**FRS FL Milestone Report SF0274.5b (Dec-2007)**

# Assessment of the potential for adaptation and wider management use of a fully modular version of the single sub-population juvenile river-phase model.

(the 'Smolt-Split' models of salmonid development from ova to smolting).

P.J. Bacon and W.S.C. Gurney

**Executive Summary.**

- The models of salmonid development, from ova to smolts, so far produced by SF0274 have appreciable potential for modularisation and further refinement.
- This document reviews a number of ways those models could be enhanced to fit certain aspects of the (juvenile) freshwater stages of salmonid life-cycles more precisely.
- It presents and discusses the biological processes, their related topics of management importance and some of the existing, and new, data sets which would need to be incorporated in order to usefully include those aspects in a more detailed model.
- The possibilities are summarised as a list of Key-Questions in an appendix.

- Parallel development of the 'marine phase' model of the salmon life cycle is presently suggesting that the crucial, controlling (but not necessarily limiting) aspects of salmon population dynamics probably take place in freshwater, and that some of these may occur during river ascent phase of returning adults.
- Available data on these 'adult return' aspects of the salmon life-cycle are much more sparse than are the data on juvenile production (the subject of this report).
- For the immediate spatial modelling purposes, of the current SF0274 contract on salmon populations, it may transpire that the populations processes during adult return appear so crucial, and the data on them so sparse, that, for our immediate purposes, rather then extend the present 'smolt-split' models, we may actually need to simplify them to obtain a balanced overall model structure.

- Accordingly we have so far left the inventory of potential enhancements to the present smolt-split model un-prioritised.

- **BACKGROUND**

**Aim of this report**

This document outlines the achievements of the Size At Age Variability models of the production, body growth and survival of Atlantic salmon between spawning and smolting achieve by project SF0274 by April 2007. It aims to emphasise potential theoretical developments and the additional field data that would allow their improvement for both scientific understanding and management. It refers specifically to the latest versions (SAAV_SSv4, without DD parr growth or a general temperature function, and SAAV_SSv5 to which both these are being added), as current in the summer of 2007. These models are described in FL milestone reports for SF0274, and key stages of their development have been published (Gurney and Veitch (2007), Gurney *et al* (2007), Gurney *et al* (submitted)).

The schedule of SF0274 will not allow the suggestions made herein to be implemented within the duration of the current project (to March 2009). The intention is to document possible avenues for further investigation while they are fresh in our minds, so that any continuation of the present contract will be able draw upon them, to hit the ground running.

**Context of the Freshwater Phase Model**

The aim of the overall SF0274 project is to contrast two paradigms of salmon population and structure. The simplest, advocated *fauté de mieux* by ICES, is that salmon populations within large watersheds (several hundred square kilometres) can be managed as a single entity. The more complex paradigm, which is believed more realistic for the important and diverse Scottish salmon populations, is that salmon populations are critically sub-structured within large watersheds, and that these separate sub-populations need separate management if they are to thrive.

The SF0274 project aims to build a realistic model of salmon sub-populations within a watershed and investigate the effects of the different management paradigms on the any structured or unstructured components.

In brief, the structuring within large Scottish watersheds is thought to comprise preponderances of both early-running and multi-sea-winter adults (MSW) which breed preferentially in upland environments, and preponderances of later running and one-sea-winter fish (grilse or 1SW) breeding in lowland environments. The extremes of the life-styles and life-history strategies are thus envisaged to be structured by altitude, and thus to have inherently different general environments with regard to length of the growing season, water temperatures, water flow regimes, water quality (*eg* eutrophication from agricultural inputs), pollution, and so on. There is also persuasive evidence that the different life-styles represent genetically different populations, and that key life history characteristics, such as run-timing, spawning date, return at 1SW (versus 2SW) and body growth rates, are all heritable.

The overall broad project strategy requires full life-cycle models for the different postulated sub-populations of salmon, able to mimic their different oceanic life-styles, with regard to the number of winters spent at sea and thus their marine survivals and achieved marine growth. The present review and models, however, only deal with the narrower freshwater-phase, from spawning to smolting. Despite this, the overall project

aim requires a model structure that can be parameterised to realistically mimic the approximate extremes of the observed population dynamics. For example, the cold, unproductive upland regions thought to be typified by early running (and mainly MSW fish), and the warmer, richer lowland regions, typified by later running (and mainly grilse) fish. The intention is to have a model structure just rich enough to capture both sets of dynamics when separately parameterised with values typical of the different regions and life history styles.

We note that, in detail, this strategy of model parameterisation is only possible if suitable detailed data are available for at least these two contrasting regions. We emphasise that one of the needs for this document is to draw attention to the fact that, while adequate data are available from the Girnock burn, to investigate and parameterise such dynamics for the upland situation, no such detailed data set is presently (2007) available for the lowlands. KQ.1.1 Will suitable data be available from the Lowlands to parameterise the models.

