

Multiple sub-population model for catchment salmon populations

Six month report - September 2006

Introduction. In the river Girnock, Atlantic salmon parr smolt between two and four years after hatch, having achieved lengths between seventy and one hundred and twenty millimetres. In warmer (southern English) waters the size at smolting is similar but the time taken can be less than a single growing season. In higher or more northerly waters the pre-smolt period can extend to over five years.

Although individuals in any given water exhibit a spread of sizes at smolting, the ranges in different waters generally overlap and one of the key differences between waters is the speed with which an individual can grow into the viable range. It is thus clear that an essential prerequisite to understanding the timing and magnitude of any given catchment's smolt output is to understand both the general pattern of individual growth and the extent of individual to individual variability around that norm.

Recognising this necessity, during the period prior to the inception of the current contract, the University of Strathclyde undertook a self-funded study of the theoretical underpinnings of the dynamics of size at age distributions in stochastic environments. This work resulted in a refereed publication [Gurney & Veitch (2006) - copy appended] which is in press at the Bulletin of Mathematical Biology.

Gurney & Veitch (2006) show that the effects of stochastic variability in the environment of functionally equivalent individuals can be exactly represented as a diffusion term in the partial differential description of the size at age distribution. They then derive an analytic condition which distinguishes between growth compensatory and depensatory dynamics. Finally they demonstrate that the combination of growth depensation arising from stochastic environmental variability and compensatory deterministic dynamics (for example von Bertalanffy individual growth) invariably leads to an initial condition independent relationship between the mean value of individual size at age and its coefficient of variation. These findings have profound implications for the identification of profitable methodologies for fitting such models to data.

Research Objective 1 – To devise document and test against existing data from the Girnock Burn, a model structure capable of describing the growth of salmon parr in a stochastic environment

Modelling Framework. The formal structure proposed by Gurney and Veitch (2006), while very well adapted to analytic treatment, is computationally cumbersome and therefore rather unsuited to data fitting. The first task under RO1 was therefore to devise a more computationally efficient description of size at age dynamics. Previous experience with high efficiency structured population models both under the N.E.R.C. Marine Productivity programme and in the construction of the Strathclyde Spatial Cod Model (STRATHCODY) suggested that a discrete time formulation would be the most appropriate solution.

We first assume, in common with much fisheries practice, that an individual grows irreversibly according to the standard von Bertalanffy prescription, which says that in the presence of food at abundance F , the individual's length L changes at a rate

$$\frac{dL}{dt} = \left[\alpha \phi(F) - \mu L \right]^+$$

where α is a constant, $\phi(F)$ is the scaled functional response, and the notation x^+ implies $\min(0, x)$. We now assume that environmental variability is represented by random variations in the value of F experienced by a given individual. We further assume that the individual's value of F remains constant over periods of length τ which we call the growth correlation time. To achieve a computationally tractable model we finally assume that $\phi(F)$ has a saturating form (such as the Holling Type II functional response) and that the values of F are either high enough for ϕ to be regarded as unity, or low enough for dL/dt to be zero (that is $\alpha\phi < \mu L$).

This picture of stochastic growth implies that any individual which survives long enough will reach a length $L_\infty = \alpha/\mu$, and that in during any given growth correlation period its growth will be described by

$$\frac{dL}{dt} = \begin{cases} \mu(L_\infty - L) & \text{with probability } p \\ 0 & \text{with probability } (1-p) \end{cases}$$

The final step in deriving a computationally efficient individual description is to change our index of size from length (L) to

$$q = -\ln \left(\frac{L_\infty - L}{L_\infty} \right)$$

and then to notice that the individual's development index (q) changes at a rate which is given by

$$\frac{dq}{dt} = \begin{cases} \mu & \text{with probability } p \\ 0 & \text{with probability } (1-p) \end{cases}$$

We notice immediately that this rate of change is independent of the individual's size, so any individual who has a development index in q to $q+\mu\tau$ at time t will either have an index in the same interval at time $t+\mu\tau$ (with probability $1-p$) or have an index in $q+\mu\tau$ to $q+2\mu\tau$ (with probability p). Hence if we write the number of individuals with development index in q to $q+\mu\tau$ at time t as $n_{q,t}$ and denote the proportion of such individuals who survive from t to $t+\tau$ by $S_{q,t}$ then we can see that

$$n_{q,t+\tau} = (1-p)S_{q,t}n_{q,t} + pS_{q-\mu\tau,t}n_{q-\mu\tau,t}$$

This update rule forms the basis for an exceptionally computationally efficient description of a population growing irreversibly with stochastic variation in individual growth performance.

