Demographic observations (estimates of size-at-age and numbers) of the marine phase of the life-cycle of Scottish salmon needed for a dynamic meta-population model.

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SF0274 Milestone 5a, Dec-2007

Executive Summary.

- This report reviews FRS FL's key Scottish data sets on those parts of the salmon life-cycle outwith our earlier modelling summary, which covered the freshwater period from spawning to smolting.
- Preliminary, strategic, models have been used to investigate which periods, aspects and mechanisms in the remaining ('marine') parts of the life-cycle, are likely exert crucial controlling influences on the dynamical stability of salmon populations.
- Analyses suggest that the former paradigm, that the extent of achieved 'early marine growth' constrained the sizes, and hence fecundities and success, at which salmon returned to breed in freshwater, is dubious.
- It appears rather that interactions between growth, sex and the heritable trait of 'sea age at return' are crucial to determining the relative fitnesses of different salmon phenotypes, and hence the dynamics of the controlling population processes.
- It is much more likely that these key control processes operate in freshwater, between river entry and ascent, through redd placement and ova survival to summer fry, than during the true 'at sea' stage.
- Key FRS FL data sets reveal differential distributions of salmon by sexes, sea-ages and sizes along an altitude response cline of breeding site selection, which parallels the month of return from the sea.
- However, the spatial extent and precision of those crucial FRS FL data are presently not quite sufficient to allow quantitative modelling of all the various response functions.
- A detailed numerical understanding of the dynamics of the interacting morphs and sub-populations of salmon within a major river catchment is vital for a model suitable for management purposes. The compositions of such sub-populations differ by sea-age, size, breeding potential, competitive ability and genetically, and their dynamic interplay must be properly understood before they can be adequately predicted.
- It is presently unclear that progressing immediately to build a model of spatially interacting salmon populations will be the best immediate option for SF0274.
- This report builds on the initial use of strategic algebraic analyses (not reported here) to highlight key aspects of the salmon life-cycle which are, or are not, adequately known. These aspects and processes are discussed, and listed in two appendices.
- The next report (Mar-08) will present the quantitative arguments about which of those processes are most important. It will thus identify any knowledge gaps, prioritise them and recommend how best they can be bridged to underpin the desired management model.

- **Background.**

This milestone report was designed to summarize, in Dec-2007, progress with developing the 'marine phase model' of SF0274 prior to a description of the eventual quantitative model, due in Mar-2008. We specified the task as to "*Prepare an FRS internal report describing the marine-phase dataset compiled under research objective 3 above*". Research objective 3 was defined as "*To assemble and evaluate a dataset of demographic observations of the marine phase of the salmon life-cycle (especially size at age estimates) for selected meta-populations. We expect data from a variety of international sources to be a critical part of this exercise*".

Our paradigm when specifying these stages and reports was based on the widely supported assumption that the growth achieved by salmon at sea would determine the ages, dates and sizes at which they returned to freshwater to breed. Basically that fast-growing fish might return early, as grilse (one SeaWinter (1SW)) whereas slower growing fish might remain at sea for longer (multiple SeaWinters (MSW)). To this end we expected to draw upon a number of data sets of salmon size-at-age whilst at sea, including some sparse, but potentially crucial ones, of fish caught when at sea, and thus from a range of international fishing sources. We expected that these international data might provide key clues to the information already held by FRS FL for Scottish salmon.

In brief, our progress to date (Dec-2007), summarized below, has not supported this paradigm. On the contrary, it has engendered the development of a (somewhat) novel concept, whereby life-history interactions between the combinations of sexes and sea-ages of salmon could be crucial to understanding their overall population dynamics. Moreover, it looks as if the key stages when these dynamics operate are probably not at sea, but rather between river-entry and spawning, and thereby overlapping with the crucial stage from spawning to summer fry identified in our last report (smolt split model).

The format of this report accordingly differs appreciably from our prior expectation. We still review the available data, and enumerate those data sets we consider most important, but from the new 'river ascent' perspective outlined above, rather than the formerly expected 'achieved marine growth' viewpoint. Indeed, we will mention an approach and data set which we consider could probably a formal invalidation of the 'achieved marine growth' paradigm, and briefly discuss whether such formal refutation would be worthwhile.

Population perspectives

The final, spatial model envisaged under project SF0274 consists of a set of inter-acting salmon meta-populations, arranged as an altitudinal gradient along a river network. The extremes would be exemplified by:

- an upland type, of early-running (both grilse and MSW fish, but predominantly MSW) experiencing low temperatures in their freshwater environment and thus showing slow freshwater growth and high smolt ages
- a lowland type, of late-running (both grilse and MSW fish, but predominantly grilse) experiencing warm temperatures in their freshwater environment and thus showing high freshwater growth and lower smolt ages

To accurately parameterise such a model it is desirable to have detailed data for both extremes (upland and lowland) and some reasonably detailed data from locations in between. The detailed upland and lowland data could then be used to derive the main parameters, and the less detailed data from the intermediate sites used to better estimate parameters about the outcomes of the interactions in situations where the proportions of the two putative types are more even.

