

Spawning escapement targets for Atlantic salmon

WRc plc

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This document reviews egg deposition targets derived from stock-recruitment data and explores novel methods of target setting based on rod and net catch returns and habitat models. The development of a methodology for transporting salmon spawning targets from a donor river in Ireland to recipient rivers in England and Wales is described.

It will be of interest to Fisheries staff involved in assessing salmon spawning success. Further refinements are likely if an additional phase of the project is progressed. It should be read in conjunction with companion report W65.

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EXECUTIVE SUMMARY

— This report examines and reviews existing stock-recruitment derived spawning targets for salmon. The relationships between alternative stock-recruitment relationships (including the relationships proposed by Cushing, Ricker, Shepherd and Beverton-Holt) is briefly discussed. Subsequently, specific case-studies (where egg deposition targets, or those of nearest surrogates, have been determined from stock-recruitment relationships) are reviewed, and the extent and causes of variation between targets are examined using published data.

It was found that the form of the stock-recruitment model that is fitted to data has considerable implications for the subsequent estimation of targets. However, river-specific stock-recruitment data is rarely good enough to determine which stock-recruitment model is most appropriate. In addition it was also found that the methods used to fit a stock-recruitment curve to data have implications for the estimation of a target.

The definition of a spawning target (such as an egg deposition target) requires a knowledge of both the stock-recruitment curve and the replacement line. When transporting a target from a donor river where this information is available to a recipient river where it is not, it must either be assumed that the stock-recruitment curve and replacement line in the donor and recipient rivers are identical, or that appropriate adjustments can be made. Methods for making such adjustments (based on the use of habitat models) are proposed. Opportunities for the transport of targets between river systems are assessed, and the use of these targets in providing guidance to Agency staff is evaluated.

The current availability of data and facilities within the Agency for the derivation of salmon stock-recruitment relationships are briefly reviewed. Also, factors influencing between-river variation in rod and net catch (e.g. catchment size, chemical productivity, fishing effort) are examined. Models are developed to predict expected catch and equivalent ova deposition optima for these.

A range of recommendations are made regarding the development and adoption of appropriate salmon spawning targets within the Agency. The assessment of compliance with such targets is addressed.

KEY WORDS

Stock-recruitment; salmon; spawning target; transport.

1. INTRODUCTION

1.1 Objectives

1.1.1 Overall Project Objectives

To examine and review existing stock-recruitment derived spawning targets for salmon, develop alternative methods and evaluate the use of these targets in order to provide guidance to Agency staff.

1.1.2 Specific Objectives

- a) To critically review case-studies where egg deposition targets (or those of nearest surrogate e.g. fry, parr) have been determined from stock-recruitment relationships, and to assess the extent and causes of variation between targets and opportunities for transportability to other river systems.
- b) To identify instances where S-R derived targets might be determined for other rivers, either through analyses of existing data or by development of established projects and facilities.
- c) To investigate the use of habitat models to predict site and river specific carrying capacities for juvenile salmonids and evaluate and attempt to develop methods to derive ova deposition optima from these.
- d) To examine factors influencing between-river variation in rod and net catch (e.g. catchment size, chemical productivity, fishing effort) and attempt to develop models to predict expected catch and equivalent ova deposition optima for these.
- e) To advise and make recommendations on the use or further development of targets a), c) and d) by the Agency, assessing their management value and potential application - including consideration of appropriate precision levels for targets and compliance criteria.
- f) To identify gaps in the available knowledge relating to objectives a) - e) and recommend a realistic programme of research to address these, indicating the resource implications of the latter.
- g) To produce an R&D Note reporting the findings of the work.

1.2 Introduction to report

This report presents the results of work undertaken to address the objectives listed above. The methods and results are presented in Sections 2 to 5 corresponding to specific objectives a) to d). Section 6 pulls together the conclusions and recommendations from the other sections.

An associated document 'The transportation of the maximum gain salmon spawning target from the River Bush (N.I.) to England and Wales' (R&D Technical Report W65) reports on the further development of the target transportation methodologies that are outlined in this document.