Although an FL project (SF0273) is starting to collect a suitable data set from one location, it will be several years before suitable initial information will be to hand. Moreover, we note that, while stream habitats in the uplands are generally amenable to field studies, often being less than some 15 m wide and 0.5 m deep, making surveys of juveniles by electro-fishing methods fairly reliable, that the lowlands are typified by much wider and deeper stretches of river known to be exploited by salmon but where existing field methods are inadequate. KQ.1.2 Will the models parameterised for the lowlands need to exclude potential differences between lowland nursery streams and lowland wide and deep rivers? Note similar implications for wide upland rivers. Indeed, initial results (by October 2007) indicate that very few of the PIT tagged individuals marked some narrow lowland tributary sites are recaptured in subsequent months, whereas at the Girnock 87% are recaptured within 20 m. This raises the more disturbing question as to whether the size data will adequately represent a 'static' population. KQ.1.2b. Are lowland populations, even of small tributaries, so much more mobile as to conform poorly to the necessary 'population estimate' assumptions?

The focus of developing the present models of the freshwater phase to date has been to utilise the most detailed available data, that from the Girnock burn, an upland tributary of the Aberdeenshire Dee, to produce a model structure that is testable, comprehensive and realistic. The present model first uses the numbers and sizes of returning adult females to estimate fry production. Then it uses water temperature data and relative fish densities at ages to estimate growth rates, given the temperatures. Finally it utilises data on smolt sizes-at-ages to estimate size-dependent rules for juvenile emigration as both autumn migrants and spring smolts.

The Girnock study site provides some forty years of high quality data on: (i) adult numbers and sizes; (ii) water temperatures; (iii) summer sizes at ages; (iv) counts, with sizes at ages, of emigrants. We emphasise that no other site in Scotland approaches either this breadth of information or its temporal extent. Although in the past decade electro-fishing results about juvenile salmon sizes have become more widespread, the number of sites for which age information is available is far less, and virtually none of them also have the adult 'input' data or the juvenile emigration records. Accordingly, two further key questions emerge. Even if the developed models are capable of mimicing the

dynamics of lowland salmon populations, KQ.1.3 can they be adequately parameterised in the absence of data on the numbers, and sizes-at-ages, of spawning adults (*ie* separate Stock-Recruitment data for the lowlands) and, KQ1.4, can they be adequately parameterised in the absence of data on the numbers and sizes-at-ages of juvenile emigrants?

**Modelling philosophy**
Our modelling philosophy is to aim to maximise our understanding by using parsimonious models that, given their process-based realism, should still work in somewhat novel situations. In designing such models one needs to account for crucial ecological processes within the limits of the available data. In the extreme, if biological theory deems a process essential to sensible understanding and there are no suitable data with which to estimate the parameters of the process, then building a model without the process is a waste of time. One has to accept that the understanding would be inadequate, and building it therefore not worth the effort. Conversely, extra biological processes should not be added to a model purely for the sake of increased realism that available data cannot support. They should be included in a model only if, following Ockham's Razor, it can be shown that a model variant without them is appreciably inferior at explaining the data to the variant including them.

**Model Development**
   Given the above modelling philosophy, we specifically chose to investigate the realism of the models of salmon populations developing to smolting (hereafter abbreviated to Smolt-Split models, to reflect the splitting of the size-distribution of parr into emigrant and resident portions) using the detailed Girnock data, as this gives us the best chance of identifying dynamic deficiencies.
   Having completed the first phase of development with the Girnock data, our assessment of future model refinements will consider two aspects.
- Firstly, which further process details might be worth adding to allow fine-tuning of the model to the salmon life-cycle, as exemplified by the Girnock data.
- Secondly, which crucial aspects of the present model cannot be adequately parameterised with data of lesser quality and degree than the Girnock and, as potentially judged by omitting them from the Girnock model, how seriously would their omission impair our understanding of other sites.

**Parameterising at novel locations: the limitations of sample sizes.**
   Details of population dynamics will depend upon the physico-chemical environment, including variables such as altitude, stream flow, water temperature and water quality. Some, if not most, of these driving variables will be correlated to each other (co-linear predictor variables). Details of population dynamics will also vary with different biotic habitats, including aspects such as bed-substrate, shelter, food supply, predators and competitive effects. All these factors could be expected to have at least some small effects on fecundity, growth, mortality and emigration. Our experience with the intensively monitored Girnock site led us to believe that, at the strategic level of between-population comparisons at which these models are presently focused, some of these

aspects are either of secondary importance or not amenable to wide spread study on cost grounds.

Field data on populations of sub-catchments typically come from a handful of electro-fishing sites. They are typically 20 to 40 metres long and about 10 metres wide, representing

- 100 to 300 square metres
- Some 100 fry and 50 parr
- Around 1% of the wider watershed

Stochastic error alone on these likely sample numbers of fish per site, representing both the size and density estimates, mean that minor factors affecting growth are not likely to be detectable, and survival can only be accurately estimated for an amalgamation of sites which will probably have different habitat compositions. Table 1 lists some obvious environmental and habitat factors pertinent to salmon population dynamics. Four of the five likely primary and secondary factors affecting growth are measurable, but are inter-correlated, so that their interpretation is hard. Only two of the six suggested primary and secondary factors on survival can be readily measured at the site level.