Unfortunately FRS does not have access to such data, nor, indeed, are we aware of any other Scottish source which does. The long term (1966~2006) Girnock data set, and the shorter Baddoch (c 1986~2006) series are highly informative about the freshwater stages of the upland situation, but they are too sparse to give accurate information on marine survival or growth. There is no comparable source of data for even the other extreme of a lowland population in freshwater.

The best source of data on marine growth and survival is the large data sets collated by FRS FL at Montrose for the North Esk. These will be described in some detail below, as they are critical. However, we must emphasise from the start that these North Esk data represent mixed populations (stocks) of fish with regard to the altitude cline. The Kineaber Mill smolt trap, where smolts are measured and aged, is near the estuary of the N Esk, and although it catches a sample of all smolts, from all tributaries, there is currently no way of distinguishing the tributary (or altitude) of smolt origin. The sample of returning adults, that is obtained from the Net and Coble fishery near the N Esk estuary and is measured and aged, also represents the mixed populations of all tributaries. However, in regards to the destination tributaries of returning adults, there is reasonable data from radio-tracking (see below) which broadly allows early, middle and late running adults to be ascribed, respectively, to high, medium and low altitude types (seasonal run-times within a year, complicated by separate run start-dates and periods for 1SW and MSW fish, as described below).

Thus, in the absence of the clear, definite, desirable data, much of the challenge in this ‘marine’ phase modelling stage will be in discerning, with reasonable confidence, patterns and underlying control processes which can be deduced from information that is indistinct and fuzzy, at least from the viewpoint of this demanding project.

Our main conclusion is that the suite of data available for the river North Esk is not only the most suitable to our needs, but also representative of the main trends in salmon populations typical of the east coast of Scotland. Regrettably, there do not seem to be similar sets of coherent and complimentary data for the North or West coast Scottish rivers.

Overview of Data Sources

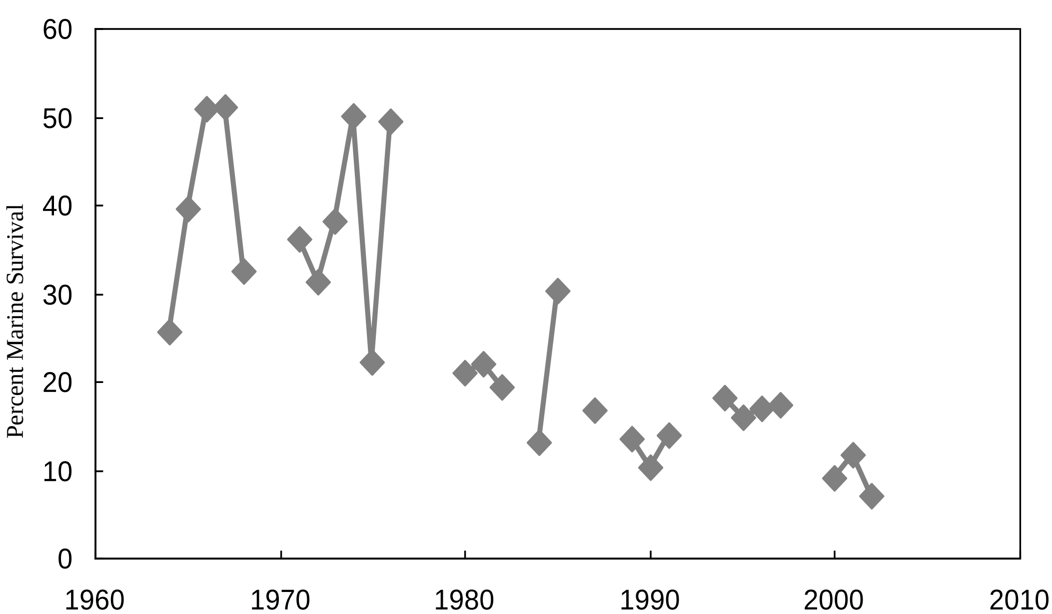
All of Scotland

National Salmon Catch DataBase. This information is curated by FRS FL at Montrose (see MDB.2 in Appendix 1). It comprises the legally-required Monthly Fishery Capture Records, from 1952 to the present, from all Scottish (salmon) fishing-right owners (see, eg, Statistical Bulletin, Scottish Salmon and Sea Trout catches, 2006). Madatorily, the data include for each ‘return site’, by year and month: numbers of fish, total weight of fish and method of capture (Fixed coastal Engine nets; net&coble esturary nets; rod-caught (and, since the early 1990s, rod-caught and released)).

At a river catchment level data these monthly data are available from the data-base. Work is in progress, but not due to be completed for a few years, to both to make the underlying data available at a finer level, potentially the individual fishing beats, and to facilitate this by a GIS 'query tool' interface, that will aid the selection of a suitable set of 'owners' for the region and period in question (given the complex histories of river stretches changing ownership on different dates, and the confidentiality of information and the individual owner level).