2. COMPARISON OF TARGETS BASED ON STOCK-RECRUITMENT CURVES

2.1 Introduction

The objective of this section is to critically review case-studies where egg deposition targets (or those of nearest surrogate, e.g. fry, parr) have been determined from stock-recruitment (S-R) relationships, and to assess the extent and causes of variation between targets and opportunities for transportability to other river systems.

2.2 The stock-recruitment curve

2.2.1 Types of stock-recruitment model

In the context of salmon, the term “stock” denotes the number of spawners in a catchment, expressed as number of adults or eggs, either in absolute terms or as numbers per unit area. The term “recruits” denotes the number of smolts leaving a catchment, in absolute numbers or as numbers per unit area. There are a number of forms of the S-R curve that have been used to describe density dependence in fish populations (Paulik, 1973), such as those by Cushing (1973), Beverton and Holt (1957), Ricker (1954), and Shepherd (1982), and these four are summarised in Table 2.1.

All of these curves have a number of features in common, for example, they all give zero recruitment for zero stock, show an initial increase in recruitment level as stock level increases, and the relationship is linear with gradient α if the parameter β is zero. The models differ, however, in how they respond to high stock levels. With the Cushing model, recruitment levels continue to increase with increasing stock levels, the Beverton-Holt model rises to an asymptote, whereas the Ricker model rises to a maximum and then decreases towards zero. The Shepherd model has three parameters, and the parameter λ determines the shape of the curve. If $0 < \lambda < 1$, the shape is similar to the Cushing model, if $\lambda = 1$, the equation becomes identical to the Beverton-Holt model, and if $\lambda > 1$, the model resembles the shape of the Ricker model.

The appropriate form of the S-R curve may be chosen from an understanding of the ecology and survival of juvenile salmonids, but in practice it is often assessed empirically, and often from inadequate data.

Table 2.1 Four stock - recruitment curves

	Cushing	Beverton-Holt	Ricker	Shepherd
S-R relationship	$R = \alpha S^{1-\beta}$	$R = \frac{\alpha S}{1 + \beta S}$	$R = \alpha S e^{-\beta S}$	$R = \frac{\alpha S}{1 + (\beta S)^\lambda}$
Gradient at S=0	∞	α	α	α
S for max R	$S = \infty$	$S = \infty$	$S = \frac{1}{\beta}$	$S = \frac{1}{\beta(\lambda - 1)^{\frac{1}{\lambda}}}$ $S = \infty, \lambda \leq 1$ $S = \frac{1}{\beta}, \lambda = 2$
Max R	$R = \infty$	$R = \frac{\alpha}{\beta}$	$R = \frac{\alpha}{e\beta}$	$R = \infty, 0 < \lambda < 1$ $R = \frac{\alpha}{\beta}, \lambda = 1$ $R = \frac{\alpha}{2\beta}, \lambda = 2$
R when $\alpha=0$	$R = 0$	$R = 0$	$R = 0$	$R = 0$
R when $\beta=0$	$R = \alpha S$	$R = \alpha S$	$R = \alpha S$	$R = \alpha S$
R when S = 0	$R = 0$	$R = 0$	$R = 0$	$R = 0$
R when S = ∞	$R = \infty$	$R = \frac{\alpha}{\beta}$	$R = 0$	$R = \infty, 0 < \lambda < 1$ $R = \frac{\alpha}{\beta}, \lambda = 1$ $R = 0, \lambda > 1$

2.2.2 Replacement line

The replacement line is often shown with the stock recruitment curve to represent all of the density-independent stages of the life-cycle. The simplest equation for the replacement line is:

$$S = \phi R;$$

where:

S is stock level (e.g. eggs);

R is number of recruits in the previous generation (e.g. smolts);

The gradient of the replacement line will be determined by factors such as marine mortality and exploitation, sea age and sex composition, and the size and fecundity of adults.

