# Development of a Lifcycle Simulation Model for Atlantic Salmon

Technical Report
W91

# Development of a Lifecycle Simulation Model for Atlantic Salmon

Scoping Study

Technical Report W91

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Any corrections or proposed amendments to this manual should be made through the regional Agency representative on the Water Resources National Abstraction Licensing Group.

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# EXECUTIVE SUMMARY

In order to make decisions on the management of salmon stocks, fisheries staff within the Environment Agency (EA) frequently have to develop basic predictive models. This can lead to an unnecessary use of resources through the duplication of effort, and may result in strategic decisions being made without the benefits of recent best practice for population modelling. There is therefore a need to develop a salmon lifecycle model that will promote a common approach to salmon management decision analysis across EA Regions. Such a model would enable the likely consequences of alternative management options to be predicted, and would provide a tool for use in the context of spawning target setting and Salmon Action Plans (SAPs). Whilst it is possible that on some rivers, available information will be insufficient to enable robust decisions to be made, a salmon lifecycle model would still assist managers in identifying outstanding information requirements and research needs.

This report reviews the different approaches that have been used to model animal populations. It is concluded that a stochastic simulation model is required for salmon management. Methods used for developing fishery simulation models are reviewed, with particular attention to the approaches taken to model formulation, calibration and validation. For many salmon models an *ad-hoc* approach has been used for model calibration. However, for the proposed Agency model, it is recommended that a Bayesian approach is used, following recent trends in marine fishery model development. This will allow parameter estimates from other fisheries to be combined with river-specific data, and will provide an appropriate probabilistic framework for decision analysis. The review concludes with a description of the reported parameter estimates for salmon populations, including values for key life-stage parameters such as juvenile survival, marine survival and exploitation rates. Particular attention is paid to the data generated from the Environment Agency's Dee Stock Assessment Programme (DSAP), on which the model will initially be calibrated.

Recommendations are made for the development of a lifecycle model, and the need for integration with the Agency's salmon spawning target procedures and proposals for a River Fisheries Habitat Inventory (FRHI) is stressed. A work programme for the development of stand-alone software, and model calibration for the River Dee, is described.

# KEY WORDS

Atlantic salmon, lifecycle model, fishery management, spawning targets, Bayesian statistics, decision analysis.

# 1. INTRODUCTION

## 1.1 Background

The Environment Agency (EA) has recognized that, in order to make decisions on the management of salmon stocks, its fisheries staff frequently have to develop what are often very basic predictive models. This somewhat *ad hoc* process can lead to an unnecessary use of resources (e.g. through the duplication of effort) and the making of strategic decisions on the basis questionable predictions. Consequently, the EA has identified a need for a more sophisticated, universal and flexible form of model.

To meet this requirement, the EA has proposed that a salmon lifecycle simulation model be developed. Such a model would enable the consequences of various management options to be simulated, and would provide a means both of prioritizing cost effectiveness and of promoting a common approach to stock prediction across the Environment Agency Regions. It is expected that investment in such a system would generate a greater confidence in stock management decisions and would facilitate risk assessment for different management options. Furthermore, the proposed project may identify particularly sensitive or poorly understood salmon lifecycle parameters, so assisting the prioritization of further strategic research.

It is expected that a salmon lifecycle simulation model would find applications in many areas of salmon fishery management (e.g. spawning target development; Environment Agency R&D Project 551) and that it would provide another tool for use in the context of Catchment Management Planning. However, the EA recognizes that there is a risk that the model's outputs may be so uncertain that they are of no management value. However, in this event the model would still enable the identification of information and (or) research needs.

The EA intends to develop a salmon lifecycle simulation model that can be applied to any salmon river. The initial calibration will be based upon its existing Dee Stock Assessment Programme (DSAP), utilizing river specific lifecycle parameters routinely generated as part of the DSAP but with the proviso that it will incorporate generic features to ensure its broader application to other UK rivers. The DSAP is a long term monitoring and research investigation of the salmon and sea trout stocks of the River Dee, in North Wales, that began in 1991. The programme is considered to have national importance, producing comprehensive data on several lifecycle parameters that may be utilized in the modelling. These include daily age, size and sex composition data from trap catches, monthly estimates of adult run size, information on spawner distribution and juvenile abundance, and estimates of exploitation and catch-effort.

## 1.2 Overall project objectives - (phases 1 & 2)

To develop a salmon lifecycle model for the Dee (but transportable to other rivers) to predict the consequences of stock management decisions, optimize management practice, and prioritize research needs.

## 1.3 Specific objectives (phase 1)

a) to review existing lifecycle models with potential for application to migratory salmonids, including models for both fish and other species, and evaluate their suitability for use in development of the Dee model or make recommendations for further modelling requirements;

b) to identify model input parameters (e.g. fishing and non-fishing mortality rates, growth rates, run timing, sea age heritability) and review observed ranges of parameter values for Atlantic salmon applicable to the British Isles;

c) to establish and describe procedures for selecting input parameters, incorporating stochastic variation and including, where appropriate, selection based on predictive relationships (e.g. such as those for density-dependent mortality);

d) to propose and cost development and validation of a computer model, outlining model structure and method of operation and adapting as necessary features from lifecycle models identified in (a) and input parameters in (b) and (c); ensure the model allows operator choice of generation run-time and adjustment of input parameters;

e) to ensure that software proposed in (d) delivers a 'user friendly' menu driven system, suggesting the format of tabulated and graphical printouts describing input parameters and life-stage outputs with respective stock-recruitment and replacement curves for various life-stages as well as facilities to identify or adjust spawning or other fishery targets and assess compliance against these;

f) to incorporate with (d) the costs of producing user and system manuals to accompany software as well as identify and cost likely software implementation and support needs.

## 1.4 Environment Agency requirements

Following an initial meeting between WRc and the EA (18 December 1995), it was decided that WRc would produce a document outlining the possible scope of the proposed salmon lifecycle model (see Appendix A). This document detailed the variables, parameters and resolution of the model, and was intended to form the starting point for further discussions which would enable the literature review and model specification to be more clearly focused on those components of the salmon lifecycle of especial interest to the EA.

The perceived requirements of the Agency (arising from subsequent discussion with the EA), together with other details pertaining to the development of a salmon lifecycle model for use as an operational management tool, are discussed in Appendix A.

# 2. APPROACHES TO MODELLING

## 2.1 Introduction

### 2.1.1 The role of models

Models are useful for investigating scenarios of coupling between the intrinsic characteristics of individual organisms and extrinsic or environmental perturbations, and the consequences of these interactions for the dynamics of the population (Batchelder and Williams, 1995). In this context, models have an important role - not just in describing population dynamics, but also in allowing the implications of management policies to be assessed through simulation rather than full implementation of new policies or the use of large-scale experimentation. Following the use of a model, the subsequent choice of management strategy may be self-evident. Alternatively, in more involved cases, it may be necessary to apply a form of scoring system (e.g. Ralls and Starfield, 1994) to the predictions of a simulation model to help differentiate between the likely 'success' of alternative management options.

### 2.1.2 Variables and parameters

Models are described mathematically in terms of the relationship between variables and parameters. The variables of a model can be defined as those quantities that are changing (e.g. over time) but can be measured, counted or otherwise evaluated. The parameters of a model can be defined as those terms that characterise a relationship between variables and which remain constant (at least over a defined period of time). Parameters can rarely be measured directly and therefore have to be estimated by statistical techniques from measurements of the variables.

In the context of a salmon lifecycle model, variables would include the annual rod and net catch, smolt output and run size. With appropriate sampling (e.g. traps and counters) and reporting (e.g. catch returns) techniques, these can be measured in each year. Parameters would include the rod and net exploitation rates, and freshwater and marine survival rates.

The distinction between variables and parameters is not always clear. The area of spawning habitat in a catchment, for example, can be measured (resembling a variable) but is constant through time (resembling a parameter). A more important issue is that in practice, parameters are rarely constant; consider marine survival, for example. The value for the marine survival rate will vary from year to year as environmental conditions change, and within a year, the survival rate will vary between individual fish according to their fitness. In stochastic models (see below), parameters may not be viewed as constant, but rather are represented by probability distributions describing the nature of the variation in the parameter.

## 2.2 Types of model

### 2.2.1 Classes of population model

A review of terrestrial models by Emlen (1989) provides a classification of models of population dynamics. Three classes of population model are described by Emlen: 'demographic'; 'energetic'; or 'population genetic'.

- **demographic** models; describe and predict changes in population size and structure.

- **energetic** models; are used to describe or predict behavioural responses to the environment or, where survival and production depend on growth rate, to describe population dynamics directly.

- **population genetic** models; are designed primarily to describe and predict changes in genome structure and adaptation to environmental change.

Demographic models may be limited by the inability to acquire all of the relevant data for a given species or scenario. It is not uncommon for them to make less than accurate predictions as they may be based on incomplete, and often erroneous, information. Fortunately, baseline estimates of demographic parameters can often be made from known, allometric relationships. Also, it is often possible to determine, *a priori*, those parameters to which the end-point predictions of interest are most sensitive (e.g. by sensitivity analysis) - see, for example, Evans and Dempson (1986).

As descriptors and predictors of processes impacting upon birth and death rates, energetic models may often be used as sub-models to a central (demographic) model that performs the task of tracking changes in population size and structure. Unfortunately, the sort of detailed information that energetic models require are rarely available, although the results of some studies involving salmonids are available in the literature (e.g. Rand *et al.*, 1993).

Population genetic models describe the changes in a population's genetic makeup in response to changes in its environment. However, as the evolution of a population's genetic makeup is a process which operates far more slowly than do changes in population size and structure, population genetic models are not generally appropriate for eco-risk assessment.

### 2.2.2 Alternative approaches to modelling & modelling specification

Whilst there is little need to justify the application of quantitative, mathematical models to the study of complex ecological systems, it is useful to define the nature of those models that are of value and interest.

There are a number of alternative approaches to modelling, and it is possible to classify models by their basic nature:

- **deterministic versus stochastic; and**
- **parametric versus non-parametric.**

and along several distinct dimensions which relate to the modelling methods that are employed:

- **empirical, conceptual, eclectic, experimental**;
- **static** versus **dynamic**;
- **individual** versus **population**;
- **analytical** versus **simulation.**

### Deterministic versus stochastic models

Deterministic models have variables that are free from random variation, whereas stochastic models contain random variables that follow probability distributions. The repeated application of a deterministic model to a predefined set of initial conditions will always produce the same output, whereas the repeated application of a stochastic model will produce a range of differing outputs.

Some authors (e.g. Dent and Blackie, 1979) consider that stochastic elements should be introduced with caution. They suggest that it is better to have a simple deterministic model which meets the objectives stated at its inception, rather than to have a complex stochastic model which is too clumsy to use or which produces results which are too obscure to be satisfactory to the user.

The need for stochastic models in fisheries management was recognised over twenty years ago, with a call for more refined models of actual fish populations and their stock-recruitment relationships including the distribution, and method of application of, random fluctuations (Allen, 1973). Lee and Hyman (1992) warn 'The caricature of reality portrayed in a deterministic model is sufficient to guide management decisions in some cases, but can be dangerously misleading in others'.

Deterministic models will, at best, capture only the central tendencies of population behaviour. However, for non-linear models the mean value of a stochastic model output, such as population size, will differ from the output produced by an equivalent deterministic model that simply uses mean parameter values.

To form a useful management tool, a lifecycle model should permit the inclusion of stochasticity, or random variability. Whilst a simple deterministic model will indicate underlying trends, it is necessary to have one or more stochastic elements in order to permit the risks (or uncertainty) associated with different management options to be fully evaluated.

Where catastrophic events are incorporated into models, they would be assigned a low probability of occurrence to reflect their rarity. As a consequence, it has been suggested that stochastic models demonstrate a general inability to incorporate truly 'catastrophic' environmental effects, and that there is always the possibility that some interactions or processes present in the real-life system may be overlooked or otherwise omitted from the model. Accordingly, Emlen (1995) suggests that, from a management perspective, outputs from stochastic models should be regarded as being 'best case'. This is somewhat misleading, in that stochastic model outputs usually reflect some form of 'average' outcome, not 'best-case'. However, whatever values are produced and output by stochastic models, they can be quoted along with some measure of their certainty, which when expressed in the correct way (e.g. as confidence intervals) can give indications of the chance of extreme events such as (near) extinction.

### Parametric models versus non-parametric models

Within the class of stochastic models, a further sub-division into parametric and non-parametric models is possible.

Parametric models are those which are based upon functional relationships (e.g. exponential decay, error structures following Normal or Poisson distributions). Although, the shapes of these functional relationships may be adjusted ('stretched' to fit the data) by changing the parameters of the model, the general nature of the model will always remain the same. Thus an implicit assumption of any parametric model is that the relationship being modelled follows (at least approximately) this functional form. If this assumption is true then the worth (predictive ability) of the model can be greatly enhanced. If it is wrong, however, it can give answers which are misleadingly precise.

Conversely, non-parametric models are those which make no such *a priori* assumptions about the relationships being modelled. Instead they allow the observed data to dictate the relationship (for example, using a neural network to model a highly complicated relationship between large numbers of explanatory variables and response variables). The advantages of non-parametric models are that they do not rely on the validity of simplifying assumptions (such as Normality of errors or exponential decay). This is quite often useful when the underlying mechanism is almost impossible to ascertain, or when the validity of assumptions cannot readily be tested. The main drawback of non-parametric models is that they usually require more data than parametric models to achieve the same quality of output.

### Empirical, conceptual methods, etc.

Establishing the model structure is the first stage in the modelling process, and several methods may be used to accomplish this. Whilst the two extremes may be represented by the empirical and the conceptual approaches, other approaches (e.g. the eclectic and the experimental) are available.

Empirical identification of model structure is based entirely on available data, effectively by asking the question 'what model describes data that looks like this?'. As the parameters in an empirical model are simply convenient values that have been derived to allow the model to fit the available data, it is not always possible to draw meaningful, ecological inferences from the parameter values that are derived. For example, the choice of transformations in the HABSCORE models (Wyatt et al, 1995) was based on inspection of the data rather than any theoretical considerations. Empirical models are often appropriate when the application is to predict an observation given the independent variables. However, with the empirical model building approach there is always the danger of over-parameterisation (i.e. increasing the number of parameters in the model until the fit to observed data is so good that one is simply modelling the noise seen in that particular data, rather than the underlying, systematic structure), which can lead to a reduction in the value of the model's predictions.

Conceptual identification of model structure is based on theoretical considerations of the model structure, with no initial reference to data. For example, the rod and net exploitation model used for the salmon escapement targets project (Wyatt and Barnard, 1997a) was conceptual. Conceptual identification of model structure is appropriate when the proposed application for the model is to assess the consequences of manipulation. This is because the model structure will (by definition) tend to reflect what is known about the ecology of the population under study, especially in terms of its potential response to environmental perturbation.

The eclectic identification of model structure is a process which is intermediate between the empirical and conceptual approaches, relying on both the inspection of data and on theoretical considerations. Often under this approach, data may be used to identify which of a number of possible theoretical models is most appropriate.

Finally, the experimental identification of model structure is achieved by manipulation of the system that is being modelled. Such an approach would be facilitated by (for example) manipulating a net-fishery whilst monitoring an upstream rod-fishery. Although based on 'cause and effect', the experimental approach may still require that ecological theory is applied to the results (i.e. use of the conceptual approach) or that a 'black-box' (i.e. empirical) approach is implemented to model the results obtained from the manipulated system. Whilst it may be impractical to manipulate a fishery specifically for model calibration, it is likely that monitoring the response of the fishery to management actions will be a useful means of model validation.

Under these definitions, the development of a salmon lifecycle simulation model as a robust management tool should not be entirely empirically based.

### Static versus dynamic methods

Static models represent a system at a particular time (e.g. describing the system at equilibrium), or a system in which time plays no role. Conversely, a dynamic simulation models represent a system as it evolves through time.

Quite clearly, for the purposes of developing a population simulation model which is subsequently to help direct management actions, there is the need to be able to describe the system at through time. Consequently, any derived models will necessarily be dynamic in nature.

### Individual versus population modelling methods

Individual-based models (IBMs) are based on the tenet that fish populations consist of non-identical individuals inhabiting heterogeneous environments and moving in a manner that maximises their individual fitness, and are an attempt to fully integrate these characteristics into a single model (Tyler and Rose, 1994).

However, whilst modelling populations on an individual-by-individual basis has proven to be a fruitful approach (e.g. Huston *et al.*, 1988), a major problem is that the typically large number of individuals needed requires impractically large computation times. Hence, because of the complexity of this approach, there is often seen to be the pragmatic need to assume that individuals within a population, age- or stage-class are equivalent - so simplifying the simulation model of the system that is under study.

A compromise between these two extremes, which goes part-way to retaining the ability to effectively model the individual variability that is encapsulated within the IBM approach, has been proposed by Scheffer *et al.* (1995). For each variable that represents a class of individuals within the model, they suggest that a supplementary variable is added to indicate the number of 'real' individuals that are actually represented, effectively producing a model of 'super-individuals'.

### Analytical versus stochastic methods

Mathematical models may be examined or studied through either formal analysis, using analytical methods (e.g. Evans and Dempson, 1986), or by simulation (e.g. Gee and Radford, 1982; Lee and Hyman, 1992; Friedland, 1995) - where simulation is the 'numerical abstraction of the process under study' (Van Horn, 1971).

The complex nature of population models means that it is often necessary to resort to simulation as a means of examining model behaviour.

An important advantage of simulation over analytical methods is that it allows the behaviour of complicated models to be examined, and estimates of population parameters to be made, even when the model is so complicated that an analytical approach would be unfeasible. In addition, analytical methods almost always rely heavily on the so-called parametric assumptions of the model (e.g. a Poisson distribution, exponential decay). The use of simulation methods allows one to incorporate non-parametric techniques (sometimes called robust methods) which do not make restrictive assumptions, but instead allow the observed data to dictate relationships.

### 2.2.3 Model resolution

Population models can be constructed with differing degrees of inherent detail. At one extreme are 'system' models - which incorporate significant detail into the processes to be modelled, whilst at the other extreme are holistic models which (theoretically, at least) trade complexity for generality of application (Emlen, 1995).

Complete system models include considerable life-history detail and can often accommodate the subsequent incorporation of still more detailed sub-models. This approach has problems as, although (given a precise and complete knowledge of parameter values) system models should be the most accurate, for most species many of the parameter values are little more than educated guesses. This obviously introduces the possibility of cascading errors in the projection of future population values. Holistic models, whilst being far simpler and less parameter intensive, are generally too simplistic to be reliable as trend predictors, except over short time periods.

In addition, it has been suggested (e.g. Bartell *et al.*, 1992) that a framework for risk analysis should incorporate all of what is known about the life history dynamics of the species being studied, and should not discard information on parameters in favour of generality. Inevitably therefore, the product of a modelling exercise often falls part way between the two extremes of model described above.

In the context of a salmon lifecycle model, the balance is between a detailed system model of the River Dee, or a holistic lifecycle model that can be used to manage fisheries with less available information. As the level of detail that can be covered in a model is governed, to some extent, by the quantity of data that are available for model development. Consequently, the choice of model resolution will be effectively driven by data availability.

### 2.2.4 Model scope

The ability to include detail where it is available can be facilitated through the adoption of a hierarchical approach (Lee and Grant, 1995), where what are a series of independent models are combined into a single framework. For example, 'life-stage models' can be used to form the basic simulation units at the lowest level in the proposed modelling structure. The combination of life-stage models subsequently produces a 'population model' which can be used to simulate (for example) complete lifecycles of salmonid populations. It is possible to derive a final tertiary level through the combination of these population models to an overall 'inter-population model'. Such an inter-population model would cover multiple species and stocks. By constructing a hierarchy of models in this way it is possible to maintain a logical consistency amongst models, whilst allowing unique model structure appropriate for each of the levels in the hierarchy (Lee and Grant, 1995).

### 2.2.5 Application of models to population management

In order to enable informed choices to be made regarding population management and subsequent impacts on the conservation of a given population, there is a need for the quantitative evaluation of the relative merits of alternative management options. As minimising the likelihood of extinction is often an objective, the aim becomes the assignation of the probability of extinction to each of the series of available management options (e.g. Possingham and Davies, 1995). Population viability analysis (PVA) - the process of assigning an extinction probability, within a specified time-frame and under particular circumstances - has become a widely applied tool in this context. Clearly, such techniques are not possible using deterministic models (as the probability of extinction with any given set of management options will be either zero or unity). Such a process of viability assessment involves the use of mathematical models including stochastic elements, explored using computer simulation.

The requirements of the Environment Agency may be less focused on the possibility of extinction, but rather on the possibility of spawning escapement falling below some pre-defined level (for example a formalised spawning target). It is possible to extend the concept of PVA from the simple case of examining the threat of extinction, by redefining the lower acceptable limit for population size to a nominal threshold value rather than to zero (e.g. defining the lower acceptable limit for spawning escapement as 20% of a pre-defined spawning target).