Analyses of sub-sets of this abundance data (for the rivers Helmsdale, Spey, Devron, Dee, Tay and Tweed) for rod-caught fish over many decades (Thorley *et al, in prep*) shows that there is strong temporal synchrony between the numbers of rod caught salmon at several of the major east Scottish Coast salmon rivers, showing strong coherence within years as well as discernible common decadal trends. In brief we conclude that these catch data for the North Esk (from Fixed Engines, Net&Coble and Rods), especially when combined with data from the North Esk Fish counter (since 1981) provide a powerful summary of the off-take by the various fisheries, enabling a 'Pre-Fishery Abundance' calculation to be used that allows marine survival, from smolt to coastal return, to be estimated for North Esk fish. We emphasise that it is the combination of data from the North Esk (smolt numbers, fishery off-take, adult escapement, etc) that makes the North Esk such a crucial, indeed unique, site. Figure 1 below indicates how the combination of smolt and adult return data can be used to estimate the marine survival of North Esk smolts.

Figure 1. Survival estimates for smolts leaving the North Esk and returning as adults.



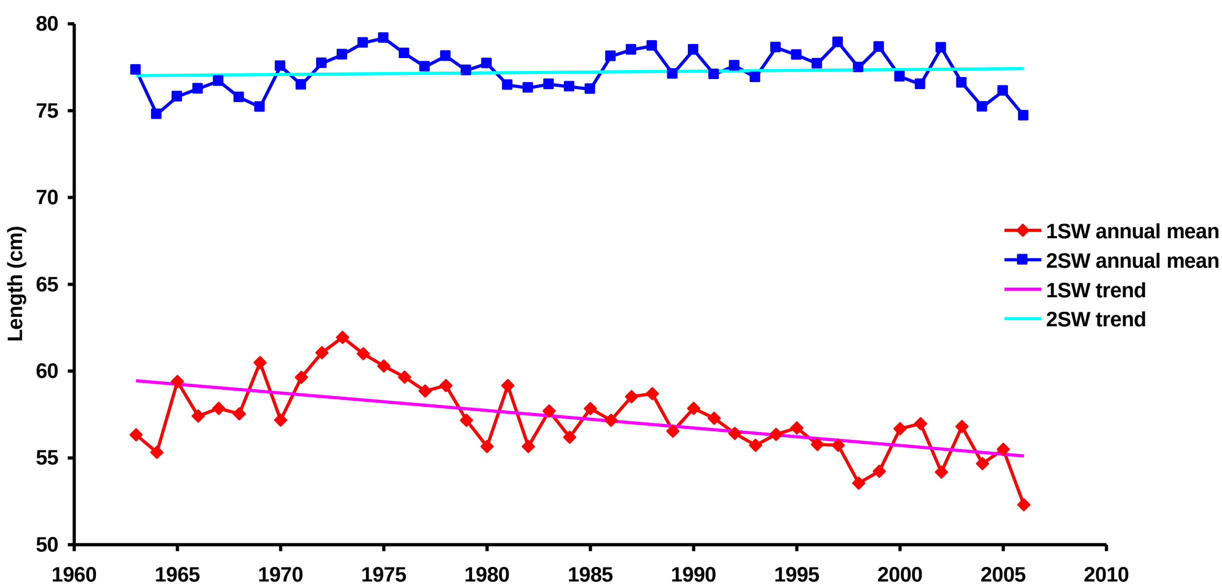
Marine survival of North Esk smolts.

Adult Salmon Catch Scale Samples, 1963 ~ present.

This data set is derived from scale samples from the commercially caught Scottish salmon (Fixed Engine and Net&Coble fishing methods). This information is also curated by FRS FL at Montrose (see MDB.1 in Appendix 1). The samples are not legally required, but are obtained 'opportunistically' by FRS FL staff. This has resulted in impressive series of records for the estuary Net&Coble fisheries on the rivers North Esk, Spey, Tay and Tweed, plus the Fixed Engine nets on the north coast at Strathy Point. Recorded data fields include, *per individual fish*, [Length, Weight, Age, Sex; and back-calculated lengths, at all Fresh-water and SeaStage winter ages, as estimated from the sampled scales]. We note that, unfortunately, the sex information is only from external characteristics, a method prone to considerable uncertainty and possible, but un-established, bias. As any bias would vary with fish size and month of the year, the possibility of bias is potentially non-trivial for some aspects (see below).

These biometric data have been subject to considerable scrutiny (Smith *et al* 2007; Bacon and Palmer, 2007; Bacon *et al* in progress; see Fig. 2 below) which have been crucial in forming our current views (see below). For the present we emphasise that, especially for the North Esk, the combination of this data set with its very large sample sizes (1,000s a year for the North Esk, comprising a relatively randomly-selected sub-set of the numbers of fish (both caught and which escaped the fisheries), for which date of return, fish length, sex, weight and sea-age are all known) is especially powerful, and key to our modelling endeavours.

Figure 2. Annual mean lengths of 1 sea-winter grilse and 2 sea-winter Atlantic salmon returning to the North Esk, 1963-2006, after adjustment for seasonal (days within years) changes in sizes of returning fish to standardize returns to a common date. The slight increases in salmon lengths and the larger decreases in grilse lengths are all statistically highly significant. (from Bacon & Palmer, 2007).



