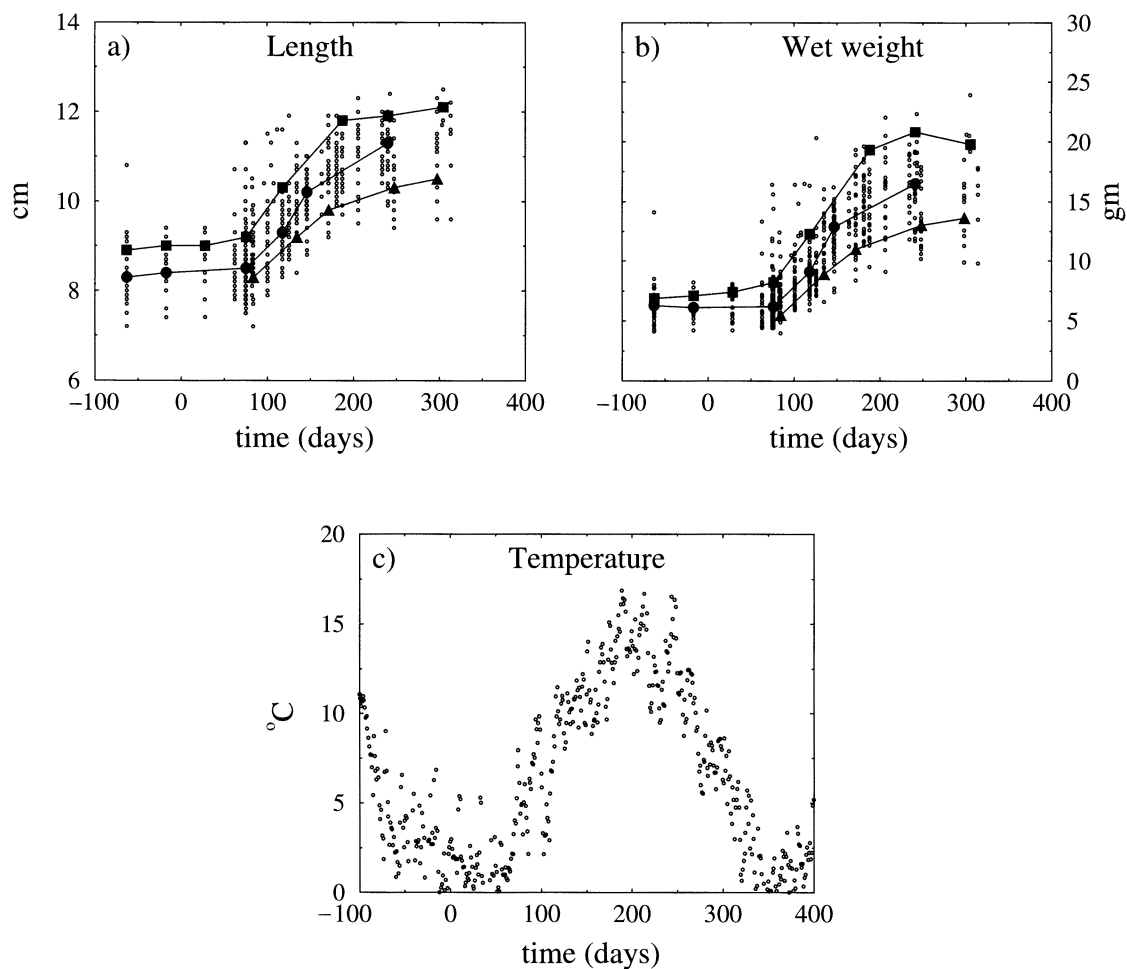
Fig. 1. Observations in the Girnock Burn during 1998/9. Measurements on individuals hatched in 1997 plotted against time in days (zero = 1/1/99). (a) Dots show the length (cm) of each fish captured. Symbols show the growth trajectories of three typical individuals (IDs: ■ = 117, ● = 37, ▲ = 2024). (b) Dots show the wet weight (gm) of each fish captured. Symbols show the growth trajectories of the same three individuals. (c) Daily water temperature in the study section.