In short, for the aims here required, the constraints of practicable fieldwork prevent the detailed study of potential components of survival estimates. Growth is more amenable to study, but even this requires replication by site within covariate combinations that have not, so far, been achieved at the level necessary to de-confound the effects of the key primary drivers. KQ1.5 Which processes can be adequately discerned at a population, as opposed to a sampling-site, level?

| Table 1 | Likely relative importance of the direct effects of different variables | | | |
|---|---|---|---|---|
| | | **Relative importance to fry and parr** | | |
| **Aspect** | **Variable** | **Growth** | **Survival** | **Notes** |
| Environ. | **Altitude** | Primary | Tertiary | 1 |
| | **Temperature** | Primary | Tertiary | 1 |
| | **Water Quality** | Secondary | Tertiary | 1, 2 |
| | Stream Flow | Tertiary | Primary | |
| Habitat | Stream bed | Tertiary | Primary (ova) | 3 |
| | Shelter | Tertiary | Primary | 3 |
| | Food supply | Primary | Secondary | 3 |
| | Predators | Tertiary | Primary | 3 |
| | **Competitors** | Secondary | Secondary | |
| | | | | |
| *Note 1* | *Altitude, Temperature and Water quality are almost certainly co-linear.* | | | |
| *Note 2* | *Effect on survival low, unless water severely polluted.* | | | |
| *Note 3* | *Hard or impractical to measure in the field* | | | |

**Scaling up from sample sites to local and regional populations.**

The historical Girnock study has six sites which are annually sampled for fry and parr densities to represent some 8 km of burn. Given that different portions of the burn are more or less accessible to natural spawning in different years, due to water levels in autumn, it is unlikely that these six sites fully represent the fry and parr stocks of the burn in all years. This density of coverage is relatively high when compared to other studies.

Accordingly the present models have not been fitted to the fry and parr densities, estimated from summer electro-fishing, as we do not believe they can be accurately scaled-up to the extent of the whole-burn, at which the model naturally operates in order to represent a realistically large population segment, and to the actual whole-burn scale represented by the trap data for immigrant adult breeders and emigrant juveniles.

KQ.1.6 Are the juvenile sample sites fully representative of the wider population?

**Resumé**

This section has considered the present state of the SF0274 Freshwater Phase Salmon Population model in the context of the wider, full life-cycle model that this project is developing. It highlights the constraints of suitable data, both local and regional, needed to invalidate unrealistic or over-complex models. The next section considers the three main components of the present model (adult production of fry; growth of fry and parr; smolting of parr) in the twin, and sometimes conflicting, lights of (i) potential model refinement and (ii) widespread parameterisation of the model to represent different and divergent Scottish salmon populations.

**Important Biological Stages and the present Models**

The present freshwater smolt-split models (v4, v5) have four main elements and life-history stages. Firstly, a stock-recruitment curve which gives the general relationship between adult female numbers to the numbers of fry found in July of the following summer (the earliest reliable censuses are feasible). Secondly, a growth module, differently parameterised for fry and parr. Thirdly a size-dependent emigration module, differently parameterised for autumn migrants and spring smolts. Fouthly a mortality module between July fry and emigration. As mentioned above, the present models do not include fitting to the juvenile densities estimated in summer by electro-fishing, as we are unconvinced of the ability to reliably scale-up the site density data to something realistic for the whole burn.

The following forward-look sections will cover these elements of the model in sequence, considering both desirable scientific investigations and those needed for more pragmatic management purposes. Management aims are likely to desire some recommendations to be made even in situations when some key elements of data, vital for proper scientific understanding and certainty, will almost certainly be lacking.

**Biological Stages**
**Stock-Recruitment: Adult female numbers to fry the following summer.**
**Rationale of present approach.**
The present models use a simple stock-recruitment curve of adult numbers to fry numbers the following summer, with a facility for fry growth (see below) to be started from sizes close to those observed for each cohort of fry sizes at their first summer census. This

pragmatic approach was adopted for several reasons. Firstly the basic analyses, supported by the final model, show a key density dependent process during this stage, which is broadly capture by the stock-recruitment relationship. Secondly, when considering the possible refinements outlined below, we were well aware of the large and variable losses during the ova and alevin stages. It is becoming clear that, even in pristine upland streams like the Girnock, many of these losses are attributable to variable ground water quality at the redds, at such fine temporal (a few days) and spatial (a hand-breadth vertically or horizontally can be critical) that their accurate prediction on a widespread basis is well-nigh impossible (see, for example, Malcolm *et al*, 2003, Malcolm *et al,* 2005). Thirdly, although we believe it would be informative and mathematically possible to model and fit the temperature dependence of fry growth, (as constrained by local food supplies), to data on fry sizes, there are presently no adequate fry size data with which to parameterise such a model. This deficiency arises from the inability to reliably sample the whole range of fry sizes from natural streams until July, about the time of the historic Girnock summer census.