The North Esk

Almost uniquely for a Scottish river, and by far the largest, the North Esk is the source of large numbers of individually (Carlin) tagged smolts, marked as they are approaching the estuary prior to going to sea. A sample of the marked smolts is returned to the river above the trap on the (Morphie dyke) lade at Kineaber Mill, and a capture-mark-recapture (Lincoln Index) approach used to estimate the numbers of smolts that went to sea down the main channel (as opposed to the mill lade) and thus allowing calculation of the total smolt output from the North Esk. These tagging details (and the biometrics of the sampled fish) are also curated at FRS FL Montrose (see MDB.3.A, Individual biometric details of North Esk smolts in Appendix 1). The smolt data is electronically available from 1975 to the present (and the earlier records are in any case so fragmentary as to be barely useable. See Appendix 1). This smolt information is complimented by the collation of similar data for returning pre-tagged adults of North Esk origin (wherever they are captured, there is a financial incentive scheme to encourage their reporting by fishermen). These recapture details (and the biometrics of the sampled fish) are also curated at FRS FL Montrose (see MDB.3.B, Adult recapture details in Appendix 1) but, as of 2006, they are only available from 1998 to 2005. It is expected that new data, and about 10 years of prior data will be added each calendar year from 2006 onwards, but this is uncertain.

These data underlie crucial Capture-Mark-Recapture estimates of survival between smolting and adult return (see Fig. 1 above). But, as it is unfortunately not yet[1] possible to distinguish 'potential grilse smolts' from 'potential MSW smolts' it is not yet possible to reliably estimate separate survival values for grilse and MSW fish[2].

The Logie Salmon counter

Staff from FRS FL Montrose also operate an exceptionally well maintained and calibrated fish counter (see Eatherly et al (2004) on the North Esk, a few kilometres above the head of the tide, at Morphie Dyke. This has operated since 1981, and electronic data are available from then to the present. The full data set, including video-camera confirmatory pictures, is very complicated, as the counter records both up- and down-stream movements of fish, but summary estimates of 'nett upstream movements' are available, by month and year and can be incorporated into estimates of salmon abundance both 'pre-fishery' (ie survival from smolting to returning to the Scottish coast) and 'fishery escapement (as an estimate of the numbers of adults surviving to breed) (see Fig.1 above).

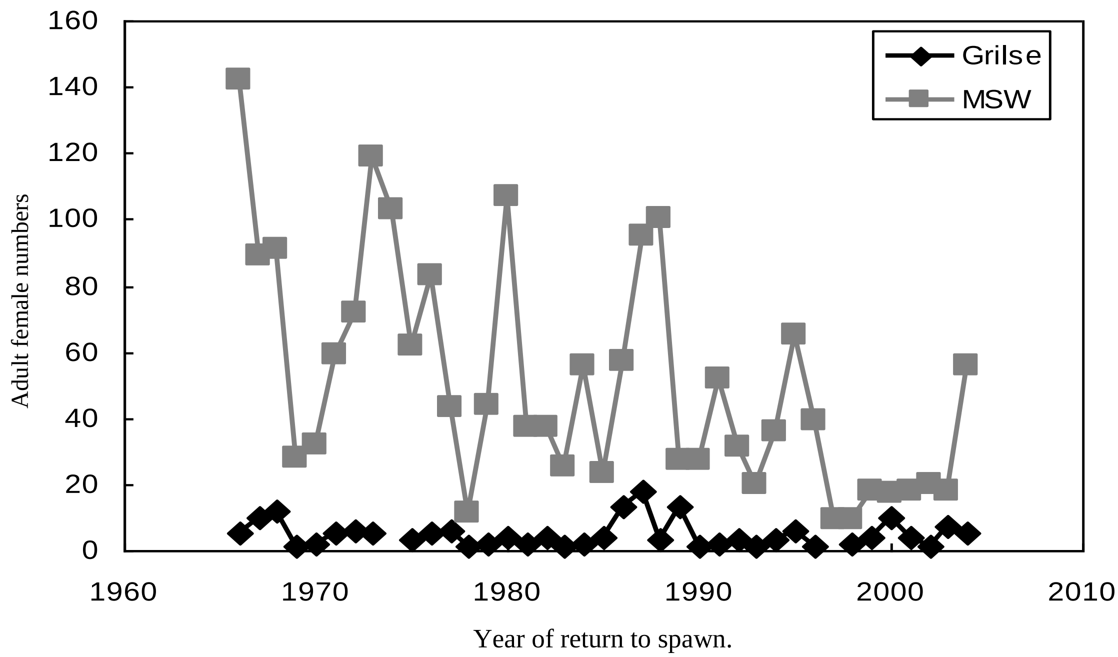
[1] The discovery and description of 'clock-genes' in salmon may, potentially and very importantly, remove this crucial obstacle in the near future.