Broekhusien *et al.* inferred a second observable, wet weight, by assuming a constant proportionality with total carbon mass. We improve on this rather unrealistic assumption by using a study of brown trout body composition reported by Elliott (1976a) and assuming that similar relationships apply in Atlantic salmon. Elliot gives a statistical relation between energy content, length and wet weight. The tight coupling between energy content and carbon mass implies that we can rearrange this expression to show that wet weight (*W*) is related to length (*L*) and total carbon mass (*R* + *S*) by

$$W = W_0 L^\beta (R + S)^\gamma \qquad \text{eqn 3}$$

where W_0 is the weight scale, β is the weight length power and γ is the weight carbon power.

ASSIMILATION AND MAINTENANCE

Broekhusien *et al.* (1994) divide the individual's metabolic processes into those which are feeding-rate dependent and those which are not, in the manner discussed by Gurney & Nisbet (1998). Because the feeding-rate independent processes may include an element of activity cost, Broekhuisen *et al.* refer to their total cost, *M*, as the maintenance cost rate. Although we emphasize the connection between these processes and basal metabolism by referring to the basal maintenance rate (b.m.r.), we retain the same functional dependence on temperature and total carbon mass, namely

$$M = M_0 (R + S)^p \exp\left[\frac{T}{T_m}\right], \qquad \text{eqn 4}$$

where M_0, p and T_m are the b.m.r. scale, power and temperature, respectively.

Feeding rate dependent metabolic processes include those parts of the activity costs associated with feeding, as well as more obvious costs such as specific dynamic action. Gurney & Nisbet (1998) argue that the totality of such costs is directly proportional to the food uptake rate and can thus be factored into an overall assimilation efficiency, ε, relating the net rate of carbon assimilation, *A*, to the gross carbon uptake rate, *U*, thus

$$A = \varepsilon U. \qquad \text{eqn 5}$$

Broekhusien *et al.*'s model was formulated to describe the growth of individuals fed a defined ration. A natural extension to describe a field situation with environmental food abundance E would represent the functional response by $U_m F(E)$ and hence write the gross carbon uptake rate as

$$U = \lambda U_m F(E) \qquad \text{eqn 6}$$

where U_m is the maximum carbon uptake rate and λ is an appetite factor whose value is normally unity but which rises under compensation conditions.

Broekhusien *et al.* assumed that the maximum carbon uptake rate scaled exponentially with temperature and allometrically with structural carbon – the allometric power being close to, but not identical with, the basal maintenance rate power. We follow their formulation, but note that it is implicit in the heuristic salmon growth model of Elliott & Hurley (1997) that maintenance and uptake have the same allometry. Hence, we write

$$U_m \equiv U_0 S^p \exp\left[\frac{T}{T_a}\right]. \qquad \text{eqn 7}$$

Although Gani (2000) derived a functional response for salmon parr, we cannot make use of equations 5–7 directly, because we have no data describing food availability in the Girnock during the study period. If we regard the environmental food abundance as a fitting function, compensatory changes in λ will be confounded with possible changes in food abundance. Hence, we choose a different strategy and define a scale constant A_0 and a dimensionless seasonality function $f(t)$ such that

$$A_0 f(t) \equiv \varepsilon\lambda U_0 F(E). \qquad \text{eqn 8}$$

In terms of these quantities, our formulation for the net carbon assimilation rate becomes

$$A = A_0 f(t) S^p \exp\left[\frac{T}{T_a}\right]. \qquad \text{eqn 9}$$

where we refer to A_0 as the assimilation scale, T_a as the assimilation characteristic temperature, and p is the basal maintenance rate power. The seasonality function, $f(t)$ represents the proportional depression of assimilation rate below the within-year maximum for an individual of the given size at the given temperature. To minimize the parameter count we assume that this function is cyclic with a period of 1 year, and takes the form of a background (winter) value f_w with a triangular peak starting at julian day t_s rising to the value unity over a period t_u and falling back to f_w over a further period t_d. We thus write

$$f(t) = \begin{cases} f_w + (1 - f_w)t'/t_u & t' \le t_u \\ 1 - (1 - f_w)(t' - t_u)/t_d & t_u < t' \le t_u + t_d \\ f_w & \text{otherwise} \end{cases} \qquad \text{eqn 10}$$