### 2.2.6 Conclusions

As discussed above, although a simple deterministic model will indicate underlying trends, it is necessary to have one or more stochastic elements in order to permit the risks (or uncertainty) associated with different management options to be fully evaluated. Consequently, it is recommended that any model that is developed should include one or more stochastic elements. In addition, due to the requirement for excessively large quantities of data in order to facilitate the development of robust non-parametric models, it is recommended that the stochastic models should be parametric in nature.

To optimise the accuracy and interpretability of developed models, identification of model structure should employ eclectic techniques. As discussed above, models will need to be dynamic, and although they are likely to be population-based, it is possible that adoption of the 'super-individual' modelling methods discussed by Scheffer *et al.* (1995) may be considered.

Finally, to maximise the value of derived models, simulation techniques (rather than analytical methods) should be used to assess the consequences of different model scenarios.

## 2.3 Construction of dynamic, stochastic simulation models

### 2.3.1 Model formulation

Two basic (dynamic) modelling methods are apparent in the literature: one making use of matrix algebra; the other being a modular system, involving the use of a series or 'chain' of sequential equations.

#### Matrix based

Modern mathematical demography, modelling the growth and decline of age-structured populations, was originated by Leslie (1945), (Ferson *et al.*, 1989). The theory uses 'Leslie matrices' (which incorporate information on the fecundity and survival of each age-class) to project a vector of age-class abundances through time. The advantages of using a matrix approach to lifecycle modelling lie in the fact that the calculations rely heavily on standard matrix algebra. Whilst the Leslie matrix is a fundamental and well accepted tool in demography (perhaps because it represents the fact that individuals in populations do only four things: they are born; they age; they reproduce; and they die) this apparent simplicity belies the mathematical complexity that can be engendered when we try to model these four things realistically (Ferson *et al.*, 1989).

An extension of the technique lies in the use of 'Lefkovitch' population projection matrices (Lefkovitch, 1965). Lefkovitch matrices represents a more general form of Leslie matrices, where the population is divided into 'stages' rather than into equal age-classes (as they are in the Leslie approach). Such applications are represented in the literature not only by studies on anadromous salmonids (e.g. Caswell *et al.*, 1984; Browne, 1988) but also by studies on non-salmonid populations (e.g. loggerhead sea turtles - Crouse *et al.*, 1987).

The theory has been further augmented by later researchers (e.g. Paulik, 1973; Levin and Goodyear, 1980) to build in, for example, density-dependence; different ways of adding stochasticity; and including threshold effects. At this stage, however, the advantages in using a matrix approach are effectively lost, as the inclusion of density dependence implies that the projection matrix becomes non-constant.

### Sequential equations

A more intuitive formulation of the relationships that are to be modelled lies in the use of sequential equations (i.e. a Markov-chain approach). In this general approach, a series of equations are formulated, each of which describes a pre-defined stage in the lifecycle. Effectively, the outputs from one stage are used as the inputs for the next, in the manner described by Larkin *et al.* (1964), Paulik and Greenough (1966) and Paulik (1973).

The combination of a modular approach using a series of sequential equations and the inclusion of stochastic elements, effectively produces a modelling form known as the Markov-chain Monte Carlo (MCMC) technique. The stochasticity of any parameters in a given stage of the lifecycle model is normally assumed to be independent of the stochasticity of the parameters of the previous stage. For example, the stochastic variability associated with a parameter describing the marine survival rate from smolt to one sea winter would be assumed to be independent of the stochasticity that is associated with the concurrent survival of fish from the one sea-winter age-class to the two sea-winter age-class.

This is by far the most flexible approach possible to lifecycle modelling, as it allows each stage in the lifecycle to be considered independently, and facilitates the inclusion or exclusion of sub-modules as is considered appropriate (both through model development and implementation). In terms of program implementation, such a modular approach also has the advantage of lending itself to the development of user-friendly, interactive computer software.

## 2.3.2 Approaches to modelling stochastic elements

### Sources of variation

There are two major sources of variability that need to be considered in the context of a lifecycle model. These are stochastic variation in the salmon lifecycle, and errors in the model itself (see Table 2.1).

**Table 2.1 Sources of variability in a lifecycle model.**

| Reference number | Type of variation / error | Focus of variability | Nature of variability |
|---|---|---|---|
| 1 | Stochastic variability | Random | |
| 2 | | Parameters | Between individuals |
| 3 | | | Temporal |
| 4 | | | Spatial |
| 5 | Model errors | Parameter estimates | |
| 6 | | Model structure | |

To illustrate these types of variability, consider the survival of smolts throughout the first winter at sea. If the probability of surviving the winter is 0.5 for all individuals in every cohort, then it would not be expected that exactly 50% of smolts would survive. The survival of 1000 (say) smolts in one cohort can be modelled by throwing 1000 dice and totalling up the number of 4s, 5s or 6s that result. Other cohorts can be modelled by throwing the dice again. The long term average for the total number of 4s, 5s or 6s for each set of 1000 throws would be 500. However, each set of 1000 throws of the dice will generate one of a range of possible totals (95% of which will be between 469 and 530). This type of variation (1, Table 2.1) becomes more pronounced for smaller populations.

The survival of smolts, however, is unlikely to be constant between individuals (2 in Table 2.1), from year-to-year (3, Table 2.1) or between different locations (4, Table 2.1). Variability between individuals may be due to genetic factors (e.g. such as size or fitness) and the variability from year-to-year may be generated by environmental variability. This variability in the parameter value will clearly generate a greater variability in the number of smolts surviving than described above.

The second source of variability arises from errors or uncertainty in the model. How do we know that the survival rate of smolts is precisely 0.5? Many parameters in the lifecycle of the salmon are very difficult to estimate, and the uncertainty in the parameter estimates (5, Table 2.1) should be reflected in the uncertainty in the predictions of the consequences of management actions. Similarly, can smolt survival be regarded as density independent, and therefore should a more complex model (6, Table 2.1) relating survival to numbers of smolts be used?

Many authors have discussed one or more of these sources of variability. For example, Burgman and Gerard (1990) describe two forms of stochasticity:

- environmental stochasticity; and
- demographic stochasticity.

They define 'environmental' stochasticity as the random variation in population parameters resulting from the variability in environmental conditions (e.g. variability in the mean growth rate due to temperature variability). 'Demographic' stochasticity is defined as that variation which arises due to chance events in the survival and reproduction of a finite, integer number of individuals. Consequently, under constant environmental conditions, demographic stochasticity may give rise to population variation and even extinction. Environmental and demographic stochasticity relate to stochastic variability sources (3) and (1) (respectively) in Table 2.1.

Similarly, Lee and Hyman (1992) defined three sources of uncertainty that can be incorporated into stochastic models:

- temporal variation in population structure and/or environmental conditions;
- intra-population variation among individuals;
- uncertainty in parameter estimates.

These relate to variation types (3), (2) and (5) in Table 2.1 respectively. They also build random variation (1) into their Stochastic Life-Cycle Model.

O'Neill *et al.* (1981) also highlight the importance of the natural, stochastic variability of the system being modelled (i.e. sources 1, 2, 3 and 4 in Table 2.1) in affecting the ability of any derived model to provide reliable predictions. In addition, they suggest that two further sources of uncertainty, namely errors in model construction (i.e. 6, Table 2.1) and uncertainty in the true value of model parameters (5, Table 2.1) will both also affect the reliability of a population model.

Other definitions of potential sources of error in the modelling process are given by Emlen (1989), although they are not entirely dissimilar to those given by O'Neill *et al.* (1981). He outlines three major sources of error:

- the model does not incorporate all influences that are likely to be encountered in the system it purports to describe;
- the model is unintentionally built on one or more erroneous relations (i.e. 6, Table 2.1); and
- incorrect parameter values are used unintentionally (i.e. 5, Table 2.1);

and points out that, whereas the first of these potential sources of error can never be entirely ruled out, the second and third are correctable. The first of these really amounts to whether an influence (such as the effects of flow on rod catch) is included in the deterministic part of the model, or whether it is 'lost' in the temporal stochastic variability in rod exploitation rate.

Peterman (1981) recognises that observed variability in salmon survival has two components - measurement error and natural process variation. Whilst he acknowledges that the former can seriously bias parameter estimates, he claims that it is only feasible to deal with the composite effect of these two sources of variation since, in practice, they can rarely be separately quantified in data. Conversely, Lee and Hyman (1992) claim that although natural stochasticity and measurement error can be expressed in identical terms mathematically, they may have different implications when the results are interpreted. In light of this, they suggest that there may be grounds for considering the contributions that are made by natural stochasticity and by parameter uncertainty independently during the development of a salmon lifecycle model.

### Approaches to modelling variation

The types of variation described above can be readily modelled using standard statistical distributions. For example, the number of fish surviving from 100 smolts, each with a probability of survival 0.5 will follow a Binomial distribution (n=1000, p=0.5); (see, for example, Pielou, 1977). If the survival rate (p=0.5) itself varies from year to year, then this variation in the parameter can be modelled using a Beta distribution. The Beta distribution is commonly used to model the frequency distributions of proportions, which must fall between 0 and 1 (e.g. Lee and Hyman, 1992). However some authors have used a normal distribution that is truncated at 0 and 1 (e.g. O'Neill et al, 1981). The combination of random variation within a year (Binomial) with variation in the parameter between years (Beta) results in the number of survivors following a 'Beta-Binomial' distribution (see, for example, Boswell et al., 1979).

A similar combination of random variation and variation in parameters can be seen with catch statistics. If all anglers on a fishery had a capture rate of exactly 4 fish per season, then by random chance, some would catch more than four fish, some less. If the process is purely random, the distribution of catch among the anglers would follow a Poisson distribution. However, the rate of capture is unlikely to be constant for all anglers, due to factors such as experience and skill. The result is that the distribution of catch is somewhat more variable than the Poisson distribution would suggest, with some (more experienced) anglers catching large numbers of fish, and other (less experienced) anglers catching no fish. The distribution of the rate of capture between anglers can be modelled by a Gamma distribution, and the resulting distribution is a Negative Binomial distribution (rather than a Poisson distribution).

The relationship between models of random variation, variation in parameter values and the resulting distribution are summarised in Table 2.2.

**Table 2.2 Combinations of parameter, and random, variation**

| Type of parameter | Examples | Variation in parameter | Random variation | Resultant distribution |
|---|---|---|---|---|
| Proportion | Marine survival, sex ratio | Beta distribution | Binomial distribution | Beta-Binomial distribution |
| Rate | Catch per unit effort | Gamma distribution | Poisson distribution | Negative Binomial distribution |

Random variation in salmon populations does not affect cohorts in isolation. The overlapping generations means that if environmental conditions cause a poor winter survival in a particular year, all cohorts present may be affected, and the influence of this random event will be seen in successive years. Populations are thus characterised by drifting levels (positive autocorrelation). One approach to modelling it is to simply introduce autocorrelation into the stochastic part of the model (for example Emlen, 1995, introduced a 1-year lag correlation into a population viability model of Chinook salmon). An alternative approach is to allow the stochastic variation to operate in a way that is likely to cause autocorrelation. For example, stochastic variation could operate each year on all cohorts present in the marine environment, and similarly in the freshwater environment.

### 2.3.3 Model calibration

#### The need for calibration

Having defined a population simulation model in terms of its inputs, life stages and outputs, it is necessary to derive suitable estimates for parameters. This process of calibration will effectively 'tune' the model to the particular situation or population under consideration. It may be possible, therefore, to produce a general salmon lifecycle simulation model that can be transported from one river to another simply by re-defining the estimates of certain of the model's parameters (i.e. by re-calibrating the model).

#### Calibration methods

In general terms there are three basic approaches to parameter estimation (outlined below); any of which may be appropriate to different components of a salmon lifecycle model:

- **Methods of shape equalisation.** The basis of the shape equalisation methodology is to choose parameters such that the shape of the fitted model is like that of the data. This is achieved by equating properties of the data sample to those of an assumed population. The most common of this type of method is the 'method of moments'. Another examples is the 'autocorrelation' structure of time-series data; a method which could be used to compare long-term fluctuations in rod catch with those predicted by a simulation model.

- **Methods of minimum deviation.** Parameters are chosen to minimise the disparity between the observed results and the chosen model. These includes the method of 'least squares' that underlies many common statistical modelling procedures, such as regression and analysis of variance, and the method of chi-squared when fitting distributions.

- **Methods of maximum explanation.** These methods try to maximise some measure of the 'explanatory' power of the fitted model by a suitable choice of parameters. The most common method used is the method of maximum likelihood, which is the natural method of estimation for both 'classical' and 'Bayesian' statistics. Maximum likelihood is the method underlying techniques such as Generalised Linear Modelling, and was used to fit the rod and net exploitation model as part of the salmon spawning escapement targets project. Bayesian methods are estimation procedures where, in addition to the calibration data, there is other prior information about the parameter of interest.

## Over-parameterisation

Proper calibration of a stochastic lifecycle model for salmon is problematic (e.g. Lee and Hyman, 1992). Rarely, if ever, is there sufficient information to provide independent estimates of all model parameters, a problem known as 'over-parameterisation'.

Consider a simple linear model:

$Y = aX$

where:

'X' is the independent variable,

'Y' is the dependent variable, and

'a' is the only parameter.

Given paired data on the variables 'X' and 'Y', one could use simple linear regression to obtain an estimate of the parameter 'a' (the gradient of the line). Assume for this illustration that the estimate obtained is the value 10. Confidence limits could also be estimated for 'a', which would be dependent on the quantity of data and the variability of the data around the model.

Now consider the model:

$Y = bcX$

where;

'b' and 'c' are two unknown parameters.

Given the same paired data on the variables 'X' and 'Y', it would clearly not be possible to separately estimate 'b' and 'c'. This is similar to the problem of calibrating a salmon lifecycle model. For many fisheries, the only available data come from rod (and perhaps net) catch returns, and yet there are a large number of unknown parameters such as marine survival, rod exploitation rate, net exploitation rate, adult freshwater survival and juvenile survival (density dependent and independent). There will be many combinations of parameter estimates that will generate the observed calibration data. The 'b' and 'c' in the above example may, for example, correspond to marine survival and rod exploitation rate. An observed time-series of rod catch data could be the result of a high marine survival with a low rod exploitation rate, or a low marine survival with a high rod exploitation rate; there is insufficient data to distinguish between these alternatives. However, the prediction of the response of the fishery to a change in the rod exploitation rate is likely to depend critically on its current value.

The solution to this problem of model calibration lies in using river-specific calibration data in combination with all other sources of information to derive a set of parameter estimates that provides the best fit to the data. For example, information from alternative sources (more intensive studies on similar rivers, published values, etc.) may suggest particular values for certain of the parameters. Thus in the above example, data from other sources may suggest that ‘b’ is very likely to have the value 5, in which case the data for ‘X’ and ‘Y’ would allow ‘c’ to be estimated as 2 (5 x 2 = 10).

A more sophisticated model would allow the user to say that he is ‘fairly certain’ that ‘b’ is 4, and ‘very uncertain’ about ‘c’ which may also be about 4. The data on ‘X’ and ‘Y’ would suggest that these initial estimates cannot be correct (4 x 4 = 16, not 10). Statistical procedures could use both the data (‘X’, ‘Y’) and the initial (‘prior’) estimates to give the final (‘posterior’) estimates of ‘a’=5 (not far from the ‘fairly certain’ initial estimate of 4), and ‘b’=2 (some way from the ‘very uncertain’ initial estimate of 4).

The correct approach for combining prior information about parameters, and calibration data, through the application of Bayesian methodologies (see below).

## Calibration of salmonid population models

The paucity of data relative to the number of unknown parameters in salmon lifecycle models has meant that many calibration exercises have had to rely on a mixture of ‘external’ estimates and expert opinion, together with river-specific calibration data. The calibration of models, however, is given scant coverage in the literature, and often where calibration is discussed, informal and intuitive methods have been used.

Emlen (1995) provides a methodology for calibrating a population viability model calibrated against a time series of redd counts. The procedure is as follows:

1. Initial values for parameters such as those relating to the stock-recruitment curve were obtained from the literature, expert judgement and in one instance (autocorrelation), pure guess.

2. 36 years of redd count data were predicted using a stochastic simulation model and the sum of squares estimated.

3. Parameter values were adjusted and step ‘2’ is repeated until the set of parameters which minimises the overall sum of squared errors (i.e. the best set of parameters to predict the observed data) has been identified.

4. Steps ‘2’ and ‘3’ were repeated 100 times for different random number sequences

5. The mean and confidence limits of the 100 parameter estimates were estimated.

Lee and Hyman (1992) suggest obtaining as many parameter estimates, relating to the system being studied, as possible. Such parameter estimates may be derived from a number of sources (e.g. from the literature; expert opinion; other models). It is necessary to be mindful of the fact that that parameters may vary between what are apparently similar systems (e.g. between salmon populations in neighbouring catchments). They suggest that a stock-recruitment curve, covering egg to pre-smolt survival, may be more general in its applicability than the other parameter estimates - even if stock-recruitment data are available (and often they are not) they are usually too scattered to allow a precise estimation of a survival function.

Their calibration procedure is summarised as follows:

1. Estimates were obtained for as many parameters as possible from the literature, expert opinion, other models and microtagging data.
2. From 1), best estimates were selected for all the parameters except the stock-recruitment curve and the total adult (tag) recovery fraction.
3. The general shape and magnitude of the stock-recruitment curve was estimated (largely based on 'professional judgement').
4. The adult recovery fraction and variability of parameters were estimated from a time series of calibration data. Parameters were adjusted systematically to minimise the sum of squared errors between observed and predicted observations. Since there were three unknown variances in the model (and insufficient data to estimate them), the user had to decide on the relative proportions of the variance to be allocated to each life stage, or alternatively must set one or two of the component variances and solve for the remainder.

Korman *et al* (1994) calibrated their model of Atlantic salmon by adjusting the parr to smolt threshold size criteria in order to produce observed parr densities. Subsequently, the marine mortality and adult 'destiny' parameters (i.e. the rates of maiden, annual and biennial spawning) were adjusted such that the predicted smolt output reproduced the maiden and repeat spawner frequencies observed in the available calibration data set.

## Bayesian Calibration

The calibration of published salmon models has involved informal methods, often assuming many parameters to be exactly known, whilst using *ad-hoc* methods to estimate the remaining parameters from calibration data. In marine fishery models, however, the use of formal Bayesian procedures is becoming common (Hilborn et al, 1994; Walters and Ludwig, 1994; Walters and Punt, 1994; McAllister et al, 1994; Kinas, 1996).

Bayesian methods are an alternative branch of statistical inference to "classical" statistical methods. A simplified comparison between these two branches of statistics is given in Table 2.3. Classical statistics adopts a narrow view of probability, defining it as the expected relative frequency in the long term. Bayesian statistics, in contrast, takes a broader view, defining probability as a degree of belief. Bayesian statistics also departs from classical statistics in that it regards unknown parameters as variables which can be described by probability distributions, representing the degree of belief in a range of possible values. In classical statistics, however, parameters are viewed as constants with single values. For example, a classical 95% confidence interval for a parameter estimate is defined as containing the true parameter value on 95% of occasions (the interval is the variable). For a Bayesian probability interval, however, the parameter has a 95% chance of being within the interval (the parameter is regarded as a variable). Perhaps the most noticeable difference between Bayesian and Classical statistics is that Classical statistics relies entirely on the data to draw inferences about unknown parameters. Bayesian inference, in contrast, requires a statement of prior belief (expressed as a prior probability distribution) about the unknown parameter. Bayesian methods then use the data to modify the prior distribution to give the posterior distribution.

**Table 2.3. Comparison between Classical and Bayesian statistical methods.**

| | Classical | Bayesian |
|---|---|---|
| Definition of probability | Expected relative frequency | Degree of belief |
| Parameters | Viewed as constants | Described by probability distributions |
| Prior information | Ignored | Required. Prior information about parameter described by "prior" (probability) distribution. |
| Inference | Data alone used to estimate parameter value | Data used to modify "prior" distribution to give "posterior" distribution. |

The posterior probability distribution is calculated from Bayes Theorem which states:

| | | | | |
|---|---|---|---|---|
| Posterior distribution of parameter values given the data | ... is proportional to ... | Likelihood of data given the parameter value | x | Prior distribution of parameter values |

In the context of a salmon lifecycle model, the model would be used to predict the rod catch given a set of parameter values for marine survival, exploitation rate and so on. The predicted rod catch can then be compared to the actual rod catch data, and the likelihood of this data occurring given the parameter values calculated. If this is then multiplied by the prior probability of these parameter values occurring, the posterior probability for the parameter values is obtained. This calculation is repeated over a range of posterior parameter values to produce the joint posterior distribution for the parameters.