   We reached the above conclusions with reluctance, as the density dependence evident in this stage of the life-cycle is clearly crucial to the overall stability of freshwater phase, and it would be highly desirable to tease this apart. We note that modern genetic methods would permit a mixture of field-enclosure and field-manipulation experiments which could greatly elucidate these key periods. This research priority was also highlighted by the EU's GENE-IMPACT workshop (Pitlochry, April-07). KQ2.1 Would a combination of field-enclosure and field-manipulation experiments involving genetic markers usefully elucidate key parameters about the ova to fry growth and survival periods?

   We note that the direct relationship between female numbers and numbers of fry recruits used in the smolt-split models omits data on ova production, by females of different body sizes, which is discussed below.

**Stock-Recruitment: Potential refinements.**
   At first sight this section should be very short. We concluded above that, even at the Girnock Burn, there are insufficient data to achieve much more than a stock-recruitment curve without a major study involving genetic markers. However, there are a few important ancillary aspects which could usefully be addressed in the short term.

   Our dilemma arises from our wish to generalise the model, especially to situations where the breeders are predominantly grilse. Recent work on the condition on returning Scottish grilse (Smith *et al*, 2007; Bacon & Palmer 2007) has shown that, since about 2000, the weight-to-length ratio of grilse has declined markedly, and their lipid reserves even further (Todd *pers comm.).* These declines are to such a degree that Todd (*loc cit*) expects appreciable declines in fecundity. Unfortunately, the crucial data to relate 'fish condition' to either egg numbers (or egg quality and egg survival) seem to be largely lacking. Despite this, it is difficult to see how a full life-cycle model developed in the next few years can totally ignore this fundamental aspect. KQ.2.2 Can we relate female salmon condition, when returning to the estuary,  to egg numbers and/or egg survival.

   Unfortunately the historic Girnock burn data do not include the weights of returning females. Historically it was argued that, as some of the fish are part-spawned before they reach the Girnock, such weights would not give a true picture (of the condition of maiden fish). With hindsight this argument, while true, is unfortunate. Weights of the genuinely

maiden fish would have been useful anyway, and weights of the part-spent fish would almost certainly have given a better estimate of the ova input to the Girnock study site than either just the number of females or just the lengths of those females. There appear to be very few data sets, from either the Girnock or Baddoch, where all three of females' lengths, weights and egg numbers have been simultaneously recorded. In view of the fact that both the Girnock and Baddoch burns now have protocols where the females are (often) stripped of eggs, there is a prime opportunity to collect this information. As the egg incubation protocols (in good quality water) keep the eggs from each fish separate, and count live and dead eggs at 'eyeing', then taking the weights of ( the female before stripping; her eggs; the associated body fluid; the female after stripping ) would not only provide useful information with regard to egg production and female condition, but the resulting 'kelt' weight to length relationships would give a useful approximation to the 'near lethal' lower limit of 'condition indices'. We note that, with few adults presently returning to the Girnock and Baddoch burns, this work might need to be repeated over a few years. KQ2.3 Collate existing, and especially get extra, information on females lengths, weights and egg numbers at spawning from the Girnock and Baddoch burns with a view to better predicting ova production by returning females, depending on their weights and lengths.

We note that, since drafting the above section (in the summer of 2007), a small initial data set on stripped females at the Girnock and Baddoch in 2007 strongly supports the above contention about predicting total productivity when this involves part-spent females. However, to be fair, such a lack of precision would probably only cause error, rather than bias, in the stock recruitment relationship so long as any discrepancy was largely constant. Unfortunately, in years when poor flows delay arrivals of adult females, it is quite plausible that more of the late-arriving females will be part-spent. Such effects (more part-spent fish when fewer females) could induce bias in the stock-recruitment estimates over time, especially if climatic changes altered the pattern of spates.

But overall, although KQ.2.3 is pertinent, that question of detail pales against the more fundamental KQ.1.6 (what could be achieved if not even the number of breeding adult females is known?)

**Stock-Recruitment: Widespread application.**

A useful degree of utility in the current models comes from the combined fitting of female numbers, via the stock-recruitment curve, and also to the numbers of emigrants (adjusting for parr mortality and smolt size). Regrettably there are hardly any other sites in Scotland where either the annual numbers of spawning females or the numbers at age of emigrating juveniles are known, let alone both. We here consider how the models might be modified if the adult numbers were unknown.

There would seem to be three possibilities.

A.1 Base the model's annual input on a (scaled relationship to) an annual rod-catch index, from a suitable local region and period (for early/ late run fish and locations).

A.2 As for A.1, but use a smoothed trend through such local or regional data

A.3 Simplify the model to start only with data on fry sizes and numbers observed in a summer census.

Either of these possibilities might work, and their relative merits could be assessed by simulating from the Girnock data. However, we caution that lacking both adult input and smolt production data, as would be the case for many real local management situations of salmon stocks, would probably be a much more severe constraint than lacking either alone.

KQ.2.4 How useful might the models be for the management of real, local, populations in the absence of data on spawning adults (beware likely simultaneous loss of data on smolt output too).