2.2.3 The stock-recruitment curve and life-cycle models

The combination of the stock recruitment curve and replacement line forms the basis of a simple deterministic model for the salmon life-cycle.

Given the stock-recruitment curve, the replacement line and exploitation rate, it is possible to estimate the theoretical equilibrium conditions for the fishery as described below. The symbols are defined in Table 2.2.

Table 2.2 Symbols used in simple deterministic life-cycle model

		Symbol
Variable	Total smolt output	S
	Smolt output per area	s
	Total escapement	E
	Escapement per area	e
	Run size	R
	Rod catch	C
	Rod effort	U
	Stream area	A
Parameter	1/(carrying capacity)	α
	1/(density-independent survival)	β
	marine survival (smolt -> egg)	ϕ
	1 - "catchability"	λ

For a Beverton-Holt stock recruitment curve, the smolt output per unit area (s) is related to the spawning escapement (measured in units of adults per unit area (e)) by:

$$s = \frac{1}{\alpha + \beta/e}$$

It is important to note that this is an alternative parameterisation of the Beverton-Holt stock-recruitment curve than that used where different forms of stock-recruitment curves are being compared (as in Tables 2.1 and 2.3).

The total smolt output from the river (S) is given by:

$$S = As;$$

and the total spawning escapement (E) in the river is given by:

$$E = Ae$$

Ignoring in-river mortality from other sources (which can readily be added to the model if required), then the total run size of adults (R) is simply the sum of the rod catch (C) and the escapement (E):

$$R = C + E$$

The adult run size (R) is also related to the smolt output (S) by the marine survival ϕ :

$$R = S\phi$$

The relationship between catch (C) and run size (R) could take a number of forms, and will include the rod effort (U). A simple example of a possible model would be:

$$C = R(1 - \lambda^U)$$

where $(1 - \lambda)$ is the catchability. The exploitation rate is therefore $1 - \lambda^U$.

The combination of these equations represent a simple life-cycle model for the salmon. From this model, the expected values for the different state variables can be estimated. The equilibrium conditions for S , E , R and C are given by:

$$S = \frac{A \left[1 - \frac{\beta}{\phi \lambda^U} \right]}{\alpha}$$

$$E = \frac{A [\phi \lambda^U - \beta]}{\alpha}$$

$$R = \frac{A \left[\phi - \frac{\beta}{\lambda^U} \right]}{\alpha}$$

$$C = \frac{A(1 - \lambda^U) \left(\phi - \frac{\beta}{\lambda^U} \right)}{\alpha}$$

These equilibrium values are shown in Figure 2.1. The lower diagonal line is the replacement line showing the number of adults returning per smolt. The lower the marine survival, the steeper the line. The upper diagonal line represents the rate of exploitation by the rods; a higher exploitation rate will result in a steeper line.