where we define

$$t' \equiv (t - t_s) \bmod 365. \qquad \text{eqn 11}$$

DYNAMICS

Broekhusien *et al.*'s (1994) model is concerned only with reproductively immature individuals, so the difference between the rate of assimilation of carbon net of costs which are proportional to that rate (A) and the rate of carbon expenditure on fixed costs (M) must represent the rate of change of the individual's total carbon mass. Remembering that the total carbon mass consists of two components, R and S, it is clear that the rate of change of reserve carbon is

$$\frac{dR}{dt} = A - M - \frac{dS}{dt} \qquad \text{eqn 12}$$

Broekhuisen *et al.* assume that the rate at which assimilated carbon is committed to new structure is proportional to the net production rate, with a variable constant of proportionality designed to keep the reserve ratio ($\rho \equiv R/S$) at a target value ρ_0 whenever possible. We modify this aspect of their model in the interests of simplicity and note that our modification introduces an added degree of realism in model behaviour. We assume that the rate of commitment to structure is proportional to the rate of carbon assimilation, with a constant of proportionality designed to ensure that (so far as is possible) the reserve ratio does not fall below a 'defended level' ρ_0. To achieve this we write

$$\frac{dS}{dt} = \kappa A \qquad \text{eqn 13}$$

where

$$\kappa = \begin{cases} \kappa_0 & \rho > \rho_0 + \rho_w \\ \kappa_0(\rho - \rho_0)^+/\rho_w & \text{otherwise} \end{cases} \qquad \text{eqn 14}$$

Whereas the Broekhuisen formulation makes the reserve ratio of individuals growing under constant conditions independent of food availability, we shall show in a future publication that our alternative assumption carries the more realistic corollary that better-fed individuals maintain higher reserve ratios.

PARAMETERS

The model described above has a total of 17 parameters of which seven can be evaluated from literature sources. We show the parameters, the number of the equation which defines them, the values used and the sources from which these values derive in Table 1.

We determined the remaining 10 parameters (Table 2) by numerical optimization against the data. The length and wet weight of each fish at first capture were used to initialize its reserve and structural carbon mass (R and S) using equations 2 and 3. Each individual's growth trajectory was determined using the fourth order Runge-Kutta method (Press *et al.* 1989) to

Table 1. Parameters determined from the literature

Param	Interpretation	Def. eqn	Value	Units	Source
W_0	Weight scale	3	0·01394	$\mathrm{g\,cm^{-\beta}\,mg\,C^{-\gamma}}$	E76a
β	Weight-length power	3	0·684	–	E76a
γ	Weight-carbon power	3	0·720	–	E76a
M_0	b.m.r. scale	4	0·014	$\mathrm{d^{-1}\,mg\,C^{1-p}}$	W92, C92
p	b.m.r. power	4	0·75	$\mathrm{d^{-1}\,mg\,C^{1-p}}$	E76b, FR84
T_m	b.m.r. temp	4	12·0	°C	E76b
T_a	Assimilation temp	9	6·0	°C	E76b, B79

B79 = Brett (1979), C92 = Carter *et al.* (1992), E76a = Elliott (1976a), E76b = Elliott (1976b), FR84 = From & Rasmussen (1984), W92 = Waiwood *et al.* (1992).

Table 2. Parameters determined by fitting, together with their best-fit values

Par	Interpretation	Def. eqn	Units	Best fit value Population A_0	Individual A_0
A_0	Assimilation scale	9	$\mathrm{mg\,C^{1-p}\,day^{-1}}$	0·095	see Fig. 4a
f_w	Rel. winter assimilation	10	–	0·162	0·183
t_s	Assimilation rise start	10	julian day	17·9	35·9
t_u	Assimilation rise duration	10	days	39·7	24·1
t_d	Assimilation fall duration	10	days	130	124
κ_0	Max. proportion to S	14	–	0·232	0·156
ρ_0	Defended reserve ratio	14	–	2·44	3·04
ρ_w	Allocation switch width	14	–	0·362	0·506
L_0	Length–structure scale	2	$\mathrm{cm\,mg\,C^{-\alpha}}$	2·35	2·06
α	Length–structure power	2	–	0·248	0·279

integrate equations 12 and 13 between the times of its first and last capture, driven by temperatures linearly interpolated between the daily values shown in Fig. 1. A squared relative error was calculated for each trajectory by comparison with all the recapture observations for that fish, and the total error for a given parameter set was calculated by summing the trajectory errors for all fish. A parameter set which minimized the overall square relative error was determined using the downhill simplex method (Press *et al.* 1989) with bootstrap restarting (Wood 2001).