Fitting to salmonid data. The computational efficiency of models based on this formalism makes them very suitable for fitting to observational data and a paper (copy appended) has been submitted to the Canadian Journal of Fisheries and Aquatic Science, describing the methodology and giving some exemplary applications to salmonids (trout in the Frome and the Girnock, and salmon parr in the Girnock) and gadoids (Cod in the North Sea). In addition, this paper shows that where the per-capita mortality rate is size independent (note that this does not preclude its being a function of age or time) the efficiency of a fitting process focussed on summary statistics for the size at age distribution can be further increased by deriving explicit equations of motion for the first two moments of the size at age distribution. The additional efficiency thus gained suffices to allow determination of the confidence intervals for the fitted parameters using re-sampling methods.

To produce a good fit to the salmonid data it was necessary to incorporate into the model the further assumption that within each year there is a 'growing season' during which rapid growth occurs (the growth probability p is large) while for the rest of each year growth is slow (the growth probability p is small). With this extension, the model produces very plausible fits (see Fig 1) to data from the 1997 salmon hatch and the 2002 trout hatch in the Girnock, and a composite picture of trout growth in the Frome derived from observations in 2002/3, with τ set to 10 days and best fit parameters as follows

parameter	Symbol	Frome trout	Girnock trout	Girnock salmon
Initial mean length	L_i (mm)	66.7	50.7	69.7
Initial length c.v.	c_i (%)	4.47	13.1	8.63
Asymptotic length	L_∞ (mm)	306	309	148
Maintenance rate	μ (%d ⁻¹)	0.456	0.122	0.746
Growth prob. (summer)	p_g	0.697	0.872	0.604
Growth prob (winter)	p_w	0.149	0.152	0.023
Growing season start	U (doy)	71.9	39.6	72.3
Growing season end	D (doy)	147	186	188

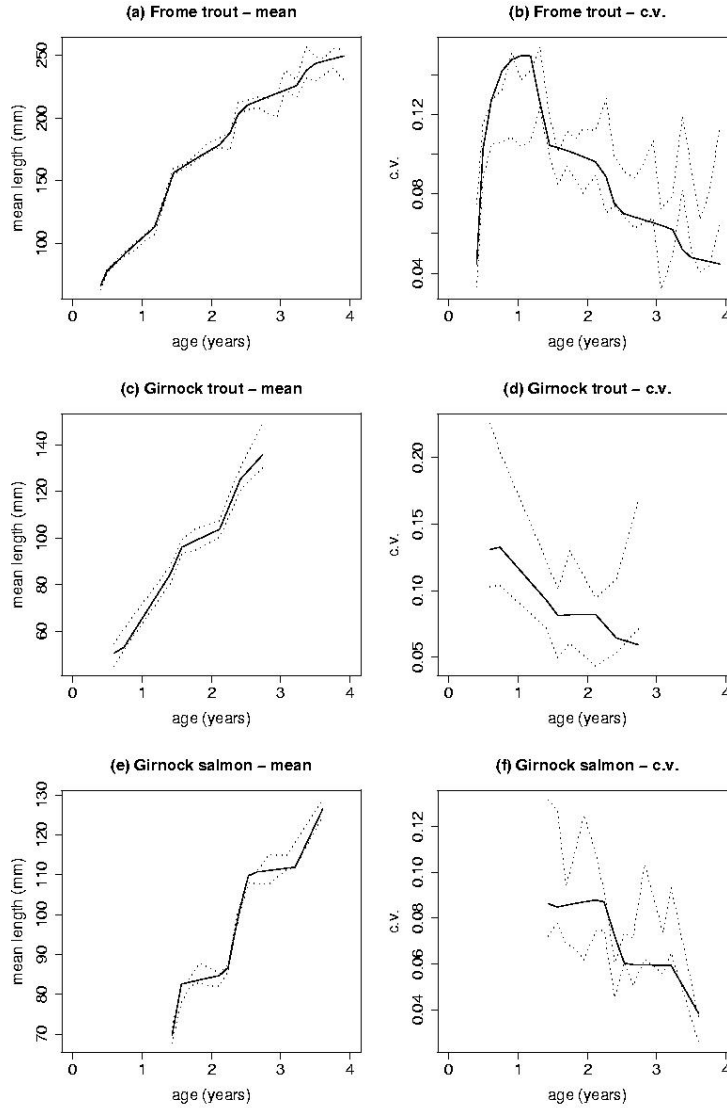


Fig 1. Fitted length at age statistics for wild salmonids. Frames a,c, and d show fitted values (solid lines) and 95% confidence limits for observed values (dotted lines) of mean length at age. Frames b,d, and f show fitted values (solid lines) and 95% confidence limits for observed values of length at age c.v. Frames a and b refer to Trout observed in the River Frome (S. England) in 2002/3, frames c and d refer to trout from the 2002 hatch in the Girnock Burn (Dee side) and frames e and f refer to salmon parr from the 1997 hatch in the Girnock Burn.