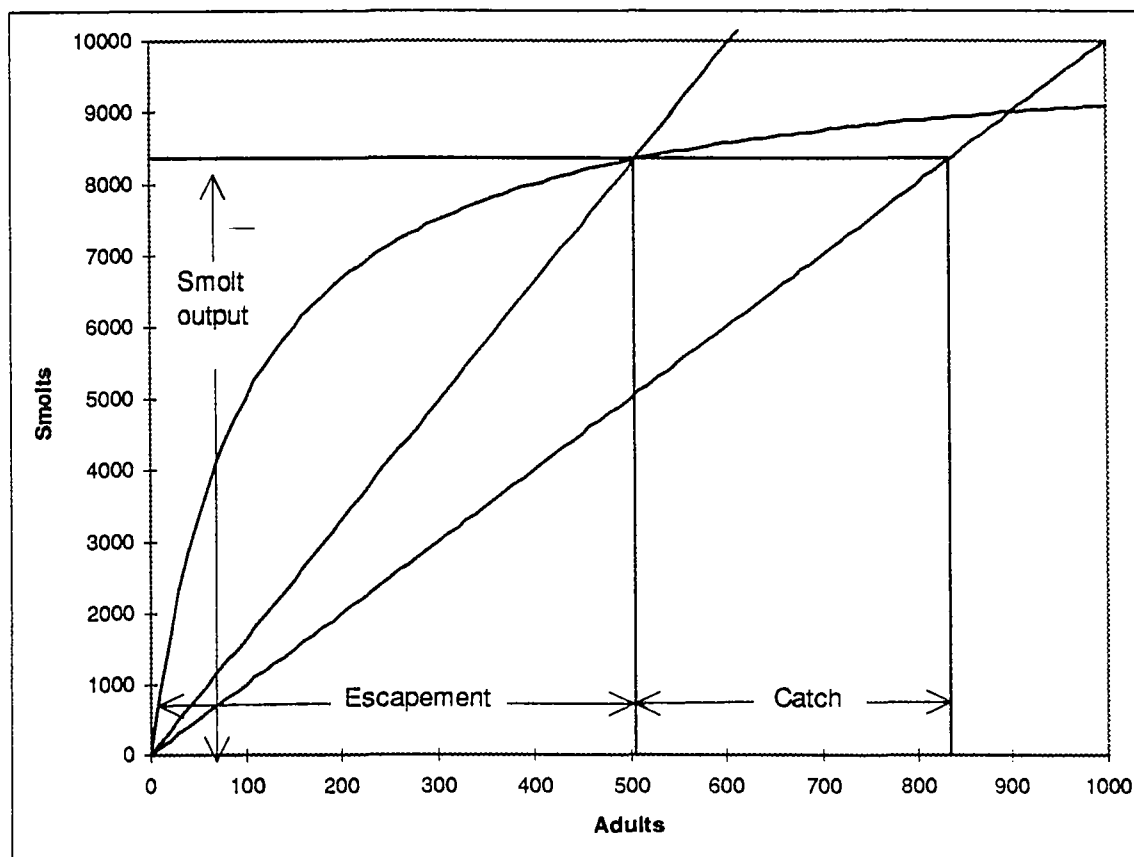


Figure 2.1 Equilibrium values for catch, escapement, smolt output and run size (= escapement + catch) from the stock-recruitment curve and replacement line

Thus any change (through time or between rivers) in the stock recruitment curve (α , β), the replacement line (ϕ), the stream area (A) or the exploitation (λ , U) will cause a change in the equilibrium levels of the smolt output (S), escapement (E), run size (R) and catch (C).

For many rivers, the only data available for the adult phase of the life-cycle are the declared catch from rods and/or nets, which can be used to estimate the actual catch (C). Even if the equilibrium conditions remain constant, the catch will vary randomly from year to year. Because of the overlapping cohorts present in a salmon population, stochastic factors will tend to affect successive cohorts, and the population will show “positive autocorrelation”. In other words, population levels will tend to “drift” above and below the equilibrium levels rather than show random variation.

The equation for the equilibrium condition for the catch (C) gives the intuitive results that if the marine survival (ϕ), freshwater survival ($1/\beta$), freshwater carrying capacity ($1/\alpha$) or useable stream area (A) decline, then the catch will also decline. For a decline in the carrying capacity ($1/\alpha$) and the stream area (A), the decline in catch will be directly proportional; for example, if the carrying capacity halves, then the catch will also halve.

2.2.4 Maximum gain

Consider Figure 2.1. Increasing the fishing effort (U) from zero will cause an steady rise in the exploitation rate, and the upper diagonal line will become steeper. The catch (C) will initially increase, but at high exploitation rates, the decline in the smolt output (S) and therefore the run size (R) will outweigh the increase in fishing effort, and the catch will decline again to zero. Given a stable fishery (stable ϕ , α , β , A, λ) there is therefore an optimal exploitation rate that will give the maximum catch, and at this point on the stock-recruitment curve, a corresponding egg deposition can be identified. The egg deposition that generates the maximum catch can be regarded as a reference egg deposition level that generates “maximum gain”.