We note that our caveat about the potential use of the models for local management in the absence of adult and smolt data does not apply to the strategic objective of the current SF0274 project, which simply needs to contrast the effects of different culling regimes (for example rod-catches) on the spatially segregated populations, simulated over a potentially wide range of adult return-time scenarios which appear to reflect the spatial sub-structuring of the populations.

**Growth of fry and parr and their density and temperature dependence.**

There are two key processes that need incorporating into the model for it to be of general use. The negative density dependence of fry and parr densities on the growth of fry, and a general temperature dependent growth function, to replace the relative temperature approximation used for the Girnock data in v4 of the model.

**Density dependent growth.**

V5 of the model includes a negative density dependent effect of fry densities on fry growth, a refinement which significantly improved the model's fit to the Girnock data. KQ.2.5 Should the density dependence be refined to include effects of *both* fry and parr on fry growth.

**Temperature dependent growth.**

More fundamentally, the temperature-dependence function of fish growth used in both v4 and v5 is presently a mathematical convenience that uses relative temperatures, and does not correspond to temperatures in $^{o}$C. The necessary algebra to achieve a fully realistic portrayal of the absolute temperature effect, over the necessary environmental temperature range in $^{o}$C, has been developed (by Gurney, in May 2007) but there has been insufficient project time to incorporate this refined formulation into the computer program. Such a degree of realism is fundamentally crucial to the spatial 'catchment' modelling envisaged for the first, present, phase of SF0274, and would ideally be added during development of the catchment scale, interacting populations model. However, if suitable fish growth and temperature data are not available to parameterise the lowland situations, a simpler representation might be adequate for the initial catchment model. In which case the issue of representing the absolute temperature relationship of fry and parr growth could stay unimplemented . KQ.2.6 At what stage will the full realistic representation of temperature dependent growth be incorporated?

### Growth of marked individuals

The SAAV models are designed to represent the growth of groups of individuals, such as families (genotypes) or small populations. They ascribe changes in size to the growth of the same group (population) of individuals, and would give misleading results in situations where the composition of the sample changes, for example due to size-specific mortality or em-/immigration. This assumption is very robust for the Girnock (and probably Baddoch and Mark) population, but the initial work on the Isla tributaries (and Stuart's results from the Tay) suggest that home-range sizes, or dispersal, are much larger in at least some lowland situations. Accordingly the assumptions of a 'closed population sample' may be violated in these situations. Sub-samples of marked individuals which are re-caught would be available, but in appreciably reduced numbers and with an unknown relevance and bias to the total population. KQ.2.7. Can the models be effectively used in lowland situations where individuals may disperse much more widely and many of them be recaptured much less frequently.

### Growth data.

We note that there is an unfortunate gap in the electro-fishing data from the Girnock between 1987 and 1999, when rather radical changes to the population were taking place. There are thus no growth data to help elucidate the process. However, in principle, an estimate the growth achieved by the different cohorts could be approximated by back-calculation of the likely fish sizes, at their 0, 1, 2, 3 freshwater winters, from the sample of scales obtained from the smolts. It is worth considering whether those data would be likely to plug a crucially informative gap. KQ.2.8 Would estimates of achieved growth, from back-calculated smolt scales, be usefully informative about the Girnock population in the changing situation of the period 1987~1999. Turning this question on its head, we note that, in situations where the same individuals are not frequently re-captured by repeated (monthly) electro-fishing visits, then examination of otoliths from large parr or smolts might be a means of approximating growth trajectories over time (but note that such methods are not yet proven or calibrated. KQ.2.8b Could otoliths from parr or smolts be used to estimate growth trajectories from widely different environments?

### Parr survival.

The present model only estimates parr survival indirectly, as the time-discounted difference between the density of fry at the start of a cohort and the numbers of emigrants (autumn parr and smolts) leaving at different ages. The starting fry densities are 'scaled up' from electro-fishing sites, but the emigrant data are estimates from the smolt-trap for the entire burn. The difficulties of scaling up from sites to the whole Girnock are considered below, as are infelicities in the emigrant data caused by trap spillage. For the present we merely note that the present model avoids compounding the scaling-up error on numbers by not using estimates of parr densities. However, if the scaling-up issue could be resolved, then fitting a model to parr numbers as well as parr sizes would clearly be a useful improvement. KQ.2.9 Under what circumstances should a future model fit to parr densities as well as parr sizes? (see: Scaling-up; trap spillage).

In principal the multiple re-capture fieldwork protocols would allow estimation of parr survival (as distinct from recapture, dispersal and death) estimates to be made from the recapture histories of marked individuals (CMR methods). However, initial attempts to

do this (Bacon & Thorley) met with limited success, for several reasons. In brief, the situation is very complex. Probabilities of being resident and recaptured (at a standard site) vary, for salmon parr, with season, body size and precocity of males to name just the more obvious. The total numbers of fish sampled at the Girnock sites are relatively small to untangle such a complex situation, and not aided by the timing of historical EF visits, which were designed to elucidate growth and not survival and dispersal. Incorporation of data about fish caught emigrating at the smolt trap is helpful, but introduces yet more complexity and uncertainty. Critically the proportion of emigrants not sampled at the trap, when it spills in spates, is unknown and is confounded with the mortality estimation, especially the mortality of (precocious parr) which may leave their summer territories in autumn and remain, un-sampled, in the burn for long periods. KQ.2.10 Are the needs to know parr survival more accurately sufficient to warrant re-structuring future field work to obtain better and more robust estimates of survival, dispersal and total (burn) population densities?