When data contain little information, the posterior distributions tend to reflect the prior distributions. However, as data become more informative (large number of years of data, and number of variables measured), the priors lose their influence over the posterior and the information contained within the data will dominate.

### Illustration of Bayes

To illustrate the use of a Bayesian approach to model calibration, a very simple lifecycle model has been produced, and calibrated against a time series of rod catch data. For simplicity, most of the parameters in the model have been fixed and are assumed exactly known (eg fecundity); only marine survival and rod exploitation are to be estimated from the rod catch data. This simplification is required only to help illustrate the methodology; in practice, all parameters could be estimated in this way. The first step with Bayesian calibration is the specification of the prior belief about the parameters in the form of a probability distribution (the prior distributions). These may be obtained from expert judgement, similar fisheries, other river-specific investigations (eg tracking or tagging studies). Figure 2.1 shows the prior probability distribution for rod exploitation rate and marine survival in the form of a contour plot. The centre of the concentric circles represents an area of highest probability, which decreases towards the extreme parameter values (0 and 1). The user in this example has specified prior distributions with modal values of 0.3 for marine survival, and 0.5 for the rod exploitation rate. There is considerable uncertainty in these two parameters, represented by wide spacing of the contours.

The likelihood is calculated from the population model and the calibration data. In this simple example, the lifecycle model was used to predict the rod catch for a pair of values for the rod exploitation rate and marine survival (eg 0.5 and 0.5). The likelihood of the observed rod catch occurring, given these parameter values is then calculated. The calculation of the likelihood is then repeated over a suitable range of parameter values. In this example, the likelihood was calculated over a grid of survival and exploitation values (Hilborn et al, 1994), in steps of 0.1. This is sufficient to illustrate the method, but would be insufficient in practice. Figure 2.2 shows the joint likelihood for marine survival and rod exploitation rate given calibration data for rod catch. The data is relatively unhelpful in estimating the parameters as there is a wide range of combinations of rod exploitation rate and marine survival that could generate the observed data. For example, a high marine survival (0.75) and low rod exploitation rate (0.15) is just as likely to generate the observed rod catch as a low marine survival (0.25) and a high rod exploitation rate (0.85).

Having specified the prior distributions, and calculated the likelihood of the data across the grid of possible parameter values, it is possible to estimate the posterior distribution. Figure 2.3 shows the posterior distribution for the marine survival and rod exploitation parameters obtained from the prior distribution (Figure 2.1) and the likelihood (Figure 2.2). In all applications of Bayesian statistics, the spread of the posterior distribution is reduced in comparison with the prior distribution, reflecting the additional information about the parameters contained within the calibration data. The posterior distributions can then be used to obtain summary statistics if required, such as the mode or median of the distribution, or the variance or percentile probability intervals (eg 95% posterior probability intervals). In this example, the posterior distribution gives a modal value for marine survival of 0.25, and for rod exploitation rate, 0.45. Both are slightly lower than the modal values of the prior distributions. This would suggest that the prior marine survival of 0.3 and exploitation rate of 0.5 would generate a higher rod catch than that observed.

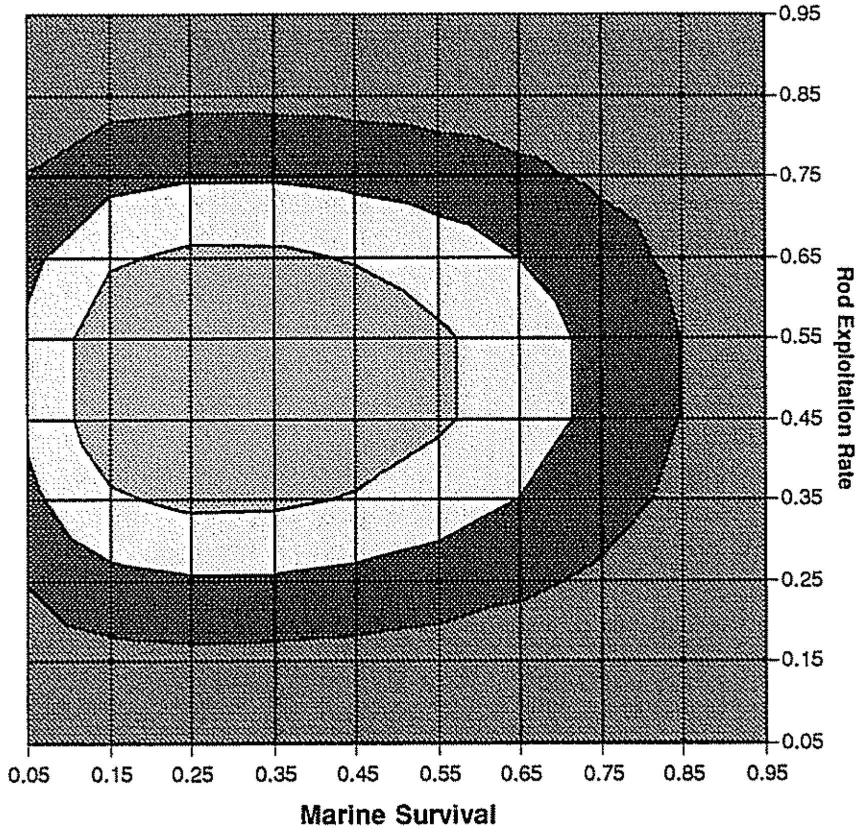


Figure 2.1. Specification of prior probability distribution for marine survival and rod exploitation rate.

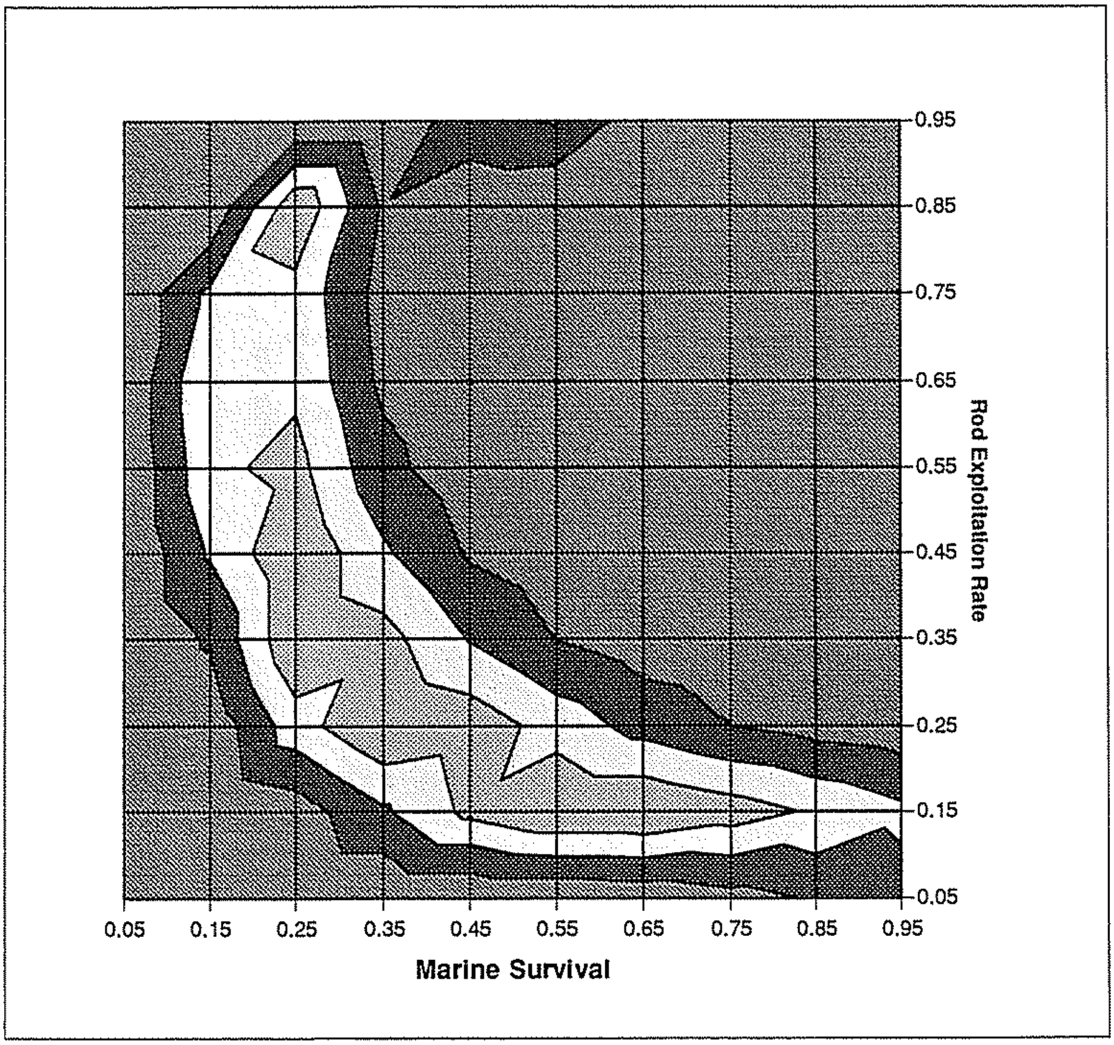


**Figure 2.2. Joint likelihood for marine survival and rod exploitation rate calculated from rod catch data.**

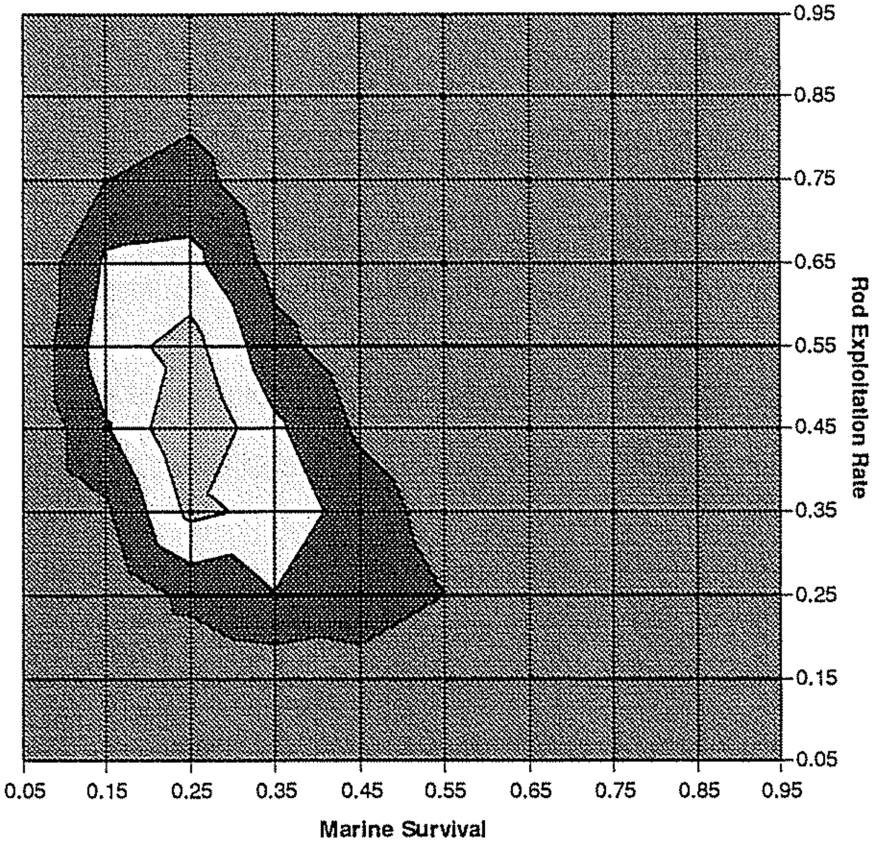


**Figure 2.3. Joint posterior distribution for rod exploitation and marine survival based on prior distributions and rod catch data.**

## Calculation of the posterior

In the above example, a grid approach was used to estimate two parameters, and the grid consisted of nine parameter values (0.1, 0.2, 0.3, ... ). To achieve this, the salmon lifecycle model had to be run 81 times (=$9^2$), and for a complex simulation model, each of the 81 runs would involve many thousands of iterations. In practice, a grid of nine points is insufficient; Walters and Ludwig (1994) suggest that at least 40 discrete levels should be used for each parameter. For the above example, this would involve 1,600 (=$40^2$) runs of the simulation model. A more complex model involving parameters for sea age specific survival and exploitation rates for a range of fisheries (high seas, coastal, net, rod), plus juvenile density dependent survival parameters will have far more than 2 parameters! The number of times that the simulation model will need to be run becomes very large for more complex models:

3 parameters $40^3$ = 64,000
4 parameters $40^4$ = 2,560,000
5 parameters $40^5$ = 102,400,000
10 parameters $40^{10}$ = $1.05 \times 10^{16}$
15 parameters $40^{15}$ = $1.07 \times 10^{24}$

These practical problems have given rise to a range of methods for calculating the posterior distribution which are computationally more efficient. Some of the approaches used in fisheries models include:

1. Analytical methods for mathematically simple models (e.g. Thompson, 1992).

2. Calculating the posterior probability at each point in a grid of parameter combinations, as above (e.g. Hilborn et al, 1994)

3. Integrating out nuisance parameters before using the grid approach (Walters and Ludwig, 1994; Walters and Punt, 1994)

4. Monte Carlo simulation methods such as (in order of likely computational efficiency):

    - Markov Chain Monte Carlo (MCMC) methods (Givens, 1993)

    - Sampling/Importance Resampling (SIR) (McAllister et al, 1994)

    - Adaptive Importance Sampling (AIS) (Kinas, 1996)

    - AIS-SIR (Kinas, 1996)

As the number of uncertain parameters increases, calculating posteriors using the first three methods becomes impractical. Monte Carlo approaches for estimating posterior distributions are then required. The SIR algorithm has been proposed as one of the simplest, most versatile Bayesian Monte Carlo methods for drawing a sample from the posterior (Rubin, 1988).

The key steps in an SIR algorithm are (after McAllister et al, 1994):

1. Choose an "importance function". For computational efficiency, this should be as close to the posterior distribution as possible, however, for simplicity, the prior distribution can be used.
2. Draw one set of parameter values ($\theta_k$) from the importance function ("Sampling").
3. Use the SLM to predict the calibration variables (eg rod catch, net catch).
4. Evaluate the likelihood, prior and importance function.
5. Calculate the importance ratio ($w(\theta_k)$, "Importance").

$$Importance\ ratio = \frac{Likelihood \times Prior}{Importance}$$

6. Repeat steps 2 to 5 a very large number of times (say m=20,000).
7. Draw a large number (say n = 5000) of sets of parameter values randomly with replacement from ($\theta_1, \theta_2, ..., \theta_m$) with probabilities proportional to ($w(\theta_1), w(\theta_2), ..., w(\theta_m)$) ("Resampling"). The resulting sample ($\theta_1, \theta_2, ..., \theta_n$) approximates a sample from the joint posterior distribution of $\theta$, and is used when performing decision analysis.

The problem with the SIR is the difficulty in finding a good importance function in Step 1. Adaptive methods (AIS, AIS-SIR) iteratively refine the importance function and can therefore be considerably more efficient than SIR.

Once the calibration exercise is complete, the sample from the posterior distribution would be saved for subsequent decision analysis.

### 2.3.4 Model validation

#### The role of validation

Once a model is at the stage where it can generate apparently useful output, there is the need to verify and validate the model. Whilst some authors have treated the terms 'verification' and 'validation' as synonyms, others have differentiated between them. Accordingly, verification can be defined as the process of ensuring that the model behaves as the experimenter intends (i.e. the model is, in relation to its purpose, an adequate representation of the real system). In this sense, verification can be thought of as the testing of the model against the original design criteria, and will include an assessment of consistency in model formulation. Subsequently, validation may be defined as 'the comparison of model behaviour against the behaviour of the real system' (Dent and Blackie, 1979) or 'the act of increasing, to an acceptable level, the confidence that an inference about a simulated process is correct for the actual process' (Van Horn, 1971).

Naylor and Finger (1967) present three classes (or philosophies) of validation: rationalism; empiricism; and positivism. Succinct descriptions of these three schools of thought (as provided by Dent and Blackie, 1979) are given below and are discussed further in the subsequent sections:

- **rationalism**; a point of view which holds that a model is simply a system of logical deductions from a set of premises, which may or may not be open to empirical verification. Therefore, if these basic premises are accepted, then the validity of the model must also be accepted.
- **empiricism**; in direct contrast to rationalism, empiricism holds that unless relationships and assumptions used in the model can be independently verified then the model can not be considered to be valid.
- **positivism**; accepts the validity of the model if it is capable of accurate prediction, regardless of the internal structure and underlying logic of the model.

#### Rationalism

Rational or 'conceptual' validation is the validation of the model not against data, but rather against prior knowledge or information. In this sense, conceptual validation (in the form of goodness-of-fit test) is an overall test, and does not test details such as model form, parameters or variables.

The types of questions that may be asked during conceptual validation are:

- is the model form correct?
- do the variable make sense in causal terms?
- do the parameter values make sense?
- does the model seem sensible to an 'expert'?

## Empiricism

Empirical validation relies upon the comparison of model predictions against data or empirical information to validate the relationships and assumptions that form the model structure. Ideally, three types of data should be available:

- **fitting data** - data specifically used to identify and fit an appropriate model;
- **validation data** - data specifically used for validation which has not been used in the initial identification / fitting of a model;
- **working data** - data arising during the routine use of the model which will provide subsequent (and ongoing) 'operational' validation, and which will facilitate the subsequent updating of the model.

In many situations, validation data may not be immediately available. In these situations a number of approaches are possible, for example:

- **data sectioning** - where the available data is divided into two, and treated as fitting and validation data. This assumes that there are sufficient data available.
- **jack-knife techniques** - where a set of n observations is available, and each of the observations is dropped in turn and the parameters of the proposed model are estimated from the remaining (n-1) observations. The model can then be used to predict the excluded observation. This procedure generates 'n' residuals which can be treated as being independent of each other.
- **recursive residuals** - this is similar to jack-knifing, although data are collected through time. For example, a salmon lifecycle model could be calibrated on two years of data and used to predict the observations (rod catch, juvenile abundance) in year three. The first three years are then used to predict year four, and so on.

## Positivism

The positivistic approach is essentially a general form of the empirical approach, in that it can be considered to be a form of empirical validation but undertaken at the 'whole model' scale. The requirements for validation data are the same as for empirical validation.

## Validation techniques in practice - utilitarian validation

A fourth approach to model validation, incorporating elements from all three of the above views, has also been proposed. This 'utilitarian' approach (Naylor and Finger, 1967; Shannon, 1975) considers that, where it is not possible to subject each of the structures or modules within a model to a formal 'empirical' assessment, but the general, 'positivistic' approach has been satisfied, then the 'rational' assessment of remaining modules is sufficient to satisfy the requirements of the validation process. In practice, population models in the literature have tended to rely on such a utilitarian approach.

### Role of sensitivity analysis in validation

As part of the validation of a given model, it is useful to assess the sensitivity of the model to any of its constituent parameters. For example, if a model is found to be extremely sensitive to one particular parameter, and it is known that estimates of that parameter are relatively imprecise, then the validity of the model may be questioned.

## 2.3.5 Sensitivity analysis

### Parameters

As indicated above, information on sensitivity may be used within the validation phase of model development. In addition, sensitivity analysis may be employed to help assess where further effort should be directed in order to produce more precise or accurate estimates of parameter values or, alternatively, where extra effort for improved precision or accuracy is unnecessary. For example, where a model is known to be sensitive to a particular parameter, it may be appropriate to direct resources into estimating the value of that parameter as accurately and precisely as possible. Conversely, where a model is relatively insensitive to changes in the value of a given parameter it may be concluded that there is less of a need to direct subsequent effort into deriving a more accurate or precise value.

Rather than using sensitivity analysis as a tool to help direct or prioritise further research and model development, Evans and Dempson (1986) describe three alternative areas where sensitivity analysis may be employed. Given the scenario where a salmon stock, and the lifecycle model which has been developed to represent it, have both reached a point of equilibrium, then sensitivity analysis may be used in at least three ways. For example, if one of the parameters in the model is changed:

- to ascertain to what extent equilibrium values (e.g. of abundance and catch) change;
- to ascertain what the immediate, transient changes are which occur as the system moves from its original equilibrium to its new one;
- to ascertain the extent to which other parameters must be changed in order for the model to remain consistent with the observed system.

Uncertainty in parameter values is explicitly included within a Bayesian model. However, it is still necessary to assess the sensitivity of the model to differences in the prior distributions (see, for example, McAllister, 1994; Kinas, 1996).

### Variables

It is also possible to assess the response of the model to changes in variables. The role played by sensitivity analysis in this context is primarily concerned with ensuring that the model as a whole behaves in a sensible way to changes in the input variables (e.g. the number of licensed nets, the timing or length of the angling season).