[2] See below. The grilse:MSW trait is about 45% heritable, so the numbers of smolts that are potentially one or the other should be a function of production, survival and numbers of breeding adults in different (unknown origin) parts of the catchment.

The Girnock and Baddoch.

The Girnock data set has been fully described in the SF0274 context in several documents (Gurney et al 2007, 2008; Bacon et al 2007 (SFO274 Milestone 5a)) and we will not elaborate on it here. Suffice it to say that it provides the crucial single-population data set to parameterise the SF0274 'upland salmon' situation. In the present context, it also serves as a test as to whether, based on the smaller numbers of Girnock fish, the deduced patterns of changes, in size and abundance, of 'early run' North Esk fish do indeed approximate those observed for a single upland population. The shorter Baddoch data set (1986 to present) could serve as a second test (although the Baddoch data are not fully quality controlled yet (Dec-2007)).

Figure 3. Annual numbers of adult females returning to the Girnock Burn.

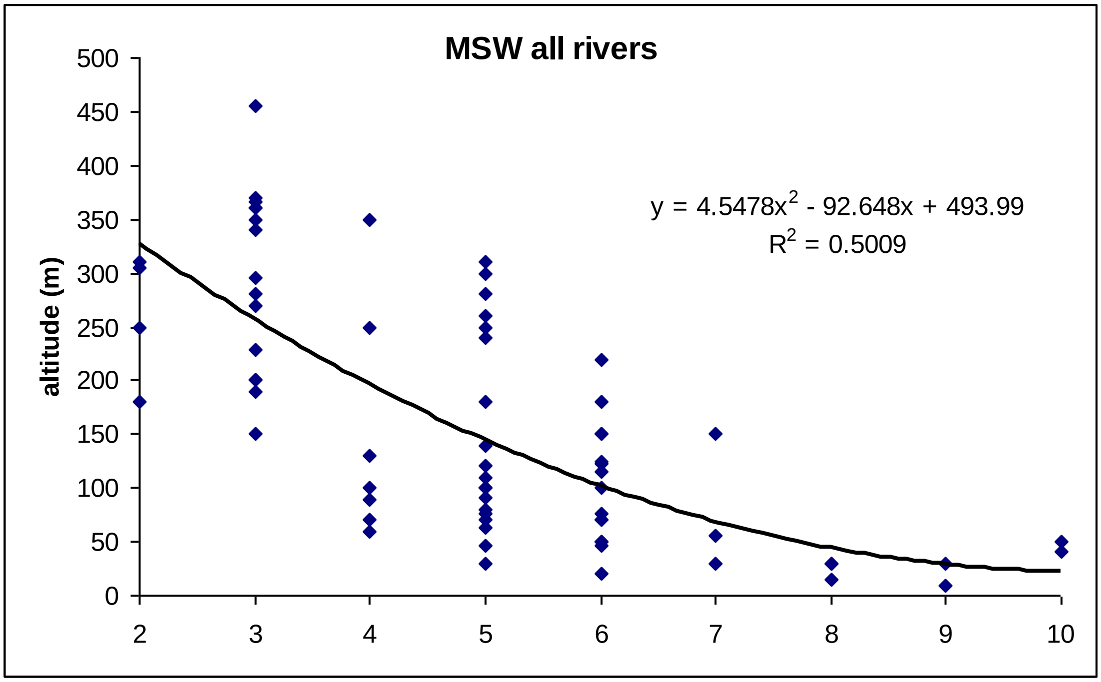


Other Data-sets

Radio-tracking data

Radio-tracking data, arising from salmon fitted with telemetry transmitters shortly after their return from the sea, and followed until they reached their spawning tributaries, is available for reasonable sample sizes of fish from five Scottish rivers (Dee, Little Gruinard, Spey, Tay and Tweed). As indicated in Fig.??nnn, there is a strong tendency for fish running early in the season, whether grilse or MSW fish, to spawn at higher altitudes than later running fish (of the same sea-age). Further details are given in (Hawkins and Smith 1986) We refer to these radio-tracking data to justify the proposed altitudinal distinction between early and late-running salmon morphs and populations, and, in the final phase of SF0274, will use them to choose appropriate altitudinal bands for the modelled inter-acting meta populations.

Figure 4. Results of radio-tracking MSW adult salmon from estuary return data to their spawning grounds, according to their month of return and the altitude of the spawning area. Combined data for rivers: Little Gruinard, Spey, Dee, Tay and Tweed. Similar results were found for the shorter period of 1SW returns. After Smith et al.



Incidental data sets

Captures at Sea (post-smolts, Scotia, etc cruises)

A very few salmon post-smolts, of UK origin, have be captured by FRS research cruises at sea (1996~1998 data available). Their biometric data (sex, size, etc) are available, but, as the numbers captured are very small and their origins unknown, they are of extremely limited worth, especially as we conclude that growth at sea is not a crucial, limiting part of the population dynamics { but see data file *\PJB_ALL\PJB_DATA\ GirBad_Dbase \SmlAtSea \ ParrPostSmolt.xls* for details}. Similarly, some 50 salmon of unknown origins were captured off the Faeroes in 1978, and biometric data (Sex, length, weight, gonad and liver weights and ages are available {see …\ Bill_Gurney \ SizeAtAge_Popn_varn \ wscg_initial_model_ideas \ Reliability Asult Salmon Sexings \ file *AlanPhil_SalmonSexDefinite _ModelData.xls* worksheet *Faroe* }.