### Scaling fry and parr densities up from EF sites to the whole burn.

The simplest way to scale-up from the electro-fishing sites to the whole of the Girnock burn (above the smolt trap) is simply *pro-rata,* by [area of whole burn / area of electro-fishing sites]. Historically (Buck and Hay) this was done within two different habitats, although the evidence for clear density differences between the two habitat types is slight. The endeavour is hampered by having just six sites in most years, allowing appreciable stochastic variation (eg which sites are near redds in which years). The difficulty would be more theoretical than practical if it could be argued both that the burn was uniform (with regard to growth and fry input) across its length and across years. Unfortunately, neither is true. On the spatial aspect, Fig.1 below shows the results of the 2005 Girnock Fry survey, indicating clear changes in both densities and achieved growth following a year when, for the first time ever, the burn was uniformly stocked to medium-high density over its entire length. On the annual aspect, it is well known that redds are clustered in particular locations (and that fry disperse only about 100 m upstream and 500 m downstream from redds), and that adult female penetration up the burn varies between years.

The Girnock Fry Survey (2005 onwards, Fig.1) data are based on relative densities from single-pass electro-fishings (due to manpower constraints). This is unfortunate, as the accuracy of the density estimates is unknown. However, for a few years in the early 1970s, there were between 30 and 12 sites fished by three (or more) passes each year. These data would give absolute density estimates, for both fry and parr. Unfortunately only about six of the sites (each year) include scales for aging. However, it is likely that the fry/ parr contrast could be adequately illuminated by comparison with the adjacent sites were taken.

KQ.2.11 Should the un-aged multiple site, 3-pass EF data from the early 1970s be worked up to elucidate the scaling-up problem along the Girnock?

KQ.2.12 How much effort is it worth expending trying to get better whole-burn estimates of salmon fry and parr in the Girnock in future, and what are the best ways of doing so?

**Fig.1.1, 1.2.** Mean fork-lengths, mean single-pass densities and biomasses of salmon fry (A.1) and parr (A.2) at some 20 sites along the Girnock burn following uniform stocking in 2005. The data are shown for two comparable surveys in August and October 2005. The fish attributes are plotted against altitude of the sampled sites, but entirely analogous results are obtained with distance upstream. Note that neither fork-length, density nor biomass are uniform along the stream.

**Fig.1.1 Date for salmon fry.**                                **Fig.1.2 Data for salmon parr.**
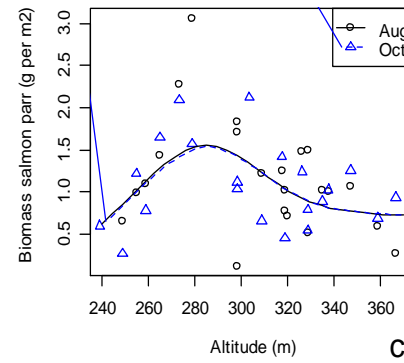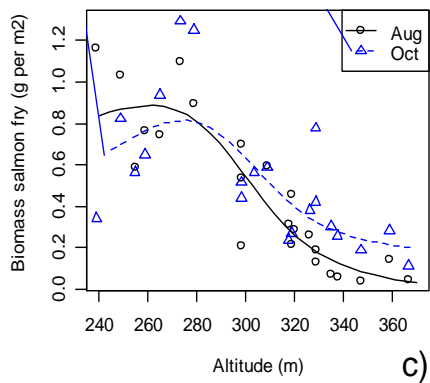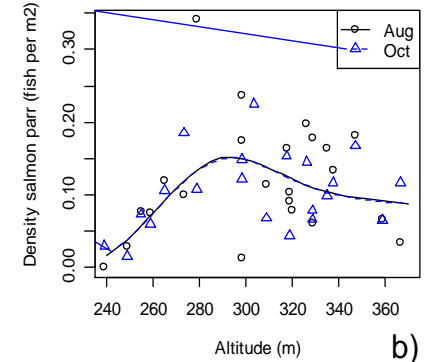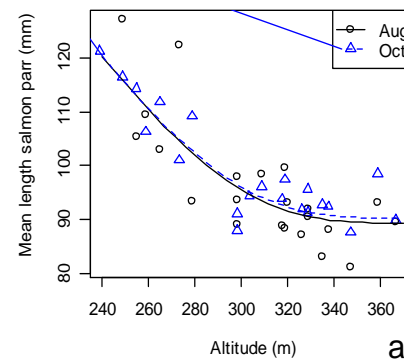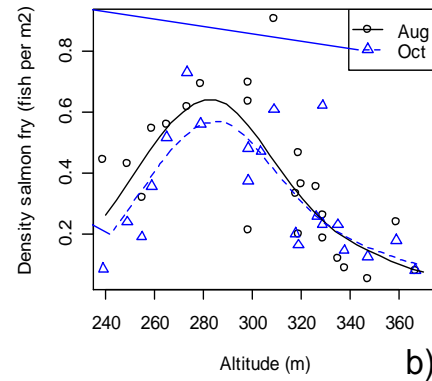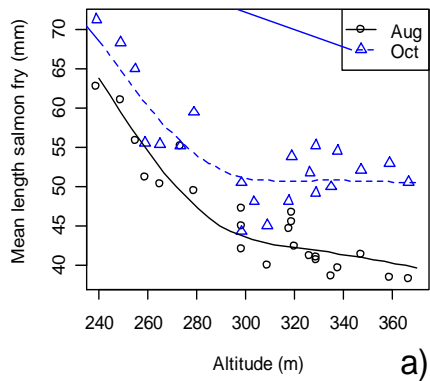
**Size dependent smolting threshold.**