For the simple life-cycle model above, the optimal level of fishing effort to achieve the maximum catch is given by:

$$U = \frac{\text{Log}\beta - \text{Log}\phi}{2\text{Log}\lambda}$$

In terms of the exploitation rate, the maximum catch is given by:

$$\text{Exploitation rate} = 1 - \sqrt{\frac{\beta}{\phi}}$$

These two equations do not include the parameter α which relates to the “carrying capacity” of the river.

The spawning escapement per unit area (e) required to give the maximum gain is:

$$e = \frac{\sqrt{\beta\phi} - \beta}{\alpha}$$

The above arguments only apply to a stable fishery (stable ϕ , α , β , A, λ). These parameters may vary considerably between fisheries, or between years within a fishery, due to different values of ϕ (marine survival, sex ratio, fecundity, sea age composition), freshwater productivity and so on. Any spatial or temporal differences in these parameters will generate different average catches (Section 2.2.3).

2.3 Egg deposition targets derived from the stock-recruitment curve

Given a model for the dynamics of a salmon fishery (most simply the S-R curve and the replacement line), there are a number of stock (e.g. egg deposition) levels identifiable that can be used as the basis for egg deposition targets. These include three broad categories which are based on:

- the egg deposition that generates the maximum catch
- the egg deposition that generates the maximum smolt output, and
- the maximum egg deposition for an unexploited fishery

These three points are illustrated in Figure 2.2, and are discussed in more detail below.