### Model structure

Finally it is possible to assess the sensitivity of the model to changes in its basic structural components. For example, where there is a choice of different sub-models it is possible to assess the implications of the different options simply by comparing the behaviour of the alternatives. For example, in a salmon lifecycle model, the choice between a Beverton-Holt or a Ricker stock recruitment curve may be unclear, but the implications for the model as a whole and the management decisions that would be made as a result of the model could be assessed by developing and comparing two versions of the model.

## 2.3.6 Model implementation

Within population viability analysis, the use of simulation models involves at least three decisions regarding the simulation process itself:

- how long the simulation needs to run before it attains equilibrium (e.g. before data can be recorded without the effects of initial conditions having an inordinately large effect on model predictions);
- how many times to repeat the simulation (i.e. how many 'games' to play); and
- how to compare alternative management strategies.

### Time for equilibrium to be reached

The former question is dealt with by Power and Power (1994) who suggest that, where simulation models do not have a natural terminating event, there is no compelling *a prioi* reason for estimating (for example) the number of smolts at any particular time. As time approaches infinity, however, the distribution of estimates generated by the model will be defined by a 'steady state distribution', Law and Kelton (1991).

This steady state distribution does not rely on the initial values of the state variables that are used to prime the model, *(I)*; such values would include, for example, the initial estimates of fry, parr, smolt and adult densities. However, in contrast to this, the time taken for the model to converge to the steady state (termed the 'transient period') is dependent on the initial conditions. Consequently, the period for which the model must be run before the steady state has been attained is not constant, but must nevertheless be eliminated from an output data set to prevent a bias being introduced into the model results. Welch (1983) provides a means by which this transient period may be identified, and therefore eliminated from the data-set that is used to calculate the steady state distribution. For example, in their model of smolt production Power and Power (1994) found that, for the particular set of initial conditions employed, the transient period lasted for 10 years. Similarly, in a modelling study of sea otter population dynamics, Eberhardt (1995) ran simulations for 10 years before data was recorded, in order to ensure that age distributions had stabilized.

### Number of games

The number of games that are played will affect the precision of the information which is generated for use in population viability analysis. The greater the number of games, then the better the description of the probability of different outcomes at each of the discrete time steps of the simulation. For example, in the examples of salmon lifecycle modelling given by Lee and Hyman (1992) their model, run for a 50 year period, was repeated 500 times. This resulted in a probability distribution (with 500 elements) for each state variable at each discrete time step of the 50 year simulation period. Other examples suggest that fewer 'games' are required (e.g. Power and Power, 1995 - who based their results on the outcome of 50 repeated model runs). Ultimately, the number of games played will be dependent on not only the desired level of precision for the probability distributions generated for each of the state variables, but also on the time and computing resources required to undertake the simulations.

In the context of Monte Carlo methods for calibration of Bayesian models, the number of simulations required will be determined by the efficiency of the simulation algorithms being employed. Increasingly efficient methods are being used (e.g. Markov Chain Monte Carlo (MCMC) methods, Sampling/Importance Resampling (SIR), Adaptive Importance Sampling (AIS), AIS-SIR). The more efficient the algorithm, the lower the number of simulations that are required, enabling considerable savings in computing time.

# 3. MODELLING SALMON POPULATIONS

## 3.1 Introduction

In this review it has proved useful to consider the salmon lifecycle as a series of discrete modules or stages, the outputs from one stage becoming the inputs of the subsequent stage. In effect, this is an extension of the proposal made by Paulik and Greenough (1966) who cite Larkin *et al.*'s earlier (1964) work on the construction of theoretical reproduction curves. In line with this, the following sections refer to:

- juvenile survival;
- smolt production;
- marine exploitation;
- marine survival;
- spawning escapement (including freshwater exploitation and egg production).

Whilst this is a gross simplification of the overall lifecycle it is not intended to reflect the structure of any subsequent models. Rather, it is intended to provide a means of grouping together information that may pertain equally to more than one facet of the lifecycle modelling process. Note that not all of the papers which were reviewed referred to complete lifecycles (these are included as a distinct section - see Section 3.7). For the most part, the references used were included as they provided valuable insights into (for example):

- modelling techniques, including the nature of functional relationships within the model and the incorporation of stochasticity;
- the derivation of parameter estimates;
- parameter estimates themselves;
- methods of model calibration; or
- subsequent interpretation of model outputs.

## 3.2 Juvenile survival

### 3.2.1 Models of juvenile survival

Whilst some authors have not employed density-dependent terms in their models (e.g. Caswell *et al.*, 1984; Korman *et al.*, 1994; Mangel, 1994) most models contain at least one function that embodies a density-dependent relationship which expresses the rate of juvenile survival. Such density-dependent relationships are usually 'compensatory' (where the survival rate decreases with increasing population size) rather than 'depensatory' (where survival increases with increasing density).

When applied to fisheries research, models of compensatory density-dependent survival are generally referred to as 'stock-recruitment' models. However, they may equally be applied to non-aquatic studies. For example, a series of alternative models tested by Elliott (1995a) had been previously applied to a diverse range of animals, including protozoa (e.g. Leslie, 1957) and various insect species (e.g. Hassell, 1975; Hassell *et al.*, 1976; Varley *et al.*, 1973).

Elliott (1985a) compared the performance of six models of density-dependence, concluding that the Ricker relationship provided the best fit for his (sea trout) data. The models he studied were:

- Ricker, 1954;
- Beverton and Holt, 1957;
- Cushing, 1973;
- Shepherd, 1982;
- Hassell, 1975; and
- Paulik, 1973.

It should be noted that the population of sea-trout in the small stream upon which Elliott's research was based would be subject to losses due to both mortality and emigration. In other instances (especially those relating to whole river systems, where stock-recruitment curves will relate to losses due to mortality alone) it has been suggested that the widely-used Ricker stock-recruitment curve may be inappropriate. For example, Solomon (1985) suggests that the evidence for a dome-shaped stock-recruitment curve (i.e. a Ricker-type curve) is 'thin'. He suggests that stock recruitment data derived from studies of natural systems with high egg deposition are not generally available, and that confirmation that increased 'mortality' is not simply the result of emigration is not always available. In addition, Solomon cites several studies (e.g. Ricker, 1954; Le Cren, 1973; Watt and Penney, 1980; Buck and Hay, 1984; Chadwick, 1985) in which there is significant 'plateau' on the stock-recruitment line - suggesting that the stream's carrying capacity has been achieved over a wide range of spawning stock size without an accompanying decrease in recruitment. Power (1993) makes use of Elliott's data to assess and compare the predictive power of the Ricker and Beverton-Holt stock-recruitment models. He concludes that, whilst the Ricker curve provides a better fit (i.e. it is a better descriptor of the available stock-recruitment data) its selection ahead of the Beverton-Holt relationship can not be supported from a predictive point of view.

In other studies, modifications of a basic Ricker function have been used to model compensatory mortality. For example, Larkin and Hourston (1964) forced a minimum (asymptotic) level of recruitment for infinite high spawning stock densities. In addition, they introduced a random element as noise about the Ricker recruitment line to represent extrapensatory mortality. This random element was combined with the rate parameter multiplicatively so as to produce a skewed distribution of recruitment for any given stock size (as seen in natural stocks). Crittendon (1994) applies a resource limitation function (which includes a stochastic element to represent extrapensatory effects - i.e. the influence of random environmental factors) to help predict the number of fry leading into an assumed stock-recruitment relationship. In effect, this resource limitation function describes mortality during the period between emergence and migration into the nursery areas.

### 3.2.2 Applicability of stock-recruitment relationships

The more commonly used models of fish population dynamics, derived from simple surplus production models (e.g. Beverton and Holt, 1957; Ricker, 1954), have found wide acceptance among fishery scientists despite the models' generally 'abysmal' fit to empirical data (Rothschild, 1986; cited by Lee and Hyman, 1992). This view is further propounded by Iles (1994) who, in abstract, comments that the relationship between stock and recruitment in fish populations has been the subject of many studies and some controversy, even to the extent that it has been questioned whether the two can be related in any meaningful way. Iles also makes reference to Rothschild's misgivings (Rothschild, 1986) and admits that the denial of a meaningful stock-recruitment relationship would have profound and disturbing influences on the science of fish population dynamics and would seem to be something of a policy of despair.

As stated above, Elliott (1985b) found strong evidence for the existence of a dome-shaped stock-recruitment curve for sea trout, and found that sea trout population density is regulated chiefly by a compensatory density-dependent survival in the early stages of the lifecycle, the 'key' factor being the spring losses soon after emergence and the onset of exogenous feeding. This theory is expanded in Elliott (1989) in which he advances the concept of a 'critical-period' for juvenile sea trout soon after hatching - during which period density-dependent loss rates are higher than seen later in life. Elliott (1985a) concluded that the Ricker curve provided the best fit to stock-recruitment data for the sea-trout population which he had studied for the period 1966-83, and subsequently made further use of the Ricker curve in a review of 25 years worth of data for sea trout (Elliott, 1993).

On a more fundamental note, some authors feel that the applicability of a simple, deterministic stock-recruitment model is not appropriate for organisms, such as teleosts, which have high fecundities (e.g. in the order of $10^6$). Under such circumstances, even a moderate level of variability in the level of pre-recruit natural mortality can lead to large changes in overall survivorship, and it is suggested that the use of fishery population models dependent upon such functions needs to be re-examined (Koslow, 1992).

Kennedy and Crozier (1993a) cite Solomon's work (Solomon, 1985) as providing a good review of the evidence for alternatives to the Ricker stock-recruitment curve. Although Solomon concluded that, for Atlantic salmon, a 'flat top' curve was most appropriate, this viewpoint was not unequivocal - there being some evidence of a 'descending' right-hand limb from some North American studies. As a way of compromising these views, Kennedy and Crozier (citing Hay, 1991) suggest that there is an envelope around an essentially flat-topped stock-recruitment curve. If penetration of spawning beds is good for a given deposition level there will be higher survival (i.e. at the upper bound of the envelope) whereas if the penetration is low then, for the same level of egg deposition, smolt production is reduced (because of an artificially raised local density, and the possible effects of, for example, overcutting of redds). This may form the conceptual basis for the inclusion of variability around the stock-recruitment curve which is related to extrapensatory factors such as river flow.

### 3.2.3 The need for habitat specific stock-recruitment relationships

Notwithstanding the debate regarding the form of the stock-recruitment relationship, several authors have suggested that there is the need not simply to assume there to be a single stock-recruitment relationship for a species, but rather to consider the potential for alternative stock-recruitment relationships applicable to discrete catchments or defined habitat types within a given catchment (see, for example, Gibson, 1993; Kennedy and Crozier, 1993b).

The fact that an increase in the productivity of a river system is likely, at least over a limited range, to result in an increase in the optimum density of egg deposition led Gibson (1993) to suggest that models should be derived to predict the productive capacity of types of habitat within appropriate biogeographic regions. Rivers should be mapped to predict the productive potential of the system. As sufficient resources may not be available to implement such work, Gibson (1993) further suggests that, because the general production of a river is controlled by characteristics of the drainage basin, an alternative approach may be to partition a river system into different habitat types according to factors such as (for example) climate; hydrological regime; fish fauna; geology; gradient; stream size; and riparian vegetation. The general level of salmon productivity could then be assessed for each of the derived habitat types. A recent example of elements of this general concept being implemented in salmon studies is provided by Korman *et al.* (1994) who used stream gradient to account for the apparently non-homogeneous spatial distribution of juvenile salmon. Initial egg deposition was calculated according to a weighting factor which related to stream-gradient (in effect, a habitat preference function based upon stream-gradient). This factor was derived from remote sensing data, through the application of an empirical transformation intended to correct for bias in gradient estimates.

In discussion, Kennedy and Crozier (1993a) suggest that measures of primary productivity and land-use patterns (together with the associated potential for the enrichment of streams) are seldom discussed in relation to salmon production in streams. However such factors have important implications for estimating optimum egg depositions and hence the applicability of so-called 'index river' data on egg-to-smolt recruitment for neighbouring catchments. Furthermore, it is evident that it is inappropriate to apply a single optimum egg density across the range of habitat types found within any one system, and that any recommended target egg deposition will be highly dependent on the proportion of different types of habitat in different river systems (Kennedy and Crozier, 1993a). This concept has been integral to recent work on the transport of spawning targets (Wyatt and Barnard, 1997b).

### 3.2.4 Parameter estimates

Lee and Hyman (1992) comment that direct estimates of smolt production resulting from different spawning levels generally are not available. Even were stock-recruitment data are available, Lee and Hyman suggest that they are often too scattered to allow precise estimation of the survival function and that, consequently, considerable 'professional judgement' is needed in its interpretation.

In general terms, the principal factors to consider in constructing a juvenile production function are:

1. Does the function have the proper shape?

2. If the production function has a maximum, does it correspond to the level of spawning adults that would be expected to produce the maximum number of pre-smolts?

3. Do the relative differences in egg-to-presmolt survival at low density and at high density seem reasonable?

It is critical that the shape of the production function for juveniles be correct, since this function directly determines the compensatory capacity of the population.

### Density-dependent recruitment

As discussed above, there is a strong conceptual basis for rejecting the use of 'generalised' stock-recruitment relationships for the early salmon life stages (i.e. egg-to-fry or egg-to-parr). Rather, it is suggested that it may be necessary to develop habitat-specific stock-recruitment relationships, and apply these on a river-by-river basis (e.g. see Wyatt and Barnard, 1997b).

### Density-dependent recruitment to later life-stages

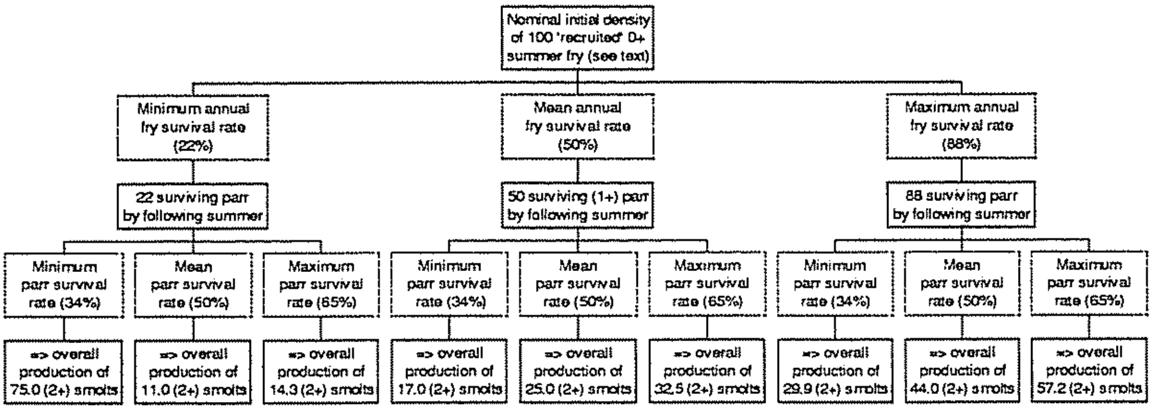
Whilst similar arguments apply to density-dependent recruitment to later life-stages, it is perhaps worth noting that some models do not differentiate between the different stages of the salmon's early life-history and, instead, use a single density-dependent relationship to model the relationship between eggs and smolts (e.g. Porter *et al.*, 1986; Lee and Hyman, 1992).

For example, although Lee and Hyman assume that density-dependent mechanisms operating in the first year or two of life play an important role in the dynamics of salmonid populations, such mechanisms operate in only a general manner, within a (single-stage) egg to pre-smolt transition.

### Subsequent density-independent freshwater survival

Based on a review of data from the British Isles, Kennedy (1988) provides figures (subsequently reproduced by Mills, 1989; and Kennedy and Crozier, 1995) indicating the wide range of variability in published values for annual survival rates for 0+ and 1+ salmon parr. They suggest that the survival rate for the period between 'recruited' 0+ fish (i.e. the summer fry population remaining subsequent to the high initial mortalities associated with the hatching and emergence phases) and 1+ fish the following summer ranges between 0.22 and 0.88. Subsequent survival rates for the transition between 1+ and 2+ (smolts) were found to range between 0.34 and 0.65. It is clear, therefore, that when applied consecutively, the upper and lower extremes of the available survival estimates can give rise to a more than seven-fold difference in the potential level of 2+ parr production (see Figure 3.1, below - reproduced from Kennedy and Crozier, 1995). Although the probabilities associated with the occurrence of either of the extremes may be low, this example serves to illustrate the overall effect of observed variability in survival over each of two successive developmental stages.

**Figure 3.1 Potential range of 2+ smolt production based on range of published annual survival rates and a nominal summer density of 0+ (recruited) fry**



Korman *et al.* (1994) provide a series of parameter estimates for natural mortality rates in Atlantic salmon (see Table 3.1), which were included in their model examining the effects of acidification. These estimates were derived from Elson (1962) and Lacroix (1985). Korman *et al.* assumed that natural mortality in freshwater was density-independent, but applied a habitat-dependent mortality rate to fry during the period of summer growth, in addition to a standard summer fry mortality rate. The habitat-dependent mortality was based on reach gradient, and was calculated for individual reaches throughout the river system being modelled. Reaches with gradients which were at the peak of a gradient-preference curve (predetermined for salmon parr, and explaining between 17% and 27% of the observed variability in parr density) were assumed to experience no habitat-dependent mortality.

**Table 3.1 Atlantic salmon freshwater mortality rates, after Korman *et al.* (1994)**

| Parameter | Rate | Period | Equivalent daily rate |
|---:|---|---|---|
| Habitat-independent emergence mortality | 85.0% | 7 months | 0.89%.day$^{-1}$ |
| Parr mortality | 40.0% | 6 months | 0.28%.day$^{-1}$ |
| Precocious parr mortality | 50.0% | 6 months | 0.38%.day$^{-1}$ |

These values are at the lower end of the range of possible values indicated by Kennedy and Crozier (1988); the two year cumulative mortality rate being effectively equal to ~87% (i.e. an overall survival rate of ~13%).

## 3.3 Smolt production

### 3.3.1 Models of smolt production

Atlantic salmon smolt production was modelled by Power and Power (1994), who proposed a framework for allowing the effects of climatic change on smolt production to be analysed. Although covering the entire lifecycle, the model structure (and hence the value of the model's outputs) is weakened by the use of relationships that have been greatly generalised. For example, no explicit allowance is made for mortality (either natural or due to exploitation) other than by correlating the displacement from the assumed mean number of alevins that are hatched in any given year (1.8 alevins.$m^{-2}$ of stream bed area) to the number of females produced three years earlier.

### 3.3.2 Estimation of smolt-age

The composition (in terms of 'river-age' or 'smolt-age') of the smolt run will represent an important component of any salmon population model, as it plays an important role in the modulation of the effects of survival through both the freshwater and the marine developmental stages. In addition, Nicieza *et al.* (1994) consider that smolt size and the timing of seaward migration are two major factors influencing subsequent marine survival of post-smolts.

The Atlantic salmon is an example of a species with a 'plastic' life-history strategy (Metcalfe and Thorpe, 1992) - the age at which smolts undertake seaward migration varying between one and eight years. Furthermore, the relationship of the duration of the freshwater and marine stages is complex (depending on the environmental conditions experienced, which will vary from year to year) and appears to be under environmental and genetic control, (Thorpe, 1989; Metcalfe and Thorpe, 1990). There is evidence that the age at which fish first turn into smolts and migrate to sea is largely determined by growth rates during the preceding summer (e.g. Thorpe *et al.*, 1992) with fish which grow faster smolting earlier. Gibson (1993) comments that life-history strategies can also change with changes in density-dependent growth rates.

Symons (1979) suggests that average smolt age can be estimated from the number of days per year on which water temperature reaches or exceeds 7°C, whilst more complex procedures have been suggested by other authors. For example, Korman *et al.* (1994) assumed that the parameters describing the proportion of 1+ parr becoming 2 year-old smolts, and of 2+ parr becoming 3 year-old smolts were 'dynamic' (density dependent). The total parr density was used to predict mean fork-length for each age-class (the assumption being that higher densities of parr give rise to a reduced growth rate and hence a lower mean fork-length). Subsequently, a nominal standard deviation of 0.78cm, assumed to be normally distributed about the mean length, was used to generate a length-frequency distribution of each age-class. These distributions were then compared against pre-determined smoltification criteria (in terms of fork-length) to arrive at the proportion of the population smolting. This methodology leads to the situation where, given a high total parr density, a lower proportion of the parr population will smolt.

Evidence for population-specific growth rates and for differential distribution between modal groups of length-at-age (e.g. Nicieza *et al.*, 1994) support the conclusion drawn from other studies (e.g. Thorpe, 1986; Taylor, 1990) that the threshold for smolting is a population-specific trait. This being the case, there is a strong argument for taking river specific information into account in this phase of the formulation of a lifecycle model. Whilst it may be possible to develop one or more sub-modules to effectively over-ride default values with estimates of smolt-age derived from environmental data (for example, in the manner described by Symons, 1979) the demands placed by such an approach, should any model need to be transportable, rapidly become excessive.