The 95% confidence limits for the fitted parameters, determined by refitting 500 random resamples of the data are

parameter	Symbol	Frome trout	Girnock trout	Girnock salmon
Initial mean length	L_i (mm)	64.1 – 68.2	47.7 – 54.1	68.3 – 72.3
Initial length c.v.	c_i (%)	1.52 – 5.38	8.49 – 15.1	6.10 – 10.1
Asymptotic length	L_{∞} (mm)	199 - 322	186 - 345	143 - 159
Maintenance rate	μ (%d ⁻¹)	0.391 – 0.498	0.110 – 0.451	0.530 – 0.981
Gr. prob. (summer)	p_g	0.619 – 0.800	0.702 – 1.00	0.561 – 0.864
Gr. prob (winter)	p_w	0.126 – 0.167	0.014 – 0.218	0.017 – 0.066
Gr. season start	U (doy)	58.0 – 83.2	30.1 - 103	71.1 – 99.6
Gr. season end	D (doy)	146 - 156	153 - 234	167 - 193

We note particularly the critical relationship between data quality and parameter uncertainty. The large sample sizes and consequently well defined temporal patterns in the Frome and Girnock salmon data lead to relatively tight confidence limits on the fitted parameters, whereas the small sample sizes

displayed by the Girnock trout data lead to confidence limits whose width would imply likely difficulty in discerning site to site differences of any degree of subtlety.

Ongoing work – smolt production. The work described in the foregoing part of this report and the submitted and/or accepted papers which arise therefrom clearly fulfil the requirements of milestones 1(Sep-06) and 2 (Dec-06) as defined in the MoU between F.R.S. and University of Strathclyde. However, before the model described here can become a useful part of a full lifecycle model, it needs to be able to describe the dynamics of smolt production. An additional benefit of this extension to the model capability is that it renders it feasible to fit the model to a significant part of the historical record from the Girnock Burn (which contains few years of highly resolved size at age data but many years which combine low resolution size at age data with size- and age- resolved smolt production data).

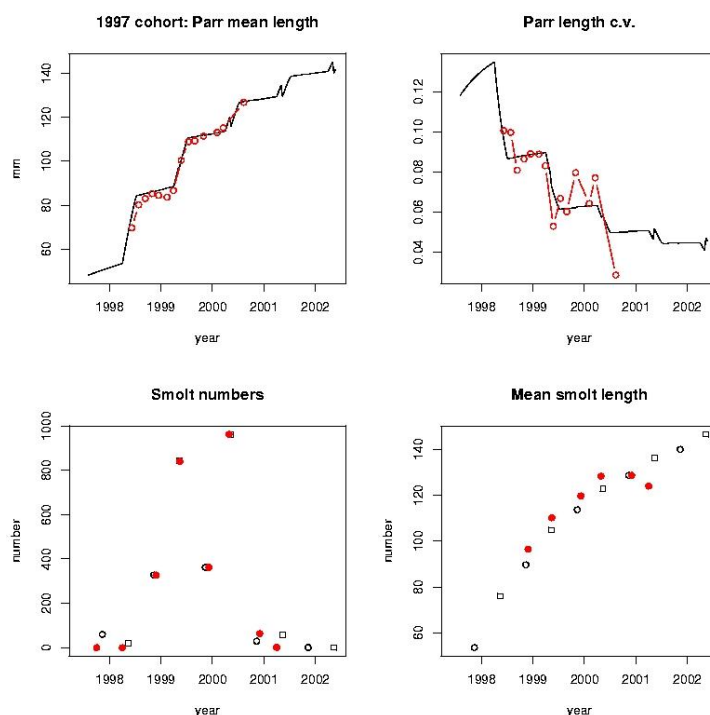


Fig 2. Prototype extension of the Strathclyde Salmon Growth Model to predict size and age resolved smolt production, fitted to the data from the 1997 cohort in the Girnock Burn.

Experiments are ongoing with a variety of different length-based trigger mechanisms for smolt emigration. A number of these show some promise, and an example of the quality of fit which can be produced is given in Fig.2. This variant of the model hypothesises that emigration is triggered by being in a band of lengths centred on a characteristic value (L_E) at two critical times of year (spring and autumn). The probability of an individual actually emigrating changes sigmoidally from zero to a saturation value (ϵ_E) over a length range L_w centred on L_E . We see that, as we would expect, it provides a slightly better fit to the size at age statistics that that shown in Fig 1, since it now accounts correctly for the removal of larger individuals by emigration. It also shows a good fit to the characteristic pattern of emigration - in which the largest number of individuals smolt in the spring smolt run, with smaller number in the two autumn runs – and also to the temporal changes in the size of the outgoing smolts.

Work is proceeding to identify the optimum formulation for the smolt trigger, after which the candidate model will be fitted to as wide a spectrum as possible of the historical record from the Girnock Burn, and any other waters for which appropriate data can be obtained. We anticipate production of a biologically focussed paper describing this phase of the work during the first half of 2007.