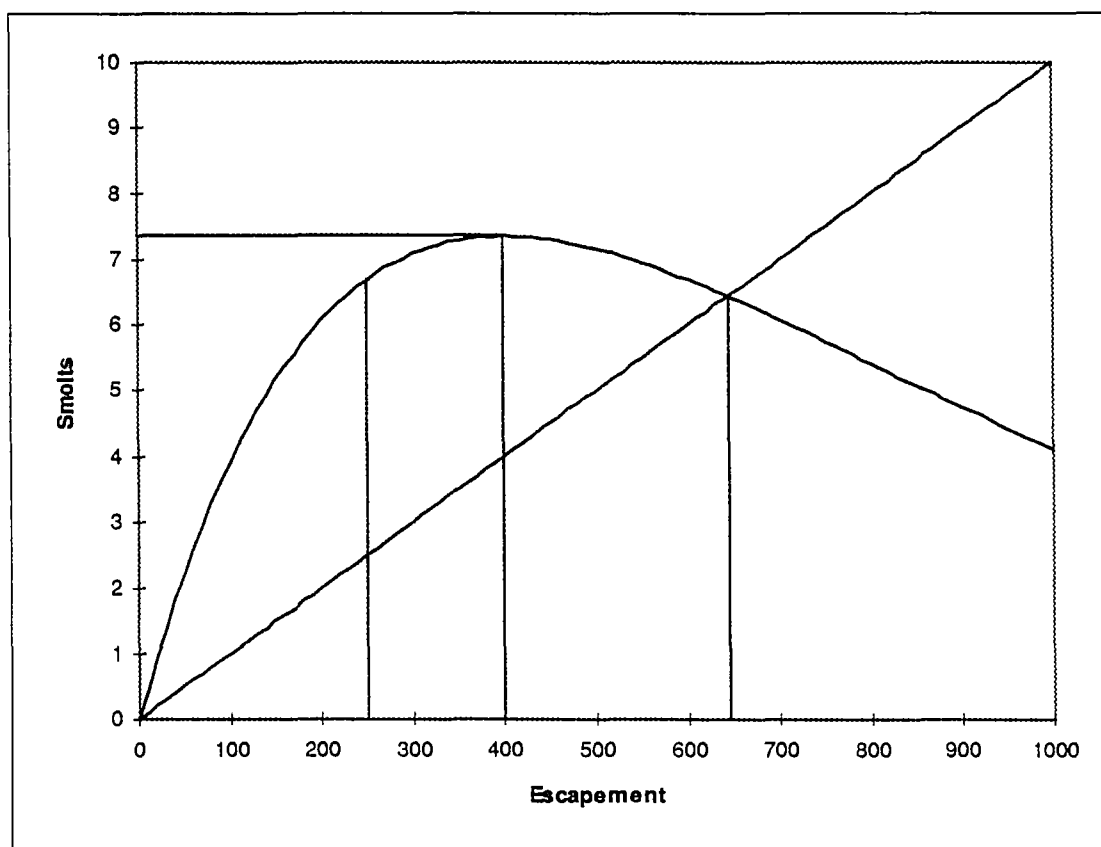


Figure 2.2 Reference points on the (Ricker) stock-recruitment curve from which targets can be derived -from left to right, escapement supporting maximum catch, escapement supporting maximum smolts, and maximum escapement for an unexploited fishery

1. **Maximum smolts.** These targets would be appropriate to protect the smolt output from a river. For dome-shaped (e.g. Ricker) stock-recruitment curve, it is possible to identify an egg deposition that results in the maximum smolt output. For stock-recruitment curves such as the Beverton-Holt curve, the maximum smolt output is produced at the maximum egg deposition. An appropriate target may not be to

achieve maximum smolt production, but perhaps some proportion (p) of the maximum production (e.g. 90%).

2. **Maximum escapement (“Replacement level”)**. These targets would be appropriate to protect the spawning escapement in a river. The replacement level represents the equilibrium level for escapement in an unexploited fishery. It is identifiable for all types of stock recruitment relationships, but requires an assessment of the relationship between the number of recruits and the number of resulting spawners in subsequent years (the “replacement” line). Estimates of parameters relating to the entire life-cycle such as sea survival, age composition, sex ratio, adult size and fecundity are therefore required. The replacement level cannot be regarded as a target itself (it would be achieved by allowing no exploitation), but spawning targets could be set as a proportion (p) of the replacement level.
3. **Maximum gain**. Maximum gain has been described in Section 2.2.4, and maximum gain would be an appropriate target where exploitation is going to be controlled to achieve the maximum catch. Failing a maximum gain target will therefore only occur when a fishery is being “over-exploited”, that is, when the catch could be increased by decreasing effort. As for the replacement level, it is identifiable for all types of S-R relationship, and requires the same information for its identification.

The targets set from stock-recruitment relationships described above can be expressed in terms of the parameters of the stock recruitment curve and the replacement line. These are shown for four stock-recruitment curves in Table 2.3.

The point of maximum gain for the Shepherd model is shown in Table 2.3 as:

$$\frac{\phi\alpha(1 + (1 - \lambda)(\beta S)^\lambda)}{(1 + (\beta S)^\lambda)} = 1$$

but for calculation purposes, let:

$$A = \phi\alpha$$

$$B = 1 - \lambda$$

$$C = (\beta S)^\lambda$$

$$C = \frac{AB - 2 + \sqrt{(AB)^2 - 4AB + 4A}}{2}$$

C can be obtained from A and B, and then the target S can be obtained from C.

Table 2.3 Spawning escapement targets (per unit area) expressed in terms of the parameters of the stock-recruitment curve and replacement line

	Cushing	Beverton-Holt	Ricker	Shepherd
S-R relationship	$R = \alpha S^{1-\beta}$	$R = \frac{\alpha S}{1 + \beta S}$	$R = \alpha S e^{-\beta S}$	$R = \frac{\alpha S}{1 + (\beta S)^\lambda}$
Replacement line	$S = \phi R$	$S = \phi R$	$S = \phi R$	$S = \phi R$
Spawning stock for maximum gain	$S = [(1 - \beta)\phi\alpha]^{1/\beta}$	$S = \frac{\sqrt{\alpha\phi} - 1}{\beta}$	$\alpha\phi e^{-\beta S'} [1 - \beta S'] = 1$	$\frac{\phi\alpha(1 + (1 - \lambda)(\beta S)^\lambda)}{(1 + (\beta S)^\lambda)} = 1$
Proportion (p) of "replacement level"	$S = p(\alpha\phi)^{1/\beta}$	$S = \frac{p(\alpha\phi - 1)}{\beta}$	$S' = \frac{pLn(\alpha\phi)}{\beta}$	$S = \frac{p(\alpha\phi - 1)^{1/\lambda}}{\beta}$
Proportion (p) of maximum smolt output*	not calculated	$S = \frac{p(\alpha\phi - 1)}{\beta(\alpha\phi - p(\alpha\phi - 1))}$	$\frac{\beta S' e^{1-\beta S'}}{p} = 1$	not calculated
Maximum smolt output (p=1)	$S = (\alpha\phi)^{1/\beta}$	$S = \frac{\alpha\phi - 1}{\beta}$	$S' = \frac{1}{\beta}$	not calculated