### 3.3.3 Smolt age on the Dee

River specific data is available for the River Dee (e.g. Davidson *et al.*, 1994, 1995). An example of this is given as Table 3.2, below. This data is based on scales sampled at Chester Weir.

**Table 3.2 Profile of smolt ages from adult fish trapped at Chester Weir, River Dee, 1993, 1994 (after Davidson *et al.*, 1994, 1995).**

| Smolt age | Percentage of fish in 1993 sample | Percentage of fish in 1994 sample |
|---|---|---|
| 1 | 37.0 | 35.2 |
| 2 | 61.7 | 63.9 |
| 3 | 1.3 | 0.9 |

## 3.4 Marine survival

### 3.4.1 Overall marine mortality

Although discussed separately below (as Sections 3.4.2 *et seq.* and Section 3.5), the two distinct mortality elements within the marine, distant-water phase of the salmon lifecycle (i.e. natural mortality and marine exploitation) have been considered by some authors as a single mortality rate.

In this respect, it has been suggested that a single value of 10% can be used to account for overall marine survival between the post-smolt stage and the return to homewaters (see, for example, Anon, 1996).

### 3.4.2 The importance of marine survival

It has been suggested that the marine survival through from the immediate post-smolt stage to the mature 'recruiting' adult stage is the most important variable affecting the level of 'recruiting' eggs and the subsequent gain (Chaput *et al.*, 1993).

However, the relationship between sea-age (i.e. the total time spent in the marine environment) and overall survival during the marine phase may be not be as straightforward it first appears. For example, it is possible that salmon displaying different marine 'strategies' (i.e. fish that remain in the marine environment for different lengths of time) may be exposed to different levels of environmental risks due to their use of different migration routes (Korman *et al.*, 1994).

In addition, the assumption that sea survival is independent of smolt density may not be valid for Atlantic salmon (Chaput *et al.*, 1993), or indeed for certain stocks of Pacific salmon (Peterman, 1978). For example, There are indications that the size of smolts affects sea survival, and that the size of smolts is inversely related to the density of smolts produced (Chadwick, 1987; cited by Chaput *et al.*, 1993).

### 3.4.3 Variability of marine survival

In a review of survival rates of Pacific salmon species, Bradford (1995) concluded that the freshwater stages contributed slightly more to the overall variation in egg-to-adult survival (where an adult is taken to be a fish at escapement) than did the ocean stages. Not surprisingly, the schedule of mortality during the egg-to-adult interval was seen to depend upon the natural history of each of the species involved.

However, data from the Western Arm Brook (Chadwick, 1988) suggests that, of the total variation in the numbers of returning adult Atlantic salmon, only about 40% can be explained by variations in smolt numbers. In addition, the variability of the overall marine survival (i.e. where a single term, equal to the sum of natural mortality plus commercial exploitation, is used for marine mortality) can be high. Chadwick, for example, provides estimates of the coefficient of variation (CV) for the marine survival rates for stock from several Canadian rivers, which range from a CV of 42% for the Little Codroy River up to 95% for the Big Salmon River, (Chadwick, 1988). In addition, it is suggested that most of this variation is due to fluctuations in the rate of natural mortality for Canadian fisheries rather than to changes in the exploitation rate, as the natural mortality is though to be higher than mortality due to fishing by a factor of perhaps eight to ten (Chadwick, 1988).

### 3.4.4 Estimating marine survival - the use of run-reconstruction techniques

To estimate survival rates (and associated fishery exploitation rates) for individual stocks it is necessary to count and tag juvenile salmon as parr, or when they emigrate as smolts, and then estimate the number remaining alive at the time that the various fisheries operate. The number of tagged fish recaptured in the fisheries can then be used to estimate the extant exploitation rate. This approach has two key weaknesses. First, natural mortality during the first year at sea (which can be both high and variable - Ritter, 1989) will affect the number of one sea-winter fish that survive from a batch of tagged smolts to become exposed to the fishery. This undefined mortality effectively introduces a major source of uncertainty at the beginning of the chain of calculations used to evaluate the exploitation rate. Second, it is necessary to know the proportion of fish of each sea-age group that mature each year, as these fish will return to home waters to spawn, and so will be unavailable to the fishery.

To resolve these problems, 'backward running' models were proposed (e.g. Potter, 1989). Such models (now usually referred to as 'run-reconstruction' models) use data on the number of fish of each sea-age class (usually tagged) returning to a river to spawn, and permit the estimation of the rates of both marine exploitation and first year (post-smolt) survival in addition to estimates of the proportion of each sea-age group maturing in each year (Potter and Dunkley, 1993).

The limitations of run-reconstruction techniques as a means of determining the level of marine exploitation lie in the requirements for tag-recapture data in the exploiting fishery and for estimates of the numbers of tagged fish of each sea-age group returning to freshwater. Some of the early estimates in the UK were for the rivers Burrishoole, Bush and North Esk (Potter and Dunkley, 1993), but data are becoming available for an increasing number of rivers.

### 3.4.5 Estimates of marine survival

Although run-reconstruction modelling is not, in itself, a form of predictive modelling, it is a valuable technique in that it provides estimates of both post-smolt survival and the proportion of stock maturing each year. Estimates of both of these parameter values are required by predictive models. For example, data presented by Potter and Dunkley (1993), which encompasses virtually all of the currently available information, provides estimates of the mean and variability of post-smolt survival and the proportion of maturing stock for five European rivers (see Table 3.3). The figures presented suggest a mean (wild-fish) post-smolt survival for the first year of 0.2 (which is approximately equivalent to an instantaneous mortality rate of $9.96\times10^{-1}.\text{day}^{-1}$).

**Table 3.3 Example of run-reconstruction estimates for post-smolt survival and proportion of stock maturing.**

| | | | Post-smolt survival | | Proportion of 1SW maturing | |
|---|---|---|---|---|---|---|
| River | Stock | Period | Mean | S.D. | Mean | S.D. |
| North Esk | Wild | 1981-89 | 0.23 | 0.06 | 0.64 | 0.04 |
| Bush | Hatchery | 1985-89 | 0.11 | 0.04 | 0.97 | 0.00 |
| Burrishoole | Hatchery | 1980-90 | 0.11 | 0.07 | - | - |
| Drammen (Norway) | 1+ hatchery smolts | 1984-89 | 0.09 | 0.07 | 0.39 | 0.14 |
| Imsa (Norway) | Wild | 1981-89 | 0.19 | 0.07 | 0.65 | 0.16 |
| | 1+ hatchery smolts | 1981-88 | 0.08 | 0.05 | 0.70 | 0.15 |
| | 2+ hatchery smolts | 1981-88 | 0.10 | 0.04 | 0.84 | 0.07 |

As they were reporting their work before the advent of run-reconstruction modelling (e.g. Potter, 1989), Gee and Radford (1982) were unable to provide direct estimates of the mortality rate for the first year at sea (all values quoted in their paper are in terms of the mortality rate per day rather than annual survival). Instead, they made use of estimates of the overall rate for the return of adults from smolts derived in other studies (e.g. Shearer, 1970; Mills and Shackley, 1971) to back-calculate an estimate for the mortality rate for the first year at sea that remains consistent with estimates from tagging experiments and with calculated mortality rates during later sea-life. Using values for the overall return rates of $5.3\times10^{-2}$, $2.7\times10^{-2}$ and $1.6\times10^{-2}$ (for one, two and three sea-winter fish respectively) Gee and Radford estimated the first year post-smolt mortality rate to be $7.0\times10^{-3}.\text{day}^{-1}$.

Assuming that post-smolts are exposed to this mortality rate for 365 days, and that mortality is both constant and density independent, the overall (annual) survival rate for post-smolts during their first year at sea is equivalent to $(1-(7.0\times10^{-3}))^{365}$, or $7.7\times10^{-2}$. Although not expressly stated, it is assumed that the mortality rates quoted by Gee and Radford are 'total' mortalities (i.e. natural mortality plus mortality due to exploitation).

Other values quoted by Gee and Radford (1982) are for the mortality of fish subsequent to their first year at sea. Because different return times are assumed for different sea-ages of fish, the period of 'residence' (during which fish are subjected to the estimated mortality rate) varies with age. The exposure periods are 148, 452 and 756 days for fish set to return as one, two and three sea-winter fish, respectively. The estimated rates of daily mortality provided by Gee and Radford ($2.6\times10^{-3}$, $2.3\times10^{-3}$, and $2.1\times10^{-3}.\text{day}^{-1}$ - respectively) therefore equate to overall survival rates of 68%, 35% and 20%. Note that the values used by Gee and Radford relate closely to the daily mortality rate of $2.4\times10^{-3}.\text{day}^{-1}$ quoted by Gardner (1976).

As with any stage where a random element is used to model the variability in a survival rate, estimates of the production of adult salmon can be biased by assuming an incorrect error structure around an assumed mean value for marine survival. In this context, Peterman (1981) suggested that a multiplicative, log-normal distribution is most consistent with the data describing the smolt-to-adult transition (i.e. marine survival).

The assumption that natural mortality in the sea varies inversely with weight-at-age (the 'inverse weight hypothesis' - Mathews and Buckley, 1976) was originally proposed for coho salmon. At the request of ICES, its applicability to stocks of Atlantic salmon was examined (Doubleday *et al.*, 1979). They estimated natural mortality rates, acting on the population between the Greenland fishery (at the nominal sea-age of 516 days) and adult return to the River Bush (at the nominal sea-age of 830 days):

- by assuming exponential growth at all ages; and
- by assuming exponential growth to sea-age one and no growth thereafter.

Data from the River Bush were found to support the hypothesis that salmon with a higher weight-at-age will have a lower natural mortality rate. However, the findings were inconclusive as the available data did not permit the precise estimation of growth in the sea, particularly during the first post-smolt year (which is most important in the inverse weight hypothesis).

However, with the growth functions used, the assumption of continuing exponential growth resulted in an overestimate of growth, and hence effectively produced an estimate of a lower-bound for the likely range of overall natural marine mortalities (mortality rates between 2.3% and 3.4% - for the 1+ and 2, 2+ smolt groups respectively). It was felt that this was a better model of mortality for the River Bush salmon than the simple assumption of no growth after the first year post-smolt (which produced mortality estimates of 5.9% and 8.6%). Similar estimates, again based on continuing exponential growth, utilising data for salmon in the Sandhill River (Labrador, Canada) ranged from 10% for the 1+ smolt group to 14% for the 2, 2+ smolt group. Consequently, Doubleday *et al.* (1979) concluded that the best general estimate for mortality during the period of return to home waters from the Greenland fishery lies in the range of 3% to 12%, and consequently suggest that, in the absence of evidence to the contrary, a natural mortality rate of 0.5% to 1.0%.month$^{-1}$ would be appropriate (equivalent to a daily rate of between $1.7\times10^{-4}$ and $3.3\times10^{-4}$). Note that the use of Bush-specific data would reduce this estimated rate to around $2.4\times10^{-4}$.day$^{-1}$ (assuming equal numbers of the 1+ and the 2, 2+ smolt groups).

## 3.5 Marine exploitation

Marine fisheries operating on the European group of Atlantic salmon stocks must be assumed to be exploiting a mixture of stocks, even when operating in estuarial waters. As a general rule, however, the extent of mixing in any catch will decrease as fisheries come closer to rivers of origin (Potter and Dunkley, 1993). Marine fisheries exploit European salmon in both 'home-' and 'distant-water' fisheries. Home-water fisheries operate from the shore, or within a narrow coastal band, extending up to 12 nautical miles from the shore. The principal distant-water fisheries exploiting European stocks are those operating at the Faroes and at Western Greenland. Both fisheries take predominantly those salmon which would have returned as two sea-winter fish, together with smaller numbers of potential three sea-winter fish. Although the Faroes fishery also catches some potential one sea-winter fish, many of these are discarded as they are under the legal size limit. Due to quota buy-outs, the importance of the Faroese fishery as major source of exploitation for European stocks has decreased considerably, although those fish that are taken are almost entirely of European origin. By contrast, the Western Greenland fishery takes both European and North American salmon. Historically, approximately equal numbers of each of these two stocks were taken, although recently the estimated proportion of European salmon in the catch has fallen to less than 40% (Anon, 1994).

Potter and Dunkley (1993) and Solomon and Potter (1992) provide information, derived from run-reconstruction models, on the exploitation rates in different commercial marine fisheries for a series of discrete salmon stocks. Information relating to wild fish from British stocks are reproduced below as Table 3.4. Note that the figures provided are the mean 'extant' exploitation rates (i.e. the catch divided by the total size of the stock at the beginning of the fishing season).

Solomon and Potter (1992) also highlight the relationships between extant exploitation rates and fishing mortality rates. Where the level of extant exploitation (U) at a fishery is known, the proportion of fish surviving the fishery (S) is given by:

$S = (1 - U)$.

The 'level of fishing mortality' (F) is defined as the 'negative of the natural logarithm of the proportion of fish surviving in a year' (Pope, 1982). That is:

$S = e^{-F}$.

Mortalities due to sequential fisheries (e.g. $F_1$, $F_2$, $F_3$ and $F_4$) can be combined to a single 'overall fishery survival' by summing the individual fishing mortalities and converting to a survival rate:

$S = e^{-Fo}$; where:

$Fo = F_1 + F_2 + F_3 + F_4$

**Table 3.4 Estimates of marine exploitation rates (mean rate with range in parentheses)**

| | | Smolt year- | Faroes | | Greenland | Homewaters (local) | |
|---|---|---|---|---|---|---|---|
| River | Stock | classes | % 1SW | % MSW | % 1SW | % 1SW | % MSW |
| North Esk | Wild | 1981-89 | <1 (0-5) | 6 (0-14) | 10 (0-48) | 54 (47-73) | 44 (34-62) |
| Bush | Wild | 1983-89 | <1 | <1 | <1 | 71 (61-81) | 45 (36-60) |
| Burrishoole | Wild | 1984-89 | <1 | <1 | <1 | 76 (54-82) | - |

Ricker (1976) suggested that, in their penultimate year of life, mortality (other than landed catch) caused by pelagic gillnetting is estimated to be equal to the catch for Pacific salmon. For salmon in their final year of life, this value falls to approximately a quarter of the reported catch. Furtehrmore, he suggests that natural mortality for sockeye (*Oncorhynchus nerka*) in their final year of life is about 0.015 per month (approximately $5.04 \times 10^{-4}.\text{day}^{-1}$) and is somewhat more in early years of pelagic life. For coho and chinook (*O.kisutch and O.tshawytscha*) the best natural mortality estimate for the last year of life is 0.013 per month (approximately $4.36 \times 10^{-4}.\text{day}^{-1}$). These estimates of 'natural' mortality are likely to include non-declared fishing mortality (i.e. non-declared landed catches).

## 3.6 Spawning escapement

### 3.6.1 Return of adults

**Available information**

As with the age at which smolts undertake their seaward migration, the length of time individual salmon spend at sea before returning to freshwater to spawn can vary greatly. There is no clear relationship between these two residence periods. For example, strong independence of river-age and sea-age was found in data from Quebec (presented by Bielak and Power, 1986) and, based on this finding, they suggested that river-age *per se* should not be taken as a determinant of potential sea-age.

Metcalfe and Thorpe (1992) suggest that the period of marine residence may range between one and six years. Both genetic and environmental factors may play a part in determining the duration of the marine phase (e.g. Gardner, 1976; Herbinger and Newkirk, 1987).

Estimates for the sea-age composition of returning adult stock for various river systems can be taken from the literature, and it is possible to use such data to produce estimates of mean return rates, together with measures of the variability of the data. Indeed, some stocks have been characterised by their periods of sea-residence.

For example, Porter *et al.* (1986) describe three stocks from North America which they term Types I, II and III. Type I stocks consist of individuals which mature after one sea-winter (i.e. as grilse). The proportion of female grilse in Type I stocks is generally >60%. Type II stocks have some individuals maturing as grilse and others that mature after two sea-winters. Type III stocks have some individuals that mature at each of three sea-ages (i.e. grilse, two sea-winter and three sea-winter fish). Grilse in stock Types II and III generally have a low proportion of females (e.g. <30%); whereas two and three sea-winter fish are predominantly female (>50%). Previous spawners occur in all stock types and sea-ages but, although varying both between stocks and annually, it is usually a low percentage (e.g. <10%) of the spawning population.

Such stock characterisation may be possible for UK salmon stocks using, for example, data on sea age and sex ratios of returning adults such as that presented for the River Dee by Davidson *et al.* (1994, 1995).

Percentage breakdowns of the returns to the North Esk (Scotland), by both smolt-age and sea-age, is presented for the period 1963-88 by Shearer (1992). This data (originally derived from net and coble catches) was used to produce the estimates shown below (Table 3.5 to 3.7, below).

**Table 3.5 Returns to River North Esk, by sea age (after Shearer, 1992)**

| | 1SW | 2SW | 3SW | 4SW | MSW (i.e. all multi-sea winter fish) |
|---|---|---|---|---|---|
| mean | 47.8 | 47.4 | 4.7 | 0.1 | 52.2 |
| sd | 13.1 | 12.1 | 2.9 | 0.1 | 13.1 |
| cv | 27.4 | 25.4 | 62.9 | 147.0 | 25.1 |

**Table 3.6 Returns of one sea winter fish to River North Esk, by river age (after Shearer, 1992)**

| | 1.1 | 2.1 | 3.1 | 4.1 |
|---|---|---|---|---|
| mean | 4.1 | 67.2 | 28.0 | 0.8 |
| sd | 2.9 | 8.7 | 9.5 | 0.7 |
| cv | 71.7 | 13.0 | 33.9 | 84.6 |

**Table 3.7** **Returns of multi-sea winter fish to River North Esk, by river age (after Shearer, 1992)**

| | 1.MSW | 2.MSW | 3.MSW | 4.MSW |
|---|---|---|---|---|
| mean | 3.3 | 62.2 | 32.6 | 1.9 |
| sd | 2.4 | 9.4 | 8.8 | 1.8 |
| cv | 71.5 | 15.0 | 27.0 | 94.6 |

Using the information in the above tables it is possible to calculate the percentage contribution made by each river- and sea-age combination to the total returning stock. For example, 47.8% of fish that have returned are one sea-winter fish (Table 3.5) and, of these, 67.2% were two year-old smolts (Table 3.6). Consequently, it may be assumed that 32.1% (i.e. 47.8% × 67.3%) of returning fish are two year-old smolts that have experienced one sea-winter.

Similar data is available for the River Dee (e.g. Davidson *et al.*, 1995) where returning adults are sampled at Chester Weir (see Table 3.8).

**Table 3.8** **Year class composition of River Dee salmon run (1992-3)**

| | **Year-class** | | | | | |
|---|---|---|---|---|---|---|
| **Sea-age** | **1987** | **1988** | **1989** | **1990** | **1991** | **All** |
| **0 SW** | - | - | - | - | - | 0 |
| **1 SW** | - | 24 | 2053 | 5935 | 2939 | 10951 |
| **2 SW** | 17 | 875 | 1449 | 649 | - | 2990 |
| **3 SW** | 71 | 55 | 13 | - | - | 139 |
| **All** | 88 | 954 | 3515 | 6584 | 2939 | 14080 |
| **Previous spawners** | - | - | - | - | - | 320 |

The drawback with this information in terms of its use in simulation modelling lies in the fact that no account is made of marine mortality. The figures simply represent the *result* of life-history strategies, and do not relate directly to the likelihood of an individual, randomly selected, fish following a particular life-history strategy and surviving to return to freshwater. However, data of this nature is still of value in that it affords a means of checking the results from sub-models that are developed (incorporating marine mortality) to describe adult return.

There are data available which relate directly to overall post-smolt survival for the period up to return the freshwater. Such data, derived by run-reconstruction, is required if the return of adults is to be adequately modelled. For example, Crozier and Kennedy (1993) present data for the River Bush, covering the period 1974-1989. This data showed that the post-smolt survival rate of returning grilse (i.e one sea winter fish) ranged from 3.9% to 12.0% (with a mean of 8.2%). The quoted coefficient of variation for the survival rate was 27.3%. The return rate of two sea winter fish over the same period was much lower (ranging from 0.4% to 1.9%, with mean of 1.1% and a coefficient of variation of 44.4%). The proportion of adults returning as grilse was high (81.0% to 96.0%; with a mean of 88.0% and a coefficient of variation of 5.9%).