The findings of the present model seem very robust in this regard, and accord well with former semi-quantitative beliefs. The emergent properties of the model show that a fixed smolting threshold can give a rich range of observed smolt sizes (due to density and temperature effects on the overall growth achieved by different ages and emigration seasons). It is likely that the estimated Threshold Smolt Size could be a national, or even an international constant. If it were, that would greatly facilitate predictions in other situations. However, this important point should be firmly established, and not assumed. Thus a couple of issues remain.

KQ.2.13 can we get data from other situations (Baddoch, N Esk smolt wheels?) to show whether the smolt threshold size is constant over space, and not just over time at the Girnock.

KQ.2.14 Would it be worth fitting the lower-limit of smolting with a bit more rigour, to elucidate just which fish, perhaps affected by age, emigrate at the smallest sizes.

**Emigrant numbers.**

We have mentioned above, in relation to dispersal and mortality estimates, the difficulties of estimating cohort growth trajectories and, particularly, survivals when the proportion of juvenile fish leaving the burn during spates (which is indeed precisely when most emigrants leave) is not accurately known from the trap data due to unknown spillage. The bias is clearly likely to be largest, and maybe serious, for survivals rather than growth. So the issue is, KQ.2.15, whether anything feasible can be done to estimate trap-spillage in different spate conditions (ie using the present spill-depth monitor on the smolt trap)

**Environmental Drivers and Processes.**

It is clear that water temperature, water quality (*eg* $O_2$ concentrtions, phosphate, nitrate; pollutants) and current velocities (food delivery and feeding opportunities, especially for fry (Critical Displacement Velocities) are inherently likely to affect the growth trajectories over time, and the survival, of juvenile salmonids. It is equally obvious that all of these will co-vary, approximately, with altitude. However, those obvious effects are not quantitatively well described, indeed they appear to be so poorly known that their relative importances are unknown. This is unfortunate, as some, such as aspects of water quality and food supply, are amenable to management alteration, whereas others are not.

Two existing FL studies (SF0727, SF0273) are directly addressing these very issues, and are working closely with this modelling endeavour (SF0274). At this stage we note that getting data from 'lowland' situations is critical to the spatial aspects of SF0274 and its potential as a management tool.

In the short term, the process based model developed from Girnock data has outrun FL's ability to supply data from other, lowland, situations with which to challenge the model, and estimate comparable parameters for lowland, probably grilse dominated, salmon populations. So, in the short term the issue is whether suitable lowland data will become available to challenge the existing model (KQ.1.1). In the longer term we note that ecology is often complex, and that if suitable data do become available, the process of fitting it is quite likely to reveal a novel process or two which may need incorporating

into an enhanced version of the present smolt-split model. Likely candidates here would be the effects of pollutants, or of competitor species, in decreasing the survival and growth of juvenile salmon when compared to the relatively pristine and competitor-sparse situation of the Girnock. KQ.2.16 As data from more widespread sites become available, will the present growth model need expanding to incorporate new processes that can only be parameterised across a range of sites?


**Discussion.**

This report is intended to summarise the applicability of the SF0274 'Smolt-Split' model of juvenile salmonid growth (versions 4 and 5) to a variety of potential uses in other FRS FL projects. In particular it is intended to draw attention both to other FRS FL data sets which might illuminate details of the model and to other FRS FL objectives which might be facilitated by use of the model. In the latter regard emphasis is placed on potential developments of the model which might enhance such wider use to aid assessment of the status of populations of juvenile salmonids.

Key aspects where such development might be worthwhile are framed as questions in the text, and collated into Appendix One.

The priority with which this topic list might be addressed would, naturally, vary depending on the priority attached to illuminating different aspects of the freshwater life-cycle to aid salmonid population management. We do not consider it appropriate to comment on this without wider discussion with FRS FL colleagues.

We had, however, expected to comment on the importance of these different issues with regard to the SF0274 modelling salmon populations, and the possible extension of the present contract (which ends in fifteen months, in March 2009).