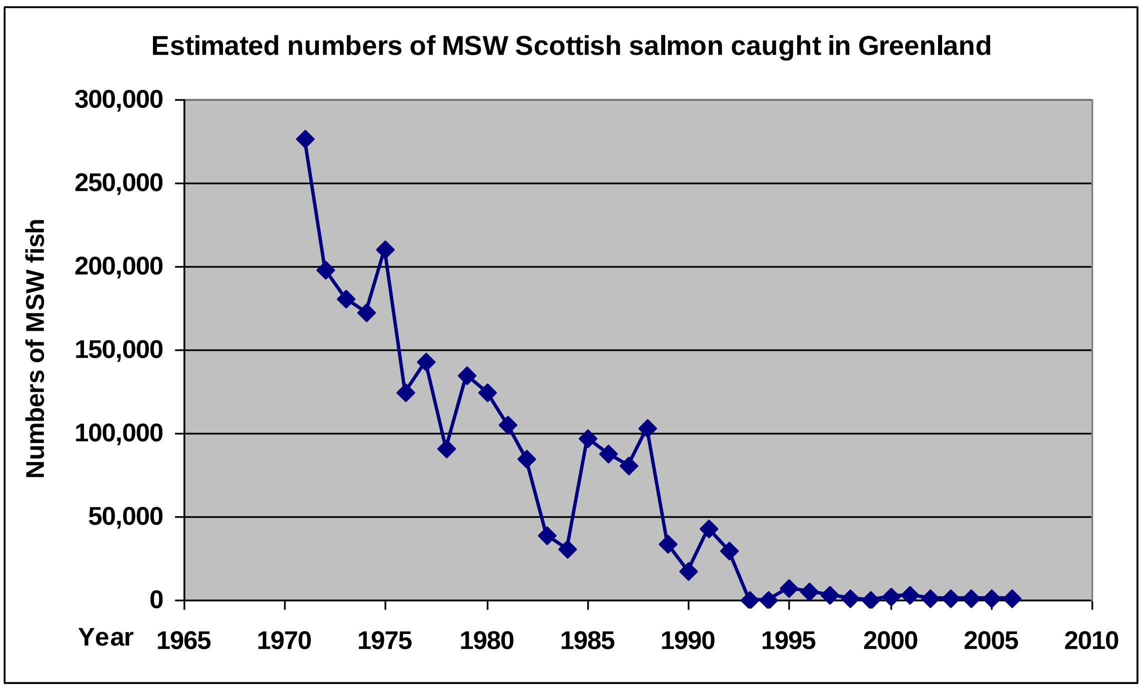
Locations of tagged smolts Recaptured at Sea (N Esk, Girnock)

Some smolts (Carlin) tagged at the Girnock or North Esk have been recaptured by commercial fishing vessels at sea (and reported via the reward scheme). Again the numbers of recaptures are limited, too limited in time and space to give any details about migration routes. The main data are summarised in *(see data files in sub-directories: {…\ SAAV_x_Marine \ Exploitation_History \ ScottishSalmonRecapturedAtSea * [various files in both the sub-directories *GirnockRecaptures* AND *N Esk Since 1980 }*)

Greenland fishery (presumed European origin fish)

The landings of the Greenland fishery, from 1971 to the present (2006) include the numbers of fish taken (all in the MSW age classes) together with an estimate of the proportion of this mixed stock (Canada and Europe) that is of European origin (Julian, Gordon? HOW is the estimate derived? How reliable is it?). The Estimated European proportion drops from 50% of 856,369 MSW fish in 1971 to 28% of 6,401 MSW fish in 2006. The Scottish stock is believed to represent 64.5% of the European stock that reaches Greenland. Accordingly these Greenland catches would represent a take of about 276,179 MSW Scottish salmon in 1971 and 1,156 MSW Scottish salmon in 2006. These Greenland catches would represent nearly twice (171%) the total of Scottish MSW caught and retained in home waters in 1971, but only 4% of the total Scottish MSW take in 2006. The annual data are summarised in {see for details *…\ AST_N_Esk_Condition_2007 \ Analysis Ideas * files [*Greenlandcatch.ppt* and *Greenland input data.xls*].

Figure 5. Estimated numbers of MSW Scottish salmon caught in Greenland by year.



Modelling implications

Over the last few months we have explored the majority of the data sets outlined above, and investigated a wide number of model components which might potentially explain them. These developing ideas were summarized in various internal discussion documents (eg *Marine_LifeCycle_0(1).pdf* to *Marine_LifeCycle_2(5).pdf*). These were circulated around FL colleagues (particularly Alan Youngson, Julian McLean, Gordon Smith and John Gilbey) and a couple of discussion meetings held to reach a consensus on progress and the best way forward.