### Stock specificity

Whilst acknowledging that there is evidence for environmental components in the determination of the age at maturity, Herbinger and Newkirk (1987) state that there is also evidence for a strong genetic component, indicating that parameters describing age at maturity are likely, to some extent, to be stock specific. The potential for there to be a genetic (and heritable) component is supported by the findings of Randall *et al.* (1986) who state that the sea-age at which Atlantic salmon mature is determined to a large extent before juveniles emigrate from their natal rivers. Thorpe and Mitchell (1981) also consider there to be strong circumstantial evidence for the existence of discrete 'river' stocks of Atlantic salmon which in turn, they suggest, implies the need for consideration of management on a stock-by-stock basis. Furthermore, although some authors have suggested that maturation at sea may be related to fluctuations of water temperature, Dempson *et al.* (1986) found that correlations between maturation and sea temperature have been contradictory.

### Timing of adult returns

Gee and Radford (1982) assumed different return dates for different sea-ages of salmon in the river Wye, which followed information presented in Gee and Milner (1980). It is obvious that, in conjunction with the identification of general life-history strategy, the identification of these return periods is important, as they will help delineate the period of exposure to different fisheries (and hence exposure to different levels of risk).

Data is available specifically for the Dee (e.g. Davidson *et al.* 1994 and 1995) which indicates the return rate of salmon (broken down by sea-age) on a month-by-month basis through the season. Such information could be used to generate 'residence' times for the different life-history strategies that are followed through the marine phase, and which can be subsequently used as indicators of the period of exposure to different levels of exploitation, etc.

## 3.6.2 Homewater commercial exploitation

The rate of homewater exploitation that is experienced by returning salmon is highly stock-specific, in that it will be strongly correlated with the existence and extent of a homewater fishery. In this sense it is only meaningful to report on homewater fishery exploitation rates for fisheries in the British Isles. In addition, the extent of some homewater fisheries may be changing due, for example, to bylaw or NLO change, or to netting rights being bought out by certain interested parties.

Estimates of exploitation rates are available for several salmon stocks (e.g. Solomon and Potter, 1992 - see Table 3.9).

**Table 3.9 Estimated exploitation rates for homewater fisheries on wild UK stocks - after Solomon and Potter (1992)**

| | | | | Percentage exploitation | |
|---|---|---|---|---|---|
| Stock | Age | Fishery | Period | Mean | Range |
| Burrishoole | 1 SW | Coastal nets | 1985-90 | 76 | 54-82 |
| Bush | 1 SW | Coastal nets * | 1984-89 | 71 | 61-89 |
| | 2 SW | | 1987-90 | 45 | 36-60 |
| North Esk | 1 SW | River nets | 1985-90 | 32 | 23-40 |
| | 2 SW | | 1985-90 | 34 | 29-37 |

* coastal netting for all of Ireland.

### 3.6.3 Freshwater exploitation and mortality

Kennedy and Crozier (1993a) cite Mills (1991) in commenting that freshwater exploitation rates from sport fisheries vary greatly between systems and that the extent and variation of non-catch fishing mortality and natural mortality in freshwater is largely unknown. In the absence of hard data, Elson (1975) has suggested that a blanket figure of 25% freshwater mortality should be applied to cover these losses. Porter *et al.* (1986) also use a value of 25% to represent angling mortality.

In place of a single blanket value for freshwater exploitation, river-specific models to estimate freshwater angling exploitation can be developed using information on angling effort.

Again, data are available for the River Dee (Davidson *et al.*, 1995) which indicate the estimated overall angling exploitation rate on a month-by-month basis (see Table 3.10) or by sea-age group (see Table 3.11).

**Table 3.10 Salmon angling exploitation rate for the River Dee, by month**

(Estimated value with 95% confidence limits given in brackets)

| Year | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | All |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1991 | - | - | - | - | - | 25.1 | 5.0 | 8.3 | 7.9 | 0.8 | 6.9 |
| | - | - | - | - | - | (9.6-64.6) | (1.7-14.7) | (5.4-12.8) | (5.3-11.8) | (0.1-4.4) | (5.3-9.1) |
| 1992 | 0.0 | 15.2 | 40.6 | 24.7 | 18.5 | 18.6 | 20.3 | 20.7 | 11.3 | 4.6 | 17.4 |
| | - | (4.0-55.7) | (20.5-80.2) | (15.8-38.6) | (11.4-30.1) | (10.4-33.4) | (15.4-26.7) | (15.1-27.1) | (7.6-16.9) | (1.9-10.7) | (15.0-20.1) |
| 1993 | - | 0.0 | 21.3 | 33.7 | 32.9 | 18.0 | 18.8 | 14.9 | 7.4 | 4.7 | 14.7 |
| | - | - | (9.0-50.0) | (15.3-73.5) | (21.5-50.4) | (10.7-30.2) | (14.4-24.6) | (11.3-19.8) | (4.9-11.1) | (1.8-12.1) | (12.7-17.0) |

**Table 3.11 Salmon angling exploitation rate for the River Dee, by sea-age**

(Estimated value with 95% confidence limits given in brackets)

| | Sea age | | | |
|---|---|---|---|---|
| Year | 1 SW | 2 SW | 3 SW | PS |
| 1991 | 6.2<br>(4.5-8.4) | 12.0<br>(6.8-20.9) | - | 5.1<br>(0.8-28.9) |
| 1992 | 16.0<br>(13.2-19.4) | 19.6<br>(15.5-24.8) | 26.7<br>(12.2-58.3) | 4.3<br>(0.6-24.3) |
| 1993 | 13.2<br>(10.9-15.9) | 18.6<br>(14.5-24.0) | 26.7<br>(11.3-62.5) | 6.7<br>(1.8-24.4) |

Additional figures are available for other river systems in the British Isles - see, for example, Anon, 1996; Solomon and Potter, 1992.

A further refinement concerning the use of information on angling exploitation rates within salmon lifecycle simulations would be to involve information on the spatial distribution of angling effort rather than to simply assume that angling effort is evenly spread throughout the catchment. The catchment of the River Dee has been split into eight sections and data exists on salmon recaptures by river section and by month, so affording an insight into the spatial component of angling exploitation. Such data is available, for example, in Davidson *et al.* (1995).

Provisional data from the River Dee (for the period 1991-1993) suggests that the combined effect of illegal fishing mortality and natural mortality in the freshwater phase, up to the time of spawning, equates to an overall mortality rate of 0.08 (Anon, 1996); a value similar to that which has been derived for the River Twyi (0.10).

The development and refinement of an angling exploitation model is likely to be an important component of the salmon lifecycle model. The management of salmon stocks in relation to spawning escapement targets in the NRA will necessitate the monitoring of compliance by rod-catch data on many rivers. The close links between target setting and compliance assessment, and the use of lifecycle models (Wyatt and Barnard, 1997a), would suggest the need for parallel approaches to the development of rod exploitation models. There have been a number of models proposed relating catch to run size and effort (see, for example, Wyatt and Barnard, 1997a; Paloheimo and Dickie, 1964; Peterman and Steer, 1981; Cryer and Maclean, 1991; Bannerot and Austin, 1983).

### 3.6.4 Egg production

#### Fecundity

Many authors have recorded differences in reproductive indices (e.g. fecundity and egg size) between different populations of Atlantic salmon (Shearer, 1992; Thorpe *et al.*, 1984 - including citations of work by Belding, 1940; Pope *et al.*, 1961; Glebe *et al.*, 1979). In addition, the life history strategies adopted by individual fish within the population may also affect the reproductive indices. For example, studies on fish from the River Almond in Scotland (Thorpe *et al.*, 1984) have indicated that, for any given sea-age and body size, fish developing faster in the freshwater phase (i.e. the lower river-age groups), had a higher fecundity than slower developing fish. However, the eggs that were produced were smaller. In addition, the fecundity of a given river-age of fish (i.e. fish of the same 'developmental rate') was positively correlated to the size of eggs produced. Whilst the larger eggs gave rise to larger fry (at age of first-feeding), the initial size advantage was not maintained through the first year of growth.

The production of eggs by returning adults has been related to the size (and hence, by inference, to the sea-age) of fish. For example, in a model developed to assess the impact of acidification on Atlantic salmon populations, Korman *et al.* (1994) assumed fecundity to be a function of female fork length, using the relationship:

$$\textit{Number of eggs} = 446.54 \times e^{(0.0362 \times \textit{Fork length}\ [\mathrm{cm}])}$$

Similarly, Pope *et al.* (1961) proposed the general relationship;

$$\log_{10}(\textit{Number of eggs}) = 2.3345 \times \log_{10}(\textit{Fork length}\ [\mathrm{cm}]) - 0.582.$$

Whilst assuming a constant gradient for this straight-line relationship, Pope *et al.* provided river-specific values for the y-axis intercept for each of a series of Scottish rivers.

Other studies have reduced the need for detailed growth information by assuming a single nominal size for returning adults of a given sea-age, and then applying a standard fecundity (in terms of eggs per kg of body weight) to these fish. The conceptual model presented by Gee and Radford (1982) follows this pattern, making use of fecundity estimates from Canadian studies (1650 $\mathrm{eggs.kg^{-1}}$) in conjunction with Wye-specific data (from Gee and Milner, 1980) on the mean weights of female one, two and three sea-winter fish. Such data is also available for the River Dee (see data presented in Table 3.12).

**Table 3.12 Estimates of mean weights (all as kg) of returning adults**

|  | Source (see below) |  |  |
|---|---|---|---|
| Sea-age | (a) | (b) | (c) |
| 1 SW | 2.72 | 3.11 | 3.06 |
| 2 SW | 5.44 | 5.42 | 6.64 |
| 3 SW | 9.07 | 7.81 | - |
| Previous spawners | - | 6.62 | 5.05 |

(a) River Wye: Gee and Milner, 1980

(b) River Dee: Davidson *et al.*, 1994 (data from fish caught in 1992)

(c) River Dee: Davidson *et al.*, 1995 (data from fish caught in 1993)

### Sex ratio

The model developed by Gee and Radford (1982) assumed an even sex ratio within each age-class. More specific information on sex ratios (estimated for separate sea-ages) of returning adults on the River Dee is available (e.g. Davidson *et al.*, 1994 and 1995).

Similar information (detailing the percentage of stock made up by females in both the 1SW and MSW classes) is available for a series of salmon stocks in UK rivers (Anon, 1996). Initial analysis of these data suggested that the proportion of females in the 1SW component may be estimated from the size of the catchment;

$$\text{Log}_{10}\ (\textit{Proportion of 1SW fish as females}\ [\%]) = 2.03 + 0.126 \times \log_{10}\ (\textit{Catchment area}\ [\text{km}^2])$$

## 3.6.5 Repeat spawners

Jonsson *et al.* (1991) found that, for fish produced in Norwegian rivers, the proportion of repeat spawners that returned to spawn biennially (rather than annually) increased with increasing sea-age at maturity (e.g. for a sea-age at maturity of 1.0-1.4 years biennial spawners made up 0-40% of repeat spawners; rising to 80-100% for sea-age at maturity of 2.0-2.3 years). Mortality rates for kelts can be found in Korman *et al.* (1994). These rates cover the period up to the end of re-acclimation to marine conditions following return from freshwater, and are given by sea-age.

Repeat spawners for the River Bush salmon stock varied between 0% and 12.0%, with a mean of 2.8% (Crozier and Kennedy, 1993). Almost all of these repeat spawners were short absence female kelts. Data for the River Dee (e.g. Table 3.8) suggest that repeat spawners made up about 2.3% of the returning stock in the 1992-3 season.

## 3.7 Complete lifecycle models

### 3.7.1 Examples of complete lifecycle models

Several examples of complete salmonid lifecycle models are to be found in the literature. Not all of these, however, relate to Atlantic salmon (see Table 3.13, over) and some are theoretical only (i.e. although the model structure and general approach are discussed, no information is available regarding the application of the model to real data sets or management scenarios). Others may describe the application software that has been developed to implement a model system, rather than describing the model itself (e.g. Ferson *et al.*, 1989).

Features of some of these models are discussed further in the following section.

### 3.7.2 Details from complete lifecycle models

**Larkin and Hourston, 1964**

Larkin (1973) refers to the early simulation model for Pacific salmon produced by Larkin and Hourston (1964) as a 'hodge-podge' of processes. Although a useful exercise in the development of model form, he did not consider it to be a useful management tool as the data inputs that were required exceeded the (then) prevailing level of understanding.

Although Larkin and Hourston's model (1964) provides a very good example of a model structure which potentially allows for a wide range of the variability that is inherent in salmonid lifecycle strategies to be included, it fails to allow for different conditions (of, for example, natural mortality, or exploitation) in different marine areas. Instead, it assumes that all stocks are similarly affected in the marine environment. The application of such a model would be likely to be inappropriate in the case of a population comprising both grilse and two sea-winter fish. By contrast, the model does permit different 'stocks' to be considered in the freshwater stage, allowing for differential compensatory, extrapensatory, and depensatory rates to be applied to different subsets of the population during the freshwater phase. In the case of extrapensatory mortality, this was achieved by applying separate scaling factors (each containing a stock-specific stochastic component) to the different 'stocks' being modelled. By contrast, extrapensatory factors in the marine environment were modelled by applying only a single scaling factor for all of the fish in the marine environment.

Compensatory effects (for the egg to fry transition) are modelled using the Ricker curve, although the otherwise severe compensatory effects seen at high egg deposition levels are avoided by setting fry production to an asymptotic value for high levels of egg deposition.

**Larkin, 1971**

Another model which encompassed the full salmon lifecycle but which effectively reported on only a limited aspect of it was that reported by Larkin (1971). His model was developed to re-create observed fluctuations in the year-on-year abundance of Adams River sockeye salmon, and only assessed the resultant temporal patterns of dominance / subdominance / and near absence.

### Paulik, 1973

Although not included in Table 3.1, Paulik (1973) presented a form of visual model by reproducing multi-axis graphs to permit the interpretation of linked stock recruitment curves and other life-stage models. These present a simple way of visualising the implications of density-dependent relationships, and can be used to demonstrate that optimum conditions for one life-stage do not necessarily represent the conditions which are optimum for the full lifecycle.

**Table 3.13 Salmonid lifecycle models**

| Reference | Subject | Notes |
|---|---|---|
| Larkin and Hourston (1964) | Pacific salmon | Model developed but not applied |
| Gee and Radford (1982) | Atlantic salmon | Model developed and executed, but not assessed with reference to existing data |
| Caswell *et al.* (1984) | Atlantic salmon | Theoretical model only |
| Evans and Dempson (1986) | Atlantic salmon (or 'equivalent') | Theoretical model, constructed simply as an example to allow development of methods for subsequent examination of parameter sensitivity |
| Ferson *et al.* (1989) | Brook trout (used as an example) | Introduces a modelling package (RAMAS) which allows non-linearity and stochastic behaviour to be modelled at the population level |
| Lee and Hyman (1992) | Pacific salmon | Developed 'SLCM' - uses stochastic process modelling (random variability assigned to processes rather than parameters) - subsequently calibrated on real data, but no simulations presented to indicate applications |
| Korman *et al.* (1994) | Atlantic salmon | Incorporated pH-related mortality to assess potential impacts of acidification on growth-rates (and, by inference, age at smolting and post-smolt survival) |
| Power and Power (1994) | Atlantic salmon | Model used to examine potential responses of salmon stocks (in terms of smolt production) due to changes in climate and alevin densities |
| Emlen (1995) | Chinook salmon | Applied model to demonstrate parameterisation techniques and methods for the assessment of population viability |
| Power and Power (1995) | Brook trout | Compared results of newly developed IBM system to those derived from an existing (population abundance style) modelling package (RAMAS; Ferson *et al.*, 1989) - highlighted weaknesses of the non-IBM approach in terms of its inability to account for the effects of environmental conditions on the size-frequency structure of the modelled population |

### Caswell *et al.*, 1984

Some salmon lifecycle models have been used as practical tools for predicting the biological consequences of management actions as recorded at the individual level. For example, Caswell *et al.* (1984) developed a model to examine the possibility that natural selection, in response to increased marine exploitation, was responsible for an observed increase in precocious maturation of male Atlantic salmon parr. Application of their model produced results which did not refute the possibility that exploitation pressures may, indeed, have initiated the observed changes. However, the validity of their particular model may be called into question as, amongst other assumptions and generalisations, no allowance is made for compensatory mortality.

### Evans and Dempson, 1986

The theoretical model produced by Evans and Dempson (1986) was based on parameter estimates from various authors in the literature and was developed primarily as a vehicle for subsequent work on the analytical approach to sensitivity analysis.

They suggest that the most serious inaccuracy of their model lies in the assumption that density-dependence enters only at one stage (in their case the transition between egg and 0+ parr - which they modelled using a Ricker relationship). They cite Symons (1979) and Buck and Hay (1984) in suggesting that high parr densities may increase the age at smolting and hence decrease the overall fry to smolt survival. They also assume that high spawning stock biomass may lead to compensatory effects through the need to use sub-optimal spawning sites and because of the disturbance of previously laid eggs.

Through analyses of their theoretical model, Evans and Dempson (1986) conclude that of all the possible fishery management options, those associated with habitat protection measures are more likely to have the desired effect (in terms of benefiting the overall fishery) than are changes in fishery regulations. In arriving at this conclusion they do not, however, appear to take into account any measure of 'confidence' in the estimation of the original rate values.

### Ferson *et al.*, 1989

The commercially available 'RAMAS' modelling package was employed to model a brook trout population, so as to provide an example of its potential application (Ferson *et al.*, 1989). Although basically an adaptation of the Leslie-matrix approach (which, as pointed out by Emlen, 1989, is generally inappropriate as it fails to take into account density-dependence in the production of population-level predictions) the RAMAS modelling package is described as a 'user-friendly Monte-Carlo simulator of age-structured population dynamics', and has the distinction of enabling density-dependent relationships to be included within the defined model.

In the example provided by Ferson *et al.* (1989) the density-dependent model used is that of Beverton-Holt, although the paper suggests that density-dependence can be changed by the user (along with fecundity, survival, immigration, emigration, together with correlations amongst fecundity, survival, and immigration / emigration). One of the suggested advantages displayed by the RAMAS package lies in its ability to specifically consider population age-structure. Whilst such a feature may be advantageous in a non-migratory population such as brook trout, for migratory populations (such as Atlantic salmon) the higher degree of spatial separation that is experienced by different age-classes or life-stages (e.g. with only a very restricted number of pre-smolt age-classes present within a stream system) may reduce this importance.

Ferson *et al.* (1989) suggest that population dynamics, both in terms of the asymptotic mean behaviour and the risk-analytic features, can be rather sensitive to the modeller's decisions about density-dependence. They further suggest that this is unfortunate, as knowledge about the existence and characteristics of density-dependence in any given species is usually the poorest demographic information available.

### Lee and Hyman, 1992

The stochastic life-cycle model (SLCM) presented by Lee and Hyman (1992) is one of the more sophisticated and adaptable models that is detailed in the literature. The model allows the user the choice between Ricker, Beverton-Holt and the logistic relationship for the density-dependent recruitment from egg to pre-smolt.

By dividing both sides of the stock-recruitment equation by the stock (i.e. the number of eggs) a probability of survival is generated. Together with an estimate of the coefficient of variation of the survival (which is a second input required from the user) this probability is used to drive the binomial-beta model for survival from egg to pre-smolt. This use of stochastic process models is thought by Lee and Hyman to represent a far more appropriate means of modelling stochastic behaviour than the use of what are effectively deterministic models modified by the inclusion of stochastically variability around mean parameter values.

### Power and Power, 1994; 1995

Power and Power's individuals based model (IBM) of a brook trout population (Power and Power, 1995) was used to assess population response to anthropogenic stress, based upon the assumption that mortality due to the effects of toxins in the environment simply represented a 'special case' of natural mortality. Within their model they only considered two density-dependent relationships: the stock-recruitment relationship describing the egg to 0+ transition and that describing the 0+ to 1+ transition. Note that, in an earlier model describing Atlantic salmon (Power and Power, 1994) they had modelled the density-dependent recruitment in two different stages: from alevin to one year-old, and from one year-old to smolt in addition to assuming a simple (exponential) model of compensatory mortality for all age classes. For all of their density-dependent compensatory mortality estimates, Power and Power used the Ricker model. In their 1995 paper, data from an earlier study (McFaddon, 1961) was used to derive the two parameters describing the Ricker curve.

In the representation of later life-stage recruitment phenomenon they assumed that adequate evidence existed for the inclusion of both stochasticity and log-normality. Accordingly, the recruitment between later stages of development (1+ to 2+, *et seq.*) was modelled probabilistically, and employed log-normal distributions about the mean survival rate. The mean survival were defined with reference to the data presented in McFadden (1961) and standard deviations were selected so as to produce a distribution of survival values that was bounded by the maximum and minimum values quoted by McFadden.

The models were run for 50 years, and repeated 50 times. The results were compared against the 14-year average of field data supplied by McFaddon (1961), and expressed as the difference between the field data and the model given as percentage of the field data.

Validation of their model was undertaken in accordance with the 'positivisic' approach in that although they considered the correspondence of field observations and model predictions was not sufficient to prove the validity of the model *per se*, it is able to do much to establish confidence in the model's predictions.