Fitting the model to the data

POPULATION A_0

Our baseline model (equations 2–4 and 9–14) has 17 parameters, of which seven (Table 1) were determined from the literature. The remainder (Table 2) were evaluated by numerical optimization against the data.

In this optimization process we calculated a separate weight and length trajectory for each fish, starting with the values observed at that individual's first capture, but assumed that the growth process thereafter is governed by the same set of parameters for all fish. The process thus found a single parameter set which minimized the total discrepancy between predicted and observed wet weights and lengths for all fish at all recaptures (880 data points).

We illustrate the quality of the resulting fits in Fig. 2. The lower frames show a regression of observed against predicted values for the length and wet weight of each fish at each recapture. These demonstrate that with 10 free parameters, the model simultaneously accounts for 90% of the variability in the 440 length observations and 83% of that in the 440 wet weight observations.

In the upper frames of Fig. 2 we show the predicted growth trajectories for the three individual fish whose observed growth trajectories we highlighted in Fig. 1. The model has clearly captured the general shape of the trajectories in both length and wet weight, and yields a visually satisfactory fit for two of our three illustrative individuals. The third individual was large at first capture and shows above average growth performance during the observation period. In this case, unsurprisingly, growth projections based on fitting the 'average' performance of the cohort seriously underpredict individual weight and length towards the end of the observation period.

INDIVIDUAL A_0

Although the fit described in the previous section successfully captures the general shape of the observed growth trajectories, there is clearly individual to individual variability in observed (within-study) growth and our next fitting exercise attempts to capture this
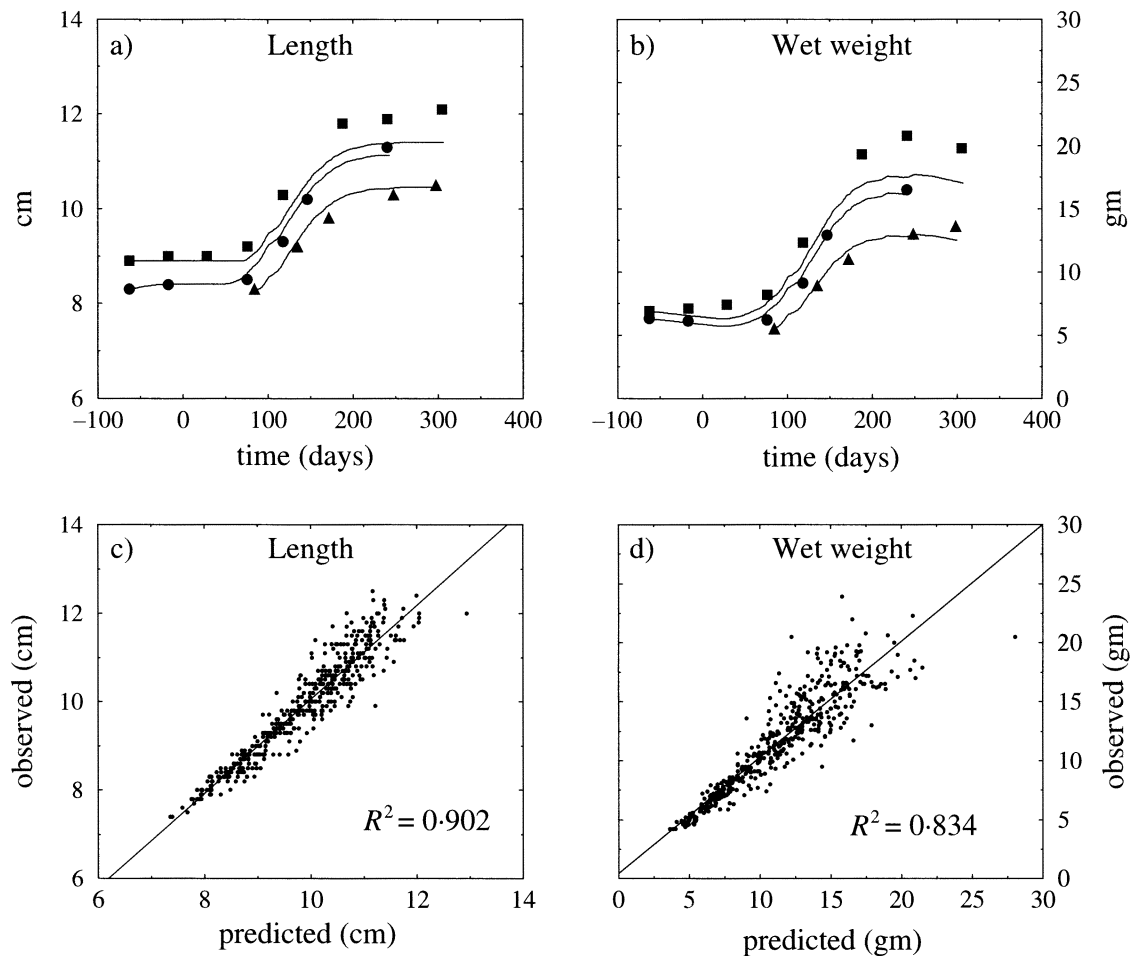
Fig. 2. Fitting the model defined by equations 2–4 and 9–14 to the Girnock Burn individual data with a single parameter set (Tables 1 & 2) for all fish. Frames (a) and (b) show the model fit to the three illustrative individual length and weight trajectories shown in Fig. 1. Frames (c) and (d) show the regression of observed against predicted length and wet weight for all recaptures of all individuals.