An early deduction from these exploratory studies was that concept that early achieved growth at sea determined both the size and the sea-age at return is almost certainly fallacious, and this is no longer a focus of our endeavors. At present (Dec-2007) we have agreed a set of some 14 crucial relationships which any satisfactory dynamic model must be able to explain. The importance of some six of these still remains uncertain. Although it is possible that the literature, or some obscure FRS FL data-sets may yet provide additional insights, some further gathering and interpretation of novel field data may be needed before we can decide how they can be accommodated. The current state of these discussions is here summarized in Appendix 2.

We already have (in the discussion documents indicated above) the great majority of the algebra and the associated computer modeling code needed to implement the various potential components of the final 'marine phase' model of SF0274. Our remaining tasks (until March 2008) are thus:

T.1 to finalise the discussions and collate the final data

T.2 to assemble the model components into a full life-cycle model

T.3 (next milestone, Mar-08) 'Prepare 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'.

ACKNOWLEDGEMENTS

We thank John Gilbey and Steve Palmer for providing and helping analyse some important aspects of the marine-phase situation, and for contributing to the discussions which assessed the importance of different potential mechanisms.

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APPENDIX ONE

Summary of FRS FL's Salmon Data Bases, as maintained by FL Montrose.

Précis of the FRS FL Montrose's Salmon Data-Holdings,
as given to Phil by Julian over the phone on Fri 27-Jan-06.

There are three major data sets which are, or are becoming, computer data bases.

MDB_ONE : Adult Catch Sample, 1963 ~ 2005.
Opportunistic samples of adults caught in some of the major salmon rivers, such as Tweed, Tay, Spey (for details, see the diagram in Montrose Sample Salmon data BY Site Year.xls). This data base is working. The data can readily be output by site sub-sets : as different files.
Data fields include, *per fish* [Length, Weight, Age, Sex and back-calculated lengths, at all Fresh-water and SeaStage winter ages, as taken from scale samples].
Summary data sheets are available (EXCEL format).

MDB_TWO : National Salmon Catch DataBase. Monthly records, 1952 ~ present.
MDB_TWO_A. The data are available on a 'catchment' basis. Work is in progress to provide the data at a local level (for 'beat' or 'owner' level, see TWO_B below…). At the catchment level this data base is up and working.
Data fields include, by 'summed locations' : [year & month]; [method of catching , eg nets, rods]; numbers caught; average weight;[effort for Nets]; catch and release by rods, since 1994 when C&R first started.
MDB_TWO_B. Access to **local data** (FORM = = 'beats' of an 'owner') of the same type is under development. This local level data will ONLY GO BACK TO 1986, and will probably not be available until late 2007 (or later).
MDB_TWO_C. Eventually there will be a **GIS query tool** developed for [**MDB_**TWO_A&B] which will produce time series summaries for chosen areas (mapped as best as possible to conform to the underlying 'ownership' data and screened for confidentiality). But it will be several YEARS before this is working, although good progress has been achieved to winter 2007, such that the underlying algorithms are now tested on a sub-set of data for the North Esk…

MDB_THREE.
MDB_THREE_A. North Esk (smolt) tagging and recapture.
These are the data used to estimate smolt numbers leaving the North Esk. Smolts are tagged at Kineaber Mmill near the estuary, and a proportion put back above the lade, and the recaptured number used to estimate the total.
Date Range. Smolts were first tagged in 1964 (but those data are lost). The1965~ data (or some of it!) may exist on paper somewhere in the Montrose attic.
Electronic data exist back to 1975: going back any further would be REALLY difficult!
Records are of (re-) captures of individual fish and record : [Site, Date]; Tag-type; Tag_IDcode; Length (nearly all records); Weight (1/10 records); Age (for the same individuals WEIGHED); and Back-Calculated Winter Lengths (for the same 1/10

Aged&weighed fish). For a very few fish that died, sex is also recorded (but this is probably a very biased sample…)

MDB_THREE_B. Adult recapture details.
The electronic data go back from 2004/5 to, currently, 1998. It is estimated that the back-log of data (back to 1964) will be added at about the rate of 10 years of data each year. *N.B. Although it might be possible to add 'early' batches of years ahead of this proposed schedule, the further back the data-archaeology goes the more surprises are expected and the slower it may get.* The records, in EXCEL format, comprise: [Date] ; Site; Sea and River Ages with back-calculated Winter-Lengths] ;Length; Weight; Gear caught on; TagIDcode where present {linking to the Smolt Data-Set }