### Emlen, 1995

Emlen (1995) provides a general stochastic population dynamics model with density feedback, age structure, and autocorrelated environmental fluctuations. This model, which was used to assess the population viability of the Snake River chinook salmon, was parameterised using 36 years of redd count data. Emlen made use of density-dependent feedback both in early life (based on Ricker, 1954; 1958) and at later stages by incorporating a continuing hatch-to-adult density-dependent feedback (based on Beverton and Holt, 1954). The simulations performed lead Emlen to suggest that population persistence depended primarily on density-independent mortality.

# 4. RECOMMENDATIONS

## 4.1 Introduction

There are a number of existing lifecycle models for salmon populations. One option is for the Environment Agency to use a model developed for salmon management elsewhere, and adapt it for UK fisheries. To do this, the model will need to fulfil a number of criteria including:

- the model should have the same broad purpose: risk assessment of alternative management options,
- the model should be able to assess the types of management options available in the UK
- the model should be constructed to an appropriate level of detail for the level of information (parameters) available for the Dee and other rivers
- the model should adopt appropriate (Bayesian) calibration methodologies
- the model should be able to be calibrated with the types of data available for UK fisheries (rod, net catch, limited effort data, counters and traps where appropriate)
- the model should be comparable to the UK target setting procedures

Even if the model is appropriate for Environment Agency salmon management, there are considerable problems associated with the modification of software developed elsewhere, and support for users.

It is recommended that for central purpose of this project (management risk assessment), that a model is developed specifically for the Dee, whilst enabling application to less intensively monitored rivers. This report has reviewed the approaches taken by other models with respect to model structure, calibration and validation. These will need to be incorporated into the Agency model.

There are a number of salmon models, such as the acidification model by Korman et al (1994), which, although not directly assessing the objectives of this project, may be of considerable use to the Environment Agency in other contexts.

## 4.2 Model stages

### 4.2.1 Introduction

The lifecycle is subdivided here into four sub-models:

- Freshwater production model
- Marine survival model
- River exploitation model
- Fecundity model

These are described in more detail in Sections 4.2.2 to 4.2.5.

### 4.2.2 Freshwater production model

#### Habitat inventory

The freshwater component of the model should be based on a habitat inventory. For the lifecycle model used in the EA target setting procedure, a simple classification is used to subdivide a river network into river types according to altitude and stream order. Each river type has been characterised in terms of its expected salmon parr densities based on a national dataset.

The Environment Agency are currently considering the options for developing a River Fisheries Habitat Inventory (RFHI). Current proposals are for a two-tier system (Wyatt and Barnard, 1997). The first tier would describe "Reach Suitability" for different fish species and age groups (including salmon) and would be driven entirely by map-based variables (such as stream-order, altitude, gradient). A catchment could therefore be divided into reaches of similar reach suitability. This would supersede the river types currently used in the targets procedure.

The second tier would measure "Relative Habitat Quality" from field surveys, and would act as a modifier of Reach Suitability. The refined habitat mapping that would be enabled through habitat surveys and the assessment of Relative Habitat Quality would benefit the lifecycle model. If the model will be used to assess the implications of habitat improvement as a management option, it will be essential that the concept of "Habitat Quality" is included in the model. It is likely that the SLM and the RFHI will be developed simultaneously. It is therefore important that the SLM is constructed in a manner that will allow the incorporation of the RFHI at a later stage.

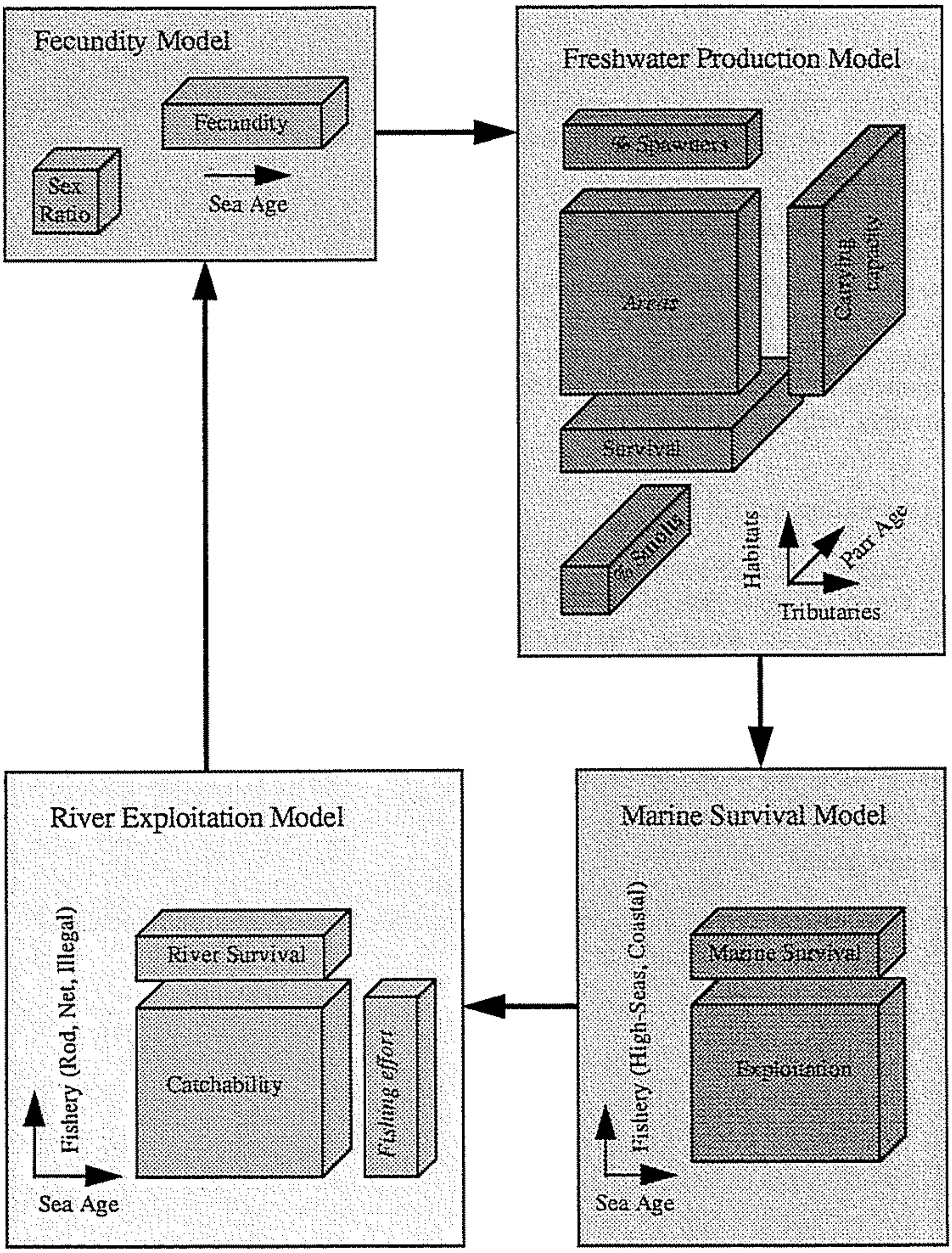


**Figure 4.1. Summary of model structure showing four sub-models. Se text for explanation.**

### Stock-recruitment model

The model for freshwater survival should follow that currently used for target setting (Appendix B). In this procedure, the river network is classified according to Reach Suitability (see above), and is also divided into sub-catchments or tributaries. Each sub-catchment will contain a mixture of different Reach Suitabilities.

The current method for target setting can utilise any stock-recruitment model, although a Ricker model uses to estimate the initial target values for rivers. For the SLM, the user should be able to select from alternative models (e.g. Ricker, Beverton-Holt, Shepherd).

### 4.2.3 Marine survival model

The marine survival model should include natural mortality and fishing mortality to different fisheries (high seas, coastal). Separate parameters for different sea-ages should be used. The parameters required by the SLM should be compatible with those available from run-reconstruction models. The prior estimates for these parameters should be comparable to those used for target setting (Appendix D).

### 4.2.4 River exploitation model

The freshwater exploitation model should include rod, net and illegal fisheries. It should be constructed to include a simple measure of fishing effort that will allow the implications of changes in exploitation to be assessed. The most appropriate form of the model should be determined in the next phase. It will be highly desirable to maintain compatibility with models used in the Agency's spawning target compliance procedures. In addition, models produced from the Environment Agency project "The use of catch statistics to determine fish stock size" should be considered in relation to this application.

### 4.2.5 Escapement model

This should include estimates of fecundity for different sea ages, and sex ratio, and should use the parameters used in the target compliance procedure.

## 4.3 Model calibration

### 4.3.1 Overview

Given that there are many more unknown parameters in the SLM than there are variables for which calibration data are available, the most appropriate method for model calibration is the use of Bayesian procedures.

### 4.3.2 Specification of prior distributions

For all model parameters, Bayesian prior distribution will need to be specified by the user. Default values will be supplied by the software where possible.

The sources of the prior distributions are likely to vary between the sub-models.

**Table 4.1. Sources of prior information of parameters.**

| Model | Parameter | Source of prior |
|---|---|---|
| Freshwater production | % spawners | Red counts, spawning habitat |
| | Carrying capacity | Habitat models (eg HABSCORE) |
| | Survival | Stock-recruitment data, River Bush |
| | % smolts | Stock-recruitment data, River Bush |
| Marine survival | Survival | Microtagging / run-reconstruction |
| | Exploitation | Microtagging / run-reconstruction |
| River exploitation | Catchability | River-specific studies |
| | Survival | River-specific studies |
| Fecundity | Sex ratio | Trap data |
| | Fecundity | Fecundity-weight relationships |

For the stock-recruitment parameters (survival, % smolts) obtained from the River Bush (or any other available egg/smolt data), there is likely to be considerable correlation between the two parameters. The prior should be specified accordingly.

A user-friendly way of specifying prior distribution should be sought. This may include the specification of a mean value with degree of certainty (high, medium or low), or a semi-graphical specification of prior distribution.

### 4.3.3 Likelihood function

The likelihood should be estimated for all prior parameter combinations using an appropriate function for all available data sources.

Likely data sources are shown in Table 4.2.

**Table 4.2. Sources of calibration data.**

| Model | Data source |
|---|---|
| Freshwater production | Juvenile densities (by age, habitat type and river reach) |
| Marine survival | None |
| River exploitation | Rod catch by sea age<br>Rod effort<br>Net catch<br>Net effort<br>Trap data (by sea age, smolt age) |
| Fecundity | None |

### 4.3.4 Estimating the posterior distribution

Given the complexity of the salmon lifecycle model, an analytical approach will not be appropriate, and given the number of parameters, a Monte Carlo approach is recommended. The most efficient algorithm is likely to be some form of Adaptive Importance Sampling (AIS) (e.g. Kinas, 1996). Posterior distributions for each parameter should be displayed graphically, together with summary statistics.

The posterior distributions for the model parameters should also be used to derive fisheries management parameters such as the maximum smolt target (Appendix C), and the maximum gain target (Appendix E).

### 4.3.5 Outputs of state variables

The distribution of all state variables (eg rod catch, egg deposition, run size) will be displayed, together with summary statistics (mean, percentiles, variance). Performance of variables (e.g. egg deposition) against target values should be reported.

## 4.4 Assessment of management action

The user will be able to assess the likely changes in the fishery by altering appropriate state variables (eg fishing effort) or parameter. The response of the fishery to alterations will be displayed as time series plots and summary statistics for any of the variables.

Two options should be available:

- the time series of variables, and
- the time series in the change in variables

This is because it may be possible to make more precise statements about how much a variable will change, than what the absolute value will be.

One possible way of displaying the time-series plots would be to plot percentiles ( eg 80, 60, 40, 20) for a period (say 50 years) representing the current status of the fishery, after which a change in fishery management is introduced, and the changes in the fishery monitored for a further 50 years. This could be done for any of the variables such as escapement (Figure 4.2) or rod catch (Figure 4.3).

## 4.5 Platform

It is proposed that the model should be developed in Delphi (1.0, 2.0), because:

- Readily programmed to give Graphical User Interface (GUI) in Windows environment
- A compiled language; will cope with computer intensive applications such as simulation
- Currently, it is the Environment Agency standard package for software development.

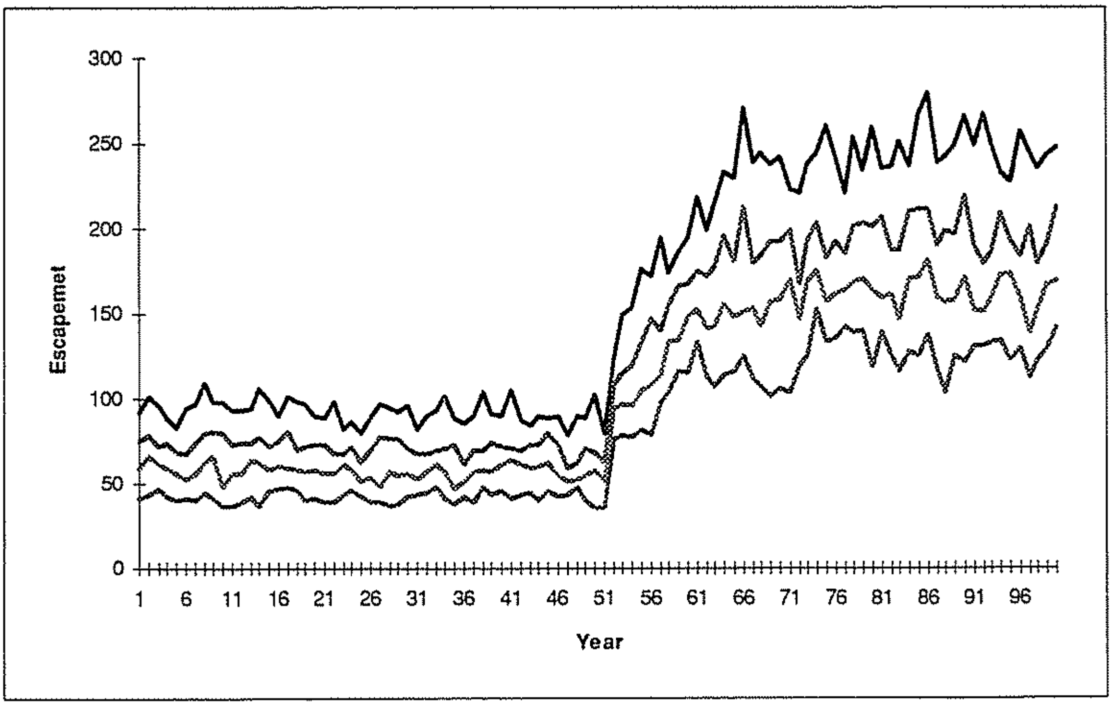


Figure 4.2. Example of time-series plot of percentiles (80, 60, 40, 20) of possible values for spawning escapement. The first 50 year period is at equilibrium, followed by a reduction in exploitation rate.

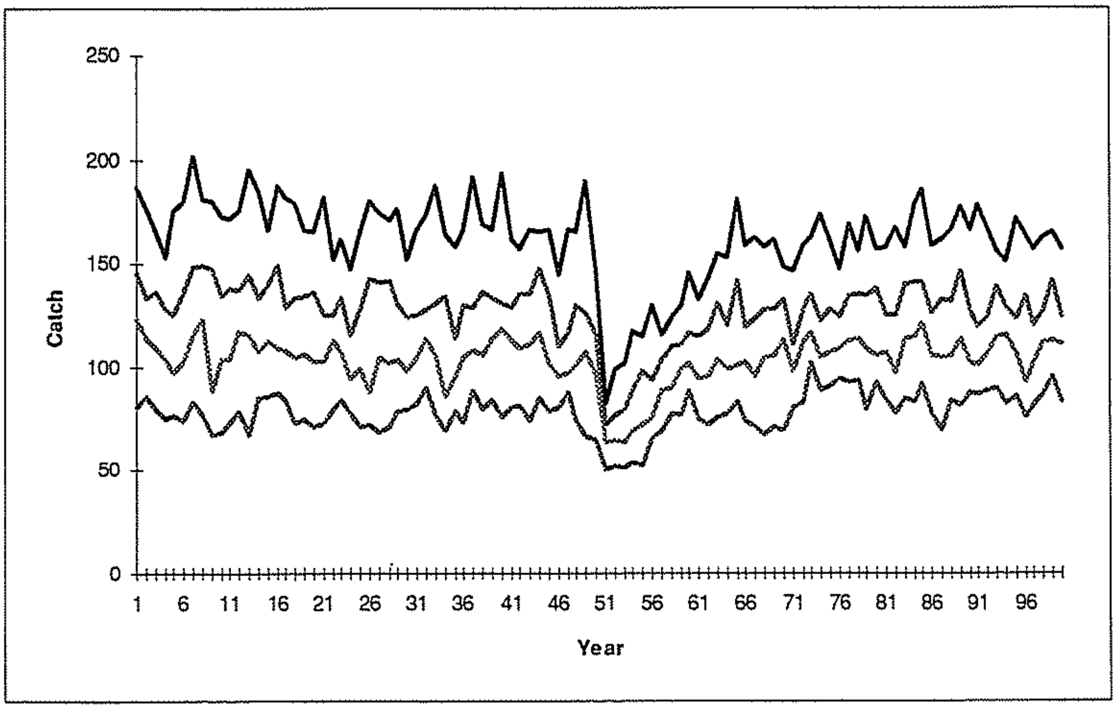


Figure 4.3. Example of time-series plot of percentiles (80, 60, 40, 20) of possible values for rod catch. The first 50 year period is at equilibrium, followed by a reduction in exploitation rate.

## 4.6 Recommended work programme

### 4.6.1 Objectives

#### Overall Objective

To develop a salmon life cycle model for the Dee (but transportable to other rivers) to predict the consequences of stock management decisions, optimise management practice, and prioritise research needs.

#### Specific Objective - Phase 2

1. To produce an operational "prototype" life cycle computer model according to Phase I specifications.

#### Specific objectives - Later phases

2. To conduct user trials to assess model application, benefits and shortfalls (eg user friendliness, operational application) and refine software where appropriate.
3. To identify and cost any further development needs following user review 12 months after software release.

### 4.6.2 Proposed Work Programme for Phase 2

The development of the software will proceed in two stages, each with a number of tasks as outlined below. By the end of Stage 1, the performance of the models will have been assessed. It is recommended that the project is reviewed at this stage before proceeding with the final development.

#### STAGE 1

1. **Construct population dynamics model**
    - Formulate detailed model structure
    - Formulate stochastic components
2. **Develop calibration methodology**
    - Identify posterior calculation methodology

- Develop prototype simulation engine

### 3. Collate data

- Estimate priors specific to the River Dee.
- Estimate joint priors for stock-recruitment parameters from the River Bush.
- Collate available calibration data for the Dee (adults and juveniles).
- Obtain relevant information from GIS (RFHI project).

### 4. Calibration

- Simulate posterior distributions for calibration data.
- Assess sensitivity of posteriors and variables to priors.

### 5. Risk analysis

- Develop risk assessment tools for predicting consequences of future management actions.
- Test methodology for Dee data.
- Assess sensitivity of performance indices to priors.

### 6. Progress report

Write report summarising model performance, and assessing likely value for decision making.

## STAGE 2

### 7. Develop user-interface

- Write specification for user-interface
- Develop prototype software
- Demonstrate software to Project Board

### 8. Develop Beta Version software

- Write Beta Version software
- Test software
- Demonstrate Software

**9. Documentation/Implementation**

- Produce documentation (user guide, software specification)
- Undertake training seminar
- Identify and cost any further development needs following user review.

### 4.6.3 Budget and timescale estimates

Budget costs are given in Table 4.1, and timescales in Table 4.2.

**Table 4.1. Budget estimates (£k) by stage.**

| Stage | | Task | Budget estimate |
|---|---|---|---|
| 1 | 1 | Construct population dynamics model | 33 |
| | 2 | Develop calibration methodology | |
| | 3 | Collate data | |
| | 4 | Calibration | |
| | 5 | Risk analysis | |
| | 6 | Progress report | |
| 2 | 7 | Develop user-interface | 39 |
| | 8 | Develop Beta Version software | |
| | 9 | Documentation | |
| | | TOTAL | 72 |

**Table 4.2. Suggested timescales.**

| Stage | Outputs | Month |
|---|---|---|
| Start | | 0 |
| Stage 1 | Report on model performance | 6 |
| Stage2 | Beta software and draft documentation | 12 |
| | Final documentation and seminar | 13 |

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# APPENDIX A

# THE ENVIRONMENT AGENGY'S REQUIREMENTS

## Introduction

Following a meeting between WRc and the (then) NRA, it was decided that WRc would produce a document (see Table A.1, below) outlining the possible scope of the proposed NRA salmon lifecycle model. This document detailed the possible variables, parameters and resolution of the model. The intention was that this should form the starting point for discussions. The results of these discussions were intended to enable both the literature review and model specification to be more clearly focused on those components of the salmon lifecycle of particular interest to the NRA / EA.