variability. Our dataset comprises 880 measurements on 179 individuals, so we can only afford to allow a single model parameter to vary from individual to individual if our fit is to retain significant statistical power.

Salmon parr are known to be territorial and the illustrative trajectories shown in Fig. 1 suggest that an individual's position within the cohort size distribution changes slowly over the study period. This would be consistent with individuals either retaining the same territory for prolonged periods, or always occupying a territory of the same relative quality.

We therefore hypothesize that individual growth variation is driven by time-independent individual to individual differences in ingestion rate relative to the current norm. To evaluate this possibility we re-fit the dataset using the same model as before, with all the parameters (Tables 1 and 2) identical for all fish, *except* for the assimilation scale, A_0 which we now assume to have an independent value for each individual.

Since we now have 16 global and 179 individual parameters, the fitting process appears intimidatingly complex. However, although each individual trajectory depends on all the global parameters, it is only affected by a single A_0 value. This allows us to adopt a nested optimization strategy which greatly increases computational efficiency. For a particular set of global parameter values, we treat each growth trajectory independently and optimize its A_0 value so as to obtain the best fit to that subset of observations which can be achieved with those global parameter values. The sum of the individual trajectory errors for these partially optimized trajectories defines the overall error for the global parameter set, which we minimize using the downhill simplex method, with bootstrap restarting to avoid being trapped in subsidiary local mimima.