APPENDIX TWO

The observational context

1. The observational context

1.1. Observations the model must encompass

1. Grilse (one sea-winter fish) coexist with multi sea-winter (MSW) fish over a wide range of habitats.
2. Early maturity is known to be heritable in farmed fish and estimates from the Norwegian rivers suggest a heritability of 0.48 ± 0.2 for sea-age at maturity.
3. The bulk of Grilse return to their home catchment from May to November while the bulk MSW fish return January to September (Dec~Nov). Individuals returning early in `their' run are associated with high altitude habitats. Late returners are associated with low altitude habitats.
4. The distribution of returners over the grilse run is remarkably stable over the period 1967-2000. The distribution of MSW returners is also quite stable, with the exception of a strong peak in late February which is present pre-1983 and absent thereafter (Fig. 5a).
5. Early, middle and late returning grilse exhibit long-run average growth performance which is consistent over the run, as do MSW fish. The long-run average growth performance of all MSW fish is worse than that of grilse. (Fig. 5b and Table 1)
6. Accepting the present caveats about the reliability of sex-determination, it appears that returning males of a given sea age, river age and run-time are slightly larger than returning females of the same group. (Fig. 5b).
7. Grilse are systematically less abundant (relative to MSW fish) in upland habitats (Fig. 1b and 4b, red line) but are numerically dominant in lowland habitats (Fig. 4b, blue line).
8. Spawning MSW fish are roughly 60% female in all habitats. Spawning grilse are increasingly male biased as altitude rises { over 80% of Girnock grilse are male (Fig. 1d), as are early runners in the N. Esk (Fig. 4d,red line), whereas late running grilse in the N. Esk have recently been almost 50% male (Fig. 4d green line).
9. Fertilised ova have a 1:1 sex ratio. Genetic marker studies on coho smolts suggest that in-river survival is sex-independent (implying that the mechanism for observed sex ratio deviations must lie in differential sea survival
10. Sea-survivals for N. Esk fish (Fig. 6) shows a post-1980 downward trend for both grilse and MSW fish. The overall survival for grilse and MSW fish differs by only a factor of 2 so either the mortality rate for MSW fish is around 70% of that for grilse or grilse and MSW fish from a given cohort undergo the same risks while both are at sea, implying an MSW mortality rate during their extended sea-life ~ 25% of that for grilse. Unfortunately, we really have no idea of the true bsurvival rates of the different components, given that the fish have a genetic predisposition to be grilse or MSW.
11. Individual fecundity of spawning females in the Baddoch and Girnock rises faster than the cube of their length. Ova mass / L^3 (Fig. 3, 2007 data).
12. There is very strong density dependence between spawning and the following autumn's fry census, which leads to a spawning stock fry recruitment relation (_g. 2d) explaining 62% of the observed variance in fry abundance.
13. Parr mortality rates in the river seem only weakly influenced by changes in the physical and biotic environment (survival of about 0.5/year seems a workable rule of thumb in the Girnock). However, there have been climate-associated changes in riverine growth rates which have altered exposure to the apparently constant mortality risk (Fig. 2c).
14. Mortality at sea is both natural and human induced. Both almost certainly vary seasonally and spatially, but we only know their approximate, resultant, overall magnitude.
15. In addition to ongoing mortality at sea, emigrating smolts suffer significant losses from aggregating predators, and the returning spawners suffer from losses to predators and human fisheries in the coastal/estuarine setting and to sport fishermen in the river. These also have strong seasonal and spatial components.

1.2. Questions and Issues

A number of questions arise from the synthesis presented in section 1.1 above:

1. Much of the synthesis in this document is predicated on an assumption that Observation 3 can be interpreted as implying that for both male and female grilse and male and female MSW, proportion of run duration at return maps one to one onto distance of spawning from estuary. For high altitude habitats we have independent confirmation from Girnock data. We need to assemble and assess the very sparse data on proportions of grilse in lowland (N Esk) tributaries.
2. What mechanisms might have caused the (Scotland-wide) post-1980 loss of the very early (end Feb.) run of N.Esk MSW fish?
3. Differences in spawners' sex ratios (observation 8) seem attributable to differences in sea-survival (observation 9). This makes the sea survivals for N.Esk fish (observation 10) crucial. Unfortunately, the different survivals estimated for 1SW and MSW fish from the North Esk are not sound and robust for this particular interpretation.
4. The competition mechanisms underlying the stock-fry-recruitment relation are critical to population stability. If they occur before ova deposition then the size-fecundity relation (observation 11) should depend on spawner density. Although the coincidence between the 2007 data for the Baddoch and Girnock argues against this class of mechanism it seems prudent to look at more years in one or both places if this is possible.
5. If the key density dependence is not occurring pre ova deposition, then our remaining choices are: 1) at deposition; 2) between deposition and hatch; 3) between hatch and emergence; and 4) between emergence and the autumn fry survey. The later in the life history the critical mechanism operates, the more spatial mixing and hence competition between the between the offspring of different mothers will there be. More data is crucially needed to examine these possibilities.
6. Optimality calculations require a knowledge of female and male fecundity as a function of length. We have egg mass data for Girnock/Baddoch females but this data has few grilse, so the mass of data is concentrated above 65cm. It would be good to have data from a midland/lowland site where grilse are more abundant, both to fill in the gap and to see if the functional relationship between (F) and L is structurally the same as that for high altitude habitats (Julian has some egg counts for late returning 1SW and MSW females; Phil and Iain McLaren are assembling Girnock and Baddoch data). See also Shearer's book