## Description of table columns

### Module

These describe stages in the lifecycle model. The table shows 15 modules, but the subdivisions are arbitrary.

### Variables - input and output

Variables are values such as run size and smolt output which change from generation to generation in the model. Each module in the lifecycle model will have inputs from, and outputs to other modules. The module 'age of return', for example, will produce outputs for 'returning adults' which feeds into the 'coastal exploitation' module, and 'MSW fish', which feeds back into the 'marine survival' module. The 'spawning targets' module only uses parameter estimates to calculate spawning targets of the users choice, and so does not utilize variables used for the simulation.

The model would be able to print or plot raw data for each variable, together with summary statistics (means, ranges, etc.).

### Variables - user outputs

Some output variables are not used as inputs to another module, but are produced for user information only. An example would be the predicted rod catch for each year which would not form an input elsewhere in the model. The variable would be valuable to the user of the model for calibration purposes, etc.

### Parameters

Parameters are values that the user of the model will need to enter, and will remain constant throughout the simulation.

## Table A.1 Table of possible scope of lifeccle model, produced for discussion

| Module | Variables | | | Parameters | Resolution | | |
|---|---|---|---|---|---|---|---|
| | Model input | Output to model / user | User outputs | | Spatial | Temporal | Other |
| Marine distribution | Smolt output; Mult spawners | Adults | | % to fishery | Mar fishery | Year | |
| Marine survival* | Adults; MSW fish | Surviving adults | | Marine survival, stochastic variation | Mar fishery | Year | Sea age |
| Marine exploitation | Surviving adults | Marine escapement | | Commercial catch | Mar fishery | Year | Sea age |
| Age of return | Marine escapement | Returning adults, MSW fish | | % returning | Mar fishery | Year | Sea age |
| Coastal exploitation | Returning adults | Run size | | Exploitation rate | - | Year | Sea age |
| Arrival | Run size | Estuary run size | | % in month | Estuary | Month | Sea age |
| Net exploitation | Estuary run size | River run size | Net catch, net exploitation rate | Net effort (tides), net catchability | Estuary | Month | Sea age, Gear type |
| Rod exploitation | River run size | Uncaught | Rod catch, rod exploitation rate | Rod 'catchability', bag limit, rod effort (hours), stochastic variation, reporting rate | Angling section | Month | Sea age, method |
| Freshwater mortality | Uncaught | Freshwater escapement | | Freshwater adult mortality | Angling section | Month | Sea age |
| Spawner density | Freshwater escapement | Spawner density | | Area, % spawners in reach | River Reach, Angling section | Year | Sea age |
| Fecundity | Spawner density | Egg density | Compliance | Fecundity, sex ratio | River | | Sea age |
| Mult spawners | Freshwater escapement | Mult spawners | | % multiple spawners | River | Year | Sea age |
| SR curve** | Egg density; juvenile density | Juvenile density; smolt density | | Density independent mortality, carrying capacity, shape (dome etc), % smolts, stocked fish, stochastic var. | River Reach, Angling section | Year | Age class |
| Smolt output | Smolt density | Smolt output | | Area | River Reach | Year | Smolt age |
| Spawning targets | | | Target values | | River | | Sea age, target type |

* Could include marine environmental parameters

** Could include freshwater environmental parameters (e.g. temperature)

### Resolution

The resolution columns provide information on the possible resolution (such as spatial and temporal) of the model. The resolution will apply to variables and parameters, and so while a high resolution will produce a more detailed output, it will require a greater number of inputs from the user of the model. For example, for the 'rod exploitation' module, the rod catch (user output) could be produced for each angling section (as on the Dee), for each month of the season, for each sea-age and for each fishing method. This may require separate estimates of the 'catchability' or exploitation rate for each of these categories to be entered by the user. Similarly, stock-recruitment curves could be specified for different river reaches (perhaps including angling sections), and for different age classes of juvenile.

The model could be run at lower resolutions than those specified on rivers where less detailed information is available, however, the maximum resolution will dictate the complexity of the model and therefore the development costs.

## Requirements

### Facilities

The Project Leader commented that a lifecycle model could be usefully employed in predicting the outcome of management options at a particular life-stage (e.g. the potential levels of smolt output resulting from stocking at different fry densities). Due to the modular nature of the proposed modelling approach, it should be possible to use the software that is developed through Phase II of this project to run 'life-stage' models in isolation, rather than the whole 'lifecycle' model.

### Calibration

It was suggested by the Project Leader that thought should be given to developing a facility for 'internal calibration' procedures within the software. Such internal calibration would provide a 'fast track' approach to simulating a population which behaves as we observe at present. The alternative to this would be to simply rely on the user repeatedly entering input parameters until the model generates the required output.

There are several issues associated with model calibration, which, in part, relate to the problem of over-parameterisation. These issues, and possible solutions, will be covered in the final report.

### Outputs

It is likely that model outputs of key variables will be produced graphically. For example, the model software would facilitate the production of a graphical output of model variables (e.g. escapement, rod catch) both:

- initially, over a 'calibration' period (through which the population would be stable);

  and subsequently;

- after a change in the management of the fishery has been instigated (e.g. after a change in the length of the rod-season).

Such an approach would allow the user to visualise the likely impact that a change in management would have on a stable system, and would show how rapidly a change occurs.

## Concerns

### Uncertainty in outputs

The Agency has recognised that, given uncertainties about the model inputs, the need to view the model outputs with caution lie more with the user than with the original developer. However, whilst there will be considerable uncertainties in many of the parameter inputs it is acknowledged that model outputs should be able to take these into account, and that the model developer should aim to help with this.

For example, whilst there may be considerable uncertainty over the rod exploitation rate, the response of the model may be very sensitive to the rod exploitation rate which is assumed. A well constructed model should, however, be capable of allowing the user to see how sensitive the model is to rod exploitation rate, together with the resulting imprecision of any predictions of the consequences of management action.

# APPENDIX B

# FRESHWATER PRODUCTION MODEL

## Introduction

To estimate the spawning escapement target for a catchment, we need the stock recruitment function that relates the egg deposition (eggs/area) in the hth cohort, to the resulting smolt production (smolts/area). Thus

$$s_h = f(x_h)$$

where

| | | |
|---|---|---|
| $x_h$ | egg deposition in the hth cohort | eggs/area |
| $s_h$ | smolt production from hth cohort | smolts/area |
| f | the stock-recruitment function | |

To enable this function to be transported between rivers, it is necessary to include information on the relative proportions of different habitat types within the catchment, and information on the smolt production dynamics within each.

The model for smolt production used in this preliminary methodology is illustrated in Figure 4.1.

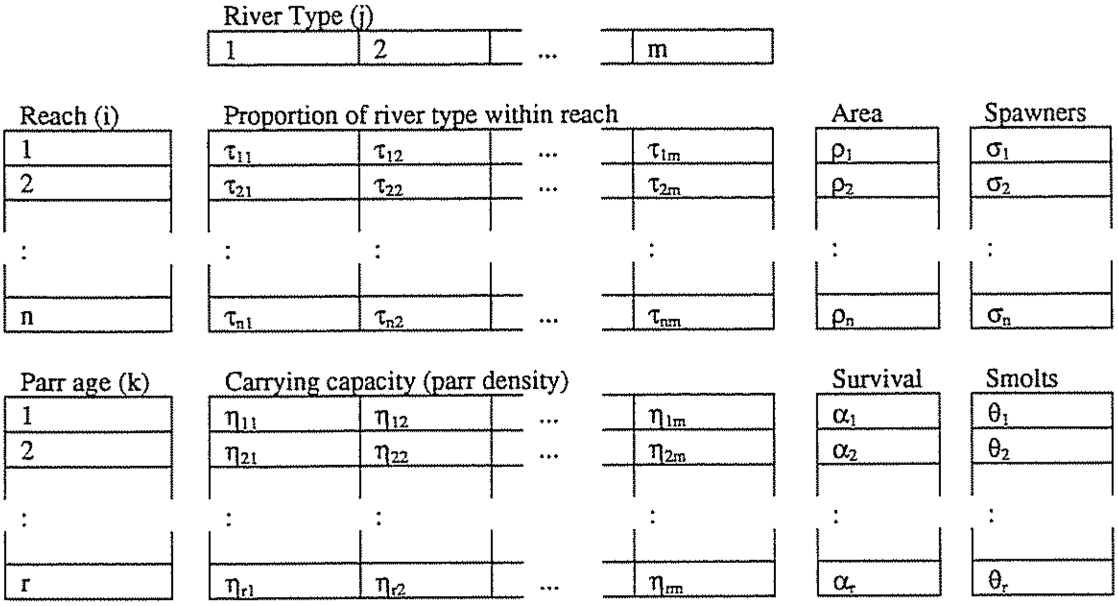

**Figure 4.1. Model of river catchment and smolt production. See text for explanation.**

## Ages of salmon parr

For the purpose of this model, juvenile salmon are divided into r age classes. The kth age class is characterised by an underlying survival rate from egg to parr ($\alpha_k$), and the proportion of those parr that successfully leave the river system as smolts ($\theta_k$). The survival rate from egg to parr of age k can be thought of as the survival rate that would operate at very low densities, at which density-dependent factors do not operate. For this simple model, the survival rates and smolt production rates are assumed to be constant throughout the catchment.

## Definition of river types

A fundamental component of the smolt production model and the transportation of spawning targets is definition of different river types, and the existence of an inventory of types for each catchment. A number (m) of river types are defined which are characterised by differences in habitat suitability for different ages of fish. The suitability of habitat in the jth river type for the kth age class of fish is described in terms of the long term average density, or "carrying capacity", of parr ($\eta_{jk}$) that could be supported at optimal spawning densities.

## Subdivision of catchment into reaches

The entire river network is considered to be divided into n reaches. These may represent major tributaries or sub-catchments of the river. The main distinction between reaches is that the density of egg deposition is allowed to be different in each.

The ith reach contains a proportion $\rho_i$ of the total wetted area of the river

$$\sum_{i=1}^{n} \rho_i = 1,$$

and each reach receives a proportion $\sigma_i$ of the total escapement

$$\sum_{i=1}^{n} \sigma_i = 1$$

If spawning occurs at a constant rate in each reach, then for all i

$$\rho_i = \sigma_i$$

Each reach will contain a mix of different river types. The proportion of the jth river type in the ith river reach is $\tau_{ij}$.

$$\sum_{j=1}^{m} \tau_{ij} = 1$$

## Smolt production model within river type and reach

Consider the jth river type within the ith river reach. The relationship between the parr density of age k with the density of eggs laid in the hth cohort is given by

$$p_{hijk} = f(x_{hi}; \alpha_k, \eta_{jk})$$

where

| | |
|---|---|
| $p_{hijk}$ | density of parr of age k in jth river type, ith river reach in hth cohort |
| $x_{hi}$ | egg density in ith reach, hth cohort |
| $\alpha_k$ | survival from egg to parr of age k at low densities |
| $\eta_{jk}$ | carrying capacity for parr of age k in jth river type |
| f | the two parameter stock recruitment function (eg Ricker, Beverton-Holt) |

The survival rate $\alpha_k$ is assumed to be constant across all reaches and river types, whereas the carrying capacity ($\eta_{jk}$) varies between river types.

If a constant proportion ($\theta_k$) of these parr turn into smolts, then the smolt output ($s_{hijk}$) is given by

$$s_{hijk} = \theta_k f(x_{hi};\alpha_k,\eta_{jk})$$

## General smolt production model for entire catchment

The relationship between the egg density in the ith river reach ($x_{hi}$) and the average egg density for the whole catchment ($x_h$) and is given by

$$x_{hi} = x_h \frac{\sigma_i}{\rho_i}$$

and the stock recruitment model becomes

$$s_{hijk} = \theta_k f\left(\frac{\sigma_i}{\rho_i} x_h;\alpha_k,\eta_{jk}\right)$$

The area of each river type within each reach as a proportion of the total stream area is given by

$$\rho_i \tau_{ij}$$

The average smolt output per unit area of age k for the entire catchment, $s_{hk}$, is therefore given by

$$s_{hk} = \theta_k \sum_{i=1}^{n} \rho_i \sum_{j=1}^{m} \tau_{ij} f\left(\frac{\sigma_i}{\rho_i} x_h;\alpha_k,\eta_{jk}\right) \qquad \text{Equation 1}$$

The average smolt output per unit area for all ages for the entire catchment, $s_h$, is therefore given by

$$s_h = \sum_{k=1}^{r} \theta_k \sum_{i=1}^{n} \rho_i \sum_{j=1}^{m} \tau_{ij} f\left(\frac{\sigma_i}{\rho_i} x_h;\alpha_k,\eta_{jk}\right) \qquad \text{Equation 2}$$

and this is the basic model relating average egg deposition density in the catchment $x_h$, to the average smolt density $s_h$.

## Ricker smolt production model for whole catchment

So far, the catchment model has been developed in terms of a general two parameter stock recruitment model operating within each river type within each reach. If a Ricker model is assumed, then

$$p_{hijk} = \alpha_k x_{hi} e^{-\beta_{jk} x_{hi}}$$

where

| | |
|---|---|
| $p_{hijk}$ | density of parr of age k in jth river type, ith river reach in hth cohort |
| $x_{hi}$ | egg density in ith reach, hth cohort |
| $\alpha_k$ | survival from egg to parr of age k at low densities |
| $\beta_{jk}$ | density dependent parameter of Ricker model for parr of age k in the jth river type |

We need to reparameterise the Ricker model in terms of the maximum parr density ($\eta_{jk}$).

$$\frac{dp_{hijk}}{dx_{hi}} = \alpha_k e^{-\beta_{jk} x_{hi}} \left(1 - \beta_{jk} x_{hi}\right)$$

and so the egg deposition that maximises the parr density is given by

$$x_{hi} = \frac{1}{\beta_{jk}}$$

and therefore $\eta_{jk}$ is given by

$$\eta_{jk} = \frac{\alpha_k}{e\beta_{jk}}$$

and therefore

$$\beta_{jk} = \frac{\alpha_k}{e\eta_{jk}}$$

Redefining the Ricker model in terms of carrying capacity gives

$$p_{hijk} = \alpha_k x_{hi} e^{\frac{\alpha_k x_{hi}}{e\eta_{jk}}}$$

and so

$$f(x_{hi};\alpha_k,\eta_{jk})=\alpha_k x_{hi}e^{-\frac{\alpha_k x_{hi}}{e\eta_{jk}}}$$ Equation 3

Substituting Equation 3 into Equation 1, we get the average smolt output per unit area of age k for the entire catchment,

$$s_{hk}=\theta_k\alpha_k\sum_{i=1}^{n}\sigma_i\sum_{j=1}^{m}\tau_{ij}x_h e^{-\frac{\alpha_k\sigma_i x_h}{e\eta_{jk}\rho_i}}$$ Equation 4

The average smolt output per unit area for all ages for the entire catchment, $s_h$, is therefore given by

$$s_h=\sum_{k=1}^{r}\theta_k\alpha_k\sum_{i=1}^{n}\sigma_i\sum_{j=1}^{m}\tau_{ij}x_h e^{-\frac{\alpha_k\sigma_i x_h}{e\eta_{jk}\rho_i}}$$ Equation 5

# APPENDIX C

# MAX SMOLT TARGET

To obtain the egg deposition $x_{ms}$ that maximises the smolt output $s_h$, we get

$$\frac{ds_h}{dx_h} = \sum_{k=1}^{r} \theta_k \alpha_k \sum_{i=1}^{n} \sigma_i \sum_{j=1}^{m} \tau_{ij} e^{-\frac{\alpha_k \sigma_i x_h}{e \eta_{jk} \rho_i}} \left(1 - \frac{\alpha_k \sigma_i x_h}{e \eta_{jk} \rho_i}\right)$$

and thus the egg deposition target $x_{ms}$ for maximum smolt production must satisfy

$$\sum_{k=1}^{r} \theta_k \alpha_k \sum_{i=1}^{n} \sigma_i \sum_{j=1}^{m} \tau_{ij} e^{-\frac{\alpha_k \sigma_i x_{ms}}{e \eta_{jk} \rho_i}} \left(1 - \frac{\alpha_k \sigma_i x_{ms}}{e \eta_{jk} \rho_i}\right) = 0 \qquad \text{Equation 6}$$

# APPENDIX D

# ESTIMATION OF MARINE SURVIVAL

To estimate the maximum gain target, it is first necessary to estimate the average number of eggs laid per smolt leaving the river ($\phi$), then

$$x_{h*} = \phi s_h$$

where $x_{h*}$ is the number of eggs produced in subsequent years from the hth cohort of smolts.

Data available for the estimation of $\phi$ included the proportion of females ($\upsilon$), the average female fecundity ($\omega$), the proportion of grilse ($\gamma$) and the marine survival for grilse $\pi_1$ and multi-sea winter fish $\pi_2$. It is therefore necessary to define the relationship between $\phi$ and $\upsilon$, $\omega$, $\gamma$, $\pi_1$ and $\pi_2$.

Consider $s_1$ smolts destined to return as grilse, and $s_2$ smolts destined to return as multi-sea winter fish. Let the number of grilse returning be $a_1$ and the number of multi-sea winter fish returning be $a_2$. Let the survival rates for grilse and multi-sea winter fish be $\pi_1$ and $\pi_2$ respectively. Then

$$a_1 = \pi_1 s_1 \qquad \text{Equation 7}$$

and

$$a_2 = \pi_2 s_2 \qquad \text{Equation 8}$$

Let the proportion of grilse be $\gamma$, thus

$$\gamma = \frac{a_1}{a_1 + a_2} \qquad \text{Equation 9}$$

or

$$\frac{a_2}{a_1} = \frac{1}{\gamma} - 1 \qquad \text{Equation 10}$$

The overall survival rate $\delta$ is given by

$$\delta = \frac{a_1 + a_2}{s_1 + s_2} \qquad \text{Equation 11}$$

Substituting Equation 7 and 8 into Equation 11, we get

$$\delta = \frac{a_1 + a_2}{\frac{a_1}{\pi_1} + \frac{a_2}{\pi_2}} \qquad \text{Equation 12}$$

Rearranging we get

$$\delta = \left(\frac{a_1 + a_2}{a_1}\right)\left(\frac{1}{\frac{1}{\pi_1} + \left(\frac{a_2}{a_1}\right)\frac{1}{\pi_2}}\right)$$

and substituting Equation 9 and 10 we get

$$\delta = \frac{1}{\frac{(1-\gamma)}{\pi_2} + \frac{\gamma}{\pi_1}}$$

If the proportion of females among the survivors is $\upsilon$, and the average fecundity of the females is $\omega$, then the number of eggs returning to the catchment from each smolt is

$$\phi = \frac{\upsilon\omega}{\frac{(1-\gamma)}{\pi_2} + \frac{\gamma}{\pi_1}} \qquad \text{Equation 13}$$

# APPENDIX E

# ESTIMATING THE MAXIMUM GAIN TARGET

Gain ($g_h$) can be defined as the surplus smolt production at a given egg deposition ($x_h$) over and above that required to generate the same egg deposition in future generations. Thus

$$g_h = s_h - \frac{x_h}{\phi}$$

therefore

$$g_h = \sum_{k=1}^{r} \theta_k \alpha_k \sum_{i=1}^{n} \sigma_i \sum_{j=1}^{m} \left[ \tau_{ij} x_h e^{\frac{\alpha_k \sigma_i x_h}{e \eta_{jk} \rho_i}} \right] - \frac{x_h}{\phi}$$

$$\frac{dg}{dx_h} = \sum_{k=1}^{r} \theta_k \alpha_k \sum_{i=1}^{n} \sigma_i \sum_{j=1}^{m} \left[ \tau_{ij} e^{\frac{\alpha_k \sigma_i x_h}{e \eta_{jk} \rho_i}} \left( 1 - \frac{\alpha_k \sigma_i x_h}{e \eta_{jk} \rho_i} \right) \right] - \frac{1}{\phi}$$

And so maximum gain is given by egg densities ($x_{mg}$) satisfied by

$$\phi \sum_{k=1}^{r} \theta_k \alpha_k \sum_{i=1}^{n} \sigma_i \sum_{j=1}^{m} \left[ \tau_{ij} e^{\frac{\alpha_k \sigma_i x_{mg}}{e \eta_{jk} \rho_i}} \left( 1 - \frac{\alpha_k \sigma_i x_{mg}}{e \eta_{jk} \rho_i} \right) \right] = 1 \qquad \text{Equation 14}$$

where

$$\phi = \frac{\upsilon \omega}{\frac{(1-\gamma)}{\pi_2} + \frac{\gamma}{\pi_1}}$$