We illustrate the quality of the resulting fit in Fig. 3. All three exemplary trajectories (Fig. 3a,b) now show both qualitative and quantitative correspondence between prediction and observation in both length and weight. In overall terms, the model now explains over 96% of the variation in both weight and length (Fig. 3c,d). The best fit global parameters are given in Table 2 and the frequency distribution of the optimal values of A_0 is shown in Fig. 4a.
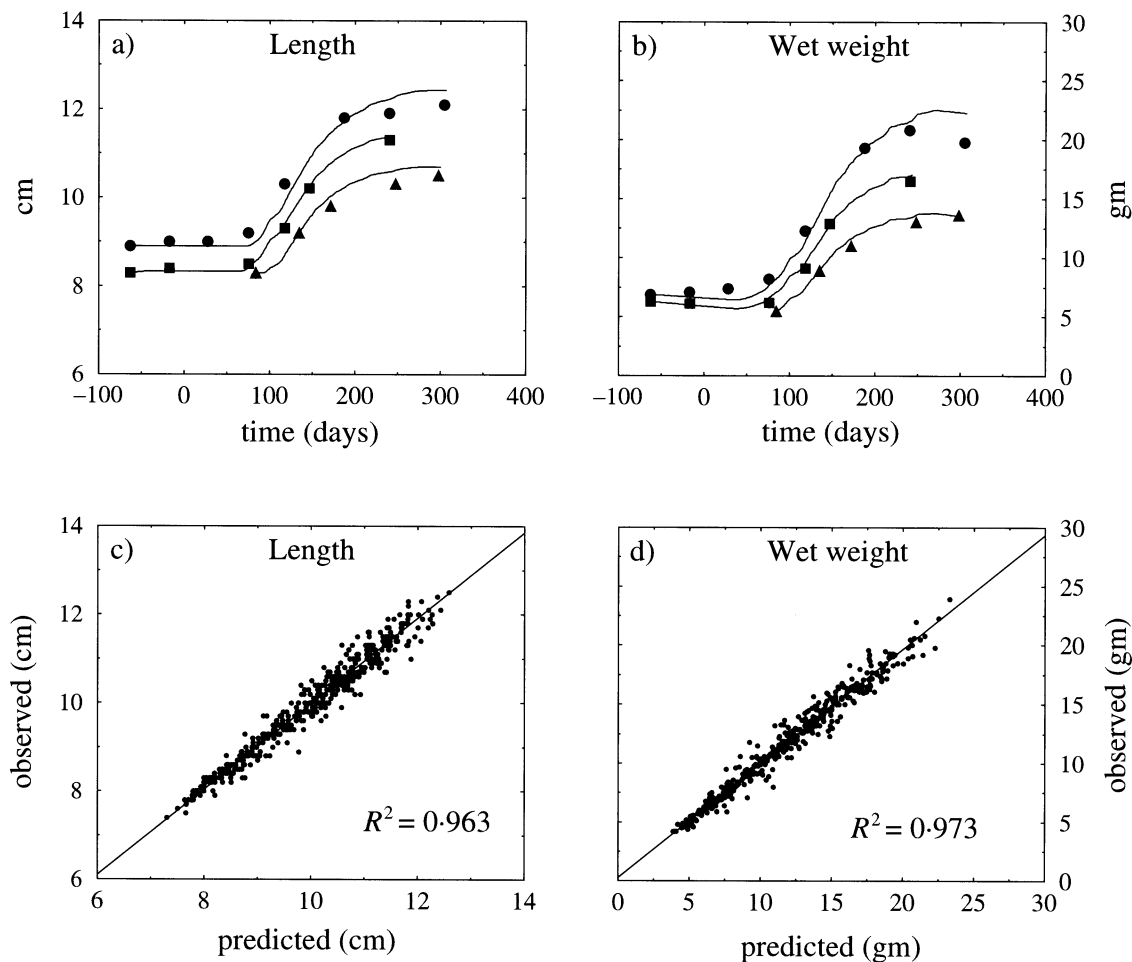
Fig. 3. Fitting the model defined by equations 2–4 and 9–14 to the Girnock Burn individual data with an independent value of A_0 for each fish and all other parameters global. Frames (a) and (b) show the model fit to the three illustrative trajectories shown in Fig. 1. Frames (c) and (d) show the regression of observed against predicted length and wet weight for all recaptures for all individuals.

Discussion

OVERVIEW

Our dataset comprises 440 measurements of wet weight and 440 corresponding measurements of length taken on 179 identified individuals recaptured repeatedly between October 1998 and December 1999. These individuals all hatched in 1997, so they were already a year old when they reached the length (7 cm) at which they could be marked, and thus included in the study.

Figure 1 shows that individuals first captured at the start of the study varied considerably in length and weight. We fitted the post-capture length- and weight-at-age data for all individuals captured twice or more, with a model based on that of Broekhusien *et al.* (1994), extended to describe a field environment, and modified to reduce the parameter count and reflect recent biological advances. Using the length and weight at first capture to initialize each trajectory and assuming a single set of 10 free parameters for all fish, our best fit explained 83% of the observed variation in length and 90% of that in wet weight.

The variability unexplained by this process represents individual to individual variation in within-study growth and can only be described by one or more individual parameters. Salmon parr are territorial and territories vary in productivity (Grant & Kramer 1990), so we hypothesize that there should be a time-independent relation between an individual's net assimilation and that of other fish of the same size at the same temperature. This would result either if individuals retain a given territory for a whole growing season or if territorial readjustments always result in a given individual occupying the same hierarchical position. To investigate this hypothesis we allowed the assimilation scale parameter, A_0, to vary between individuals (see Fig. 4a), and thus produced a fit which explained 96% of the observed variation in length and 97% of that in weight.