Since drafting the text, however, progress on the 'marine phase model' has, unexpectedly, strongly suggested that

D.1) while marine mortality may constrain the total production of salmon populations in freshwater, and can even make some populations unviable (total mortality exceeding total production to adulthood),

D.2) key aspects of the biological dynamics controlling the natural regulation of salmon population are interactions between different components of the stocks, even within single populations. These interactions occur between the Life-History strategies of both (a) the two sexes and (b) the main sea-age classes (grilse and 2SW fish). Furthermore,

D.3) that these competitive interactions most probably take place in FW, almost certainly between river entry summer-fry, and with significant controlling effects probably taking place between river entry and spawning.

Our current investigations of these aspects are still preliminary, and some key aspects are also based on rather sparse data. It is accordingly too early for us to confidengly judge the likely relative importance, to salmon management, of these complex competitive interactions and the freshwater stages in which they could occur:

FW.1 Estuary entry and river ascent to spawning sites;

FW.2 Spawning, female fecundity, ova survival to summer fry (at size f');

FW.3 Growth and survival from summer fry (size f') to smolts.

   Accordingly, until we have a better understanding of the overall complex, interacting system, it seems pointless to prioritise purely the topics within the freshwater FW.2 and FW.3 reviewed in this report.

   We therefore defer that discussion until completion (in Mar-08) of the next SF0274 milestone report (an *'FRS internal report describing the single sub-population closed life-cycle salmon model, and assessing a partitioning scheme for meta-population models constructed on this basis'*).

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## **APPENDIX ONE**

Summary of the Key Questions.

KQ.1.1 Will suitable data be available from the Lowlands to parameterise the models.

KQ.1.2 Will the model parameterised for the lowlands need to exclude potential differences between lowland nursery streams and lowland wide and deep rivers? Note similar implications for wide upland rivers.

KQ.1.2b. Are lowland populations, even of small tributaries, so much more mobile as to conform poorly to the necessary 'population estimate' assumptions.

KQ.1.3 Can the models be adequately parameterised in the absence of data on the numbers and sizes-at-ages of spawning adult numbers and sizes? (*ie* separate Stock-Recruitment data for the lowlands).

KQ1.4 Can the models be adequately parameterised in the absence of data on the numbers and sizes-at-ages of juvenile emigrants?

KQ1.5 Which processes can be adequately discerned at a population, as opposed to a sampling-site, level?

KQ.1.6 Are the juvenile sampling sites at the Girnock fully representative of the wider population?


KQ2.1 Would a combination of field-enclosure and field-manipulation experiments involving genetic markers usefully elucidate key parameters about the ova to fry growth and survival periods?

KQ.2.1.b Would details of maiden and part-spent females, their ova production and ova sizes, better inform the understanding of recruitment to the fry stage?

KQ.2.2 Can we relate female salmon condition when returning to the estuary, to egg numbers and/or egg survival.

KQ2.3 Collate existing, and especially get extra, information on females lengths, weights and egg numbers at spawning from the Girnock and Baddoch burns with a view to better predicting ova production by returning females.

KQ.2.4 How useful might the models be for the management of real, local, populations in the absence of data on spawning adults (beware of likely simultaneous loss of data on smolt output too).

KQ.2.5 Should the density dependence be refined to include effects of *both* fry and parr on fry growth.

KQ.2.6 At what stage will the full realistic representation of temperature dependent growth be incorporated?

KQ.2.7. Can the models be effectively used in lowland situations, where individuals may disperse much more widely and many of them be recaptured much less frequently.

KQ.2.8 Would estimates of achieved parr growth, from back-calculated smolt scales, be usefully informative about the Girnock population in the changing situation of the period 1987~1999.

KQ.2.8b Could otoliths from parr or smolts be used to estimate growth trajectories from widely different environments?

KQ.2.9 Under what circumstances should a future model be fitted to parr densities as well as parr sizes? (see: Survival; Scaling-up; trap spillage)

KQ.2.10 Are the needs to know parr survival more accurately sufficient to warrant re-structuring future field work to obtain better and more robust estimates of survival, dispersal and total (burn) population densities? (see: Survival; Scaling-up; trap spillage)

KQ.2.11 Should the un-aged multiple site, 3-pass EF data from the early 1970s be worked up to elucidate the scaling-up problem along the Girnock?

KQ.2.12 How much effort is it worth expending trying to get better whole-burn estimates of salmon fry and parr in the Girnock in future, and what are the best ways of doing so?

KQ.2.13 can we get data from other situations (Baddoch, N Esk smolt wheels?) to show whether the smolt threshold size is constant over space, and not just over time at the Girnock.

KQ.2.14 Would it be worth fitting the lower-limit of smolting with a bit more rigour, to elucidate just which fish, perhaps affected by age, emigrate at the smallest sizes.

KQ.2.15, whether anything feasible can be done to estimate trap-spillage in different spate conditions (*ie* using the present spill-depth monitor on the smolt trap).

KQ.2.16 As data from more widespread sites become available, will the present growth model need expanding to incorporate new processes that can only be parameterised across a range of sites?