INDIVIDUAL VARIABILITY

On the evidence of our first fit, variability in initial state and systematic growth thereafter account for about 87% (83% length, 91% weight) of the observed
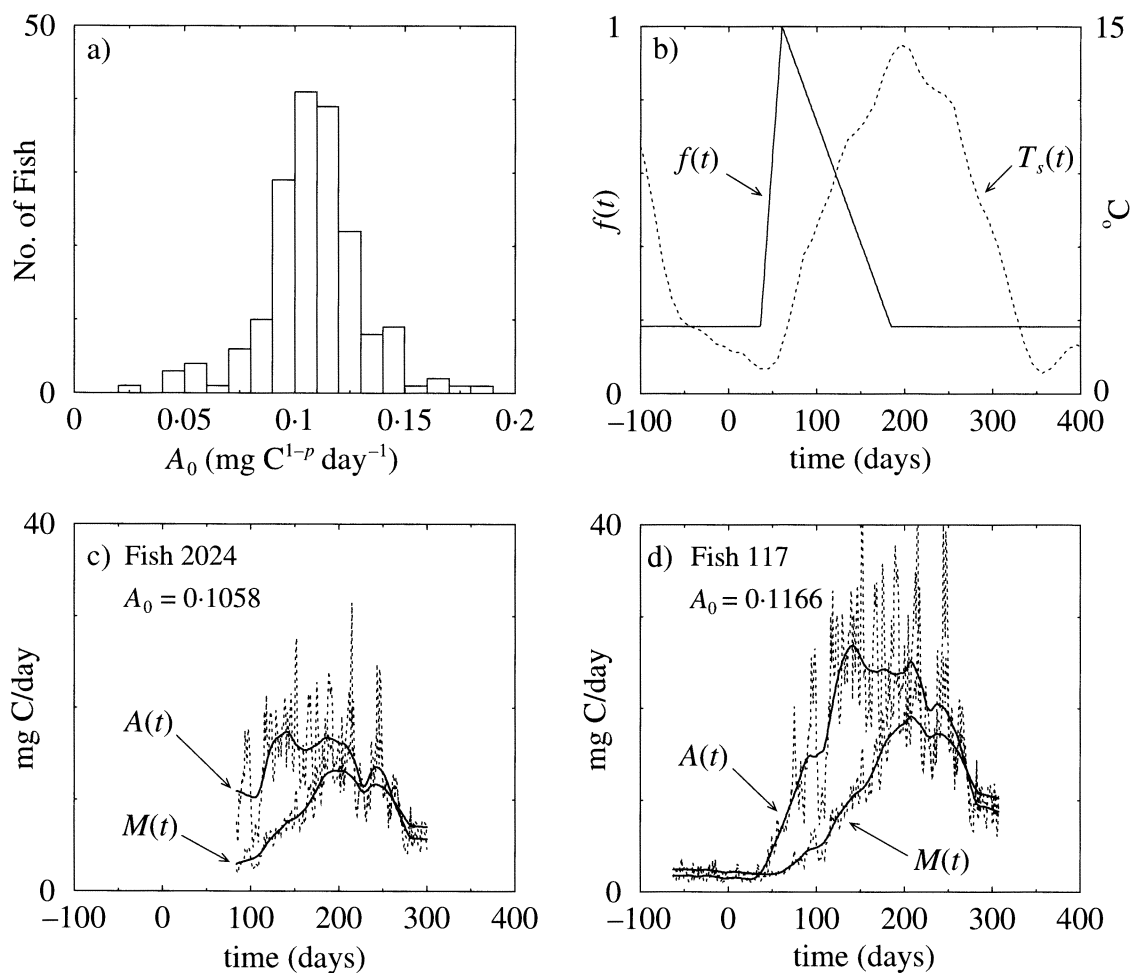
Fig. 4. (a) Frequency distribution of best-fit A_0 values. (b) Time-series of relative assimilation rate, $f(t)$, and smoothed water temperature, $T_s(t)$. For illustrative clarity the daily temperatures used to drive the simulation have been LOESS smoothed (range ≈ 25 days). (c) Best-fit assimilation and basal maintenance rates for fish 2024. (d) Best-fit assimilation and basal maintenance rates for fish 117. Dotted lines show the raw estimates driven by daily temperatures and solid lines show a LOESS smooth (range ≈ 40 days) of these raw estimates.

variability in size at age, implying that around 13% (17% length, 9% weight) is associated with individual to individual variation in growth during the study and measurement error. Our second fit explains over 96% (96% length, 97% weight) of size at age variability so it explains about three-quarters (82% length, 66% weight) of the variation associated with variability in within-study growth and measurement error. This supports our hypothesis that individual assimilation rate scales change on a timescale comparable to the length of our study.

A previous study at the present site (Jordan & Youngson 1991) reported that body length differed among three possible genotypes for the *MEP-2** locus. We thus considered the possibility that assimilation scale, which represents a combination of uptake scale and assimilation efficiency (see equation 8), is a surrogate for genetically determined characteristics such as aggression or assimilation efficiency. The most likely outcome of such causality would be a strong correlation between high relative growth one year and high relative growth the next, which would be reflected in

strong positive correlation between an individual's relative assimilation during the study and its size at first capture compared to the cohort average. We could find no such correlation; indeed, there is a weak but statistically significant negative relation (slope $= -0.08$, S.E. $= 0.03$) between an individual's A_0 and the ratio of its size at first capture to the contemporaneous cohort average. This result argues strongly against a genetic basis for the variability in A_0.

To investigate the possibility that repeated capture by electro-fishing might have biased our results, we replotted the frequency distribution of individual A_0s (Fig. 4a) with individuals categorized into those captured more than four times and those captured up to four times. The results (not shown) demonstrate that both subdistributions have essentially the same expectation (0.108 for ≤ 4 captures, 0.110 for > 4 captures) and neither is significantly skewed. The only difference between them is the dispersion, which is considerably smaller for the > 4 captures subgroup than for the ≤ 4 captures subgroup. This reduction in dispersion is probably a consequence of the decreased influence of

measurement errors, particularly errors in weight consequent upon variations in gut fullness, which are smoothed out more effectively when fitting a longer time-series. There is no evidence that repeated electro-fishing captures influence the aspects of growth performance measured by the assimilation scale.

ASSIMILATION AND MAINTENANCE RATES

The key intermediate quantities which our model estimates on its way to calculating changes in length and weight (see equations 12 and 13) are the basal maintenance rate, M, and the net assimilation rate, A, defined in equations 4 and 9, respectively. In Fig. 4 we show how our best-fit estimates of these quantities vary with time for two of the individuals whose growth trajectories are shown in Fig. 3. These estimates show intense short-term variability, reflecting day-to-day variations in water temperature (Fig. 1), so we also show LOESS smoothed time-series from which the seasonal trends can more easily be distinguished.

In Fig. 4b we show our best estimate of the relative assimilation rate, $f(t)$, which represents a combination of food availability and appetite, and a LOESS smoothed time-series illustrating the seasonal trend in water temperature. These quantities show characteristically different seasonality. Estimated relative assimilation rises very sharply in early February (day 36), reaches a peak in early March (day 60) and then declines steadily until mid July (day 200). Water temperature shows a more sinusoidal trend, being at its lowest (≈ 1 °C) in early February, peaking in late July and remaining above 5 °C until well into December.

Comparing the seasonal variation of these quantities with the smoothed time-series of net assimilation and basal maintenance reveals several noteworthy features. Net growth $(A-M)$ is high in early spring (days 100–200) because high food availability (and/or raised appetite) produces high net assimilation while temperatures, and hence basal maintenance rates, are low. Estimated assimilation, and thus (presumably) food availability, peaks before day 100 and then drops sharply to reach winter levels by day 200, but because of the rapid temperature increase then occurring, the net assimilation rate continues to rise until around day 140. Indeed, driven by high summer temperatures, net assimilation exceeds half its peak value until (roughly) day 270. However, despite continuing high net assimilation, growth essentially stops after day 200 because high summer temperatures also imply high basal maintenance rates which soak up all the ingested resource.

Acknowledgements

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