*Note: for the Beverton-Holt stock-recruitment curve, maximum smolt output is defined as the smolt output in an unexploited fishery.

The process of estimating a target for a river with stock-recruitment data is first to fit the stock-recruitment curve and estimate the replacement line, and then use the estimated parameters to obtain an estimate of the target using the equations in Table 2.3.

A number of important features regarding targets are noted below:

- Any shift in the stock-recruitment curve or replacement line will generate a shift in the run size and catch (Section 2.2.3), and the spawning escapement target (Table 2.3).
- For the Beverton-Holt, Ricker and Shepherd stock-recruitment curves, the maximum smolt output ("carrying capacity") is proportional to $1/\beta$ (α constant). All types of target in Table 2.3 are also proportional to $1/\beta$. Thus with all else constant, any differences (between rivers or through time) in the carrying capacity (smolt output /

area) will generate a proportional difference in the target, irrespective of the stock-recruitment model or the type of target considered.

- Many of the targets in Table 2.3 (including maximum gain) decrease with decreasing marine survival (ϕ) (which includes sex ratio, fecundity and age composition).

2.4 Sources of error when estimating targets

2.4.1 Introduction

The process of fitting a stock-recruitment model and then estimating spawning targets is subject to error. Two main sources of error are considered here, namely:

- choice of stock-recruitment model;
- sampling error.

The magnitude of these errors are illustrated with data from the River Bush (for background see Kennedy and Crozier, 1993).

2.4.2 Choice of stock-recruitment models

Nine stock-recruitment models were fitted to the data from the River Bush using non-linear model fitting routines in Genstat. These were the Beverton-Holt, Ricker and Shepherd deterministic models, each with a Normal, Poisson and Log-Normal stochastic error structure. The results are given in Table 2.4 to Table 2.6, and the three deterministic models with a Normal error structure are illustrated in Figure 2.3.

Table 2.4 Parameter estimates for the Beverton-Holt stock-recruitment model fitted to the River Bush

		Normal	Poisson	Log Normal
α	estimate	0.091	0.078	0.0495
	standard error	0.151	0.119	0.0503
β	estimate	0.0159	0.0135	0.0083
	standard error	0.0294	0.0237	0.0108
α - β	correlation	0.998	0.998	0.996

Table 2.5 Parameter estimates for the Ricker stock-recruitment model fitted to the River Bush

		Normal	Poisson	Log Normal
α	estimate	0.02599	0.02515	0.02215
	standard error	0.00519	0.00479	0.00413
β	estimate	0.001706	0.001649	0.001529
	standard error	0.000354	0.000330	0.000321
α - β	correlation	0.903	0.893	0.885

Table 2.6 Parameter estimates for the Shepherd stock-recruitment model fitted to the River Bush

		Normal	Poisson	Log Normal
α	estimate	0.01837	0.01775	0.01595
	standard error	0.00700	0.00646	0.00539
β	estimate	0.001624	0.001565	0.001474
	standard error	0.000678	0.000648	0.000594
λ	estimate	2.33	2.33	2.31
	standard error	1.14	1.14	1.21
α - β	correlation	0.973	0.971	0.965
α - λ	correlation	-0.884	-0.888	-0.885
β - λ	correlation	-0.893	-0.903	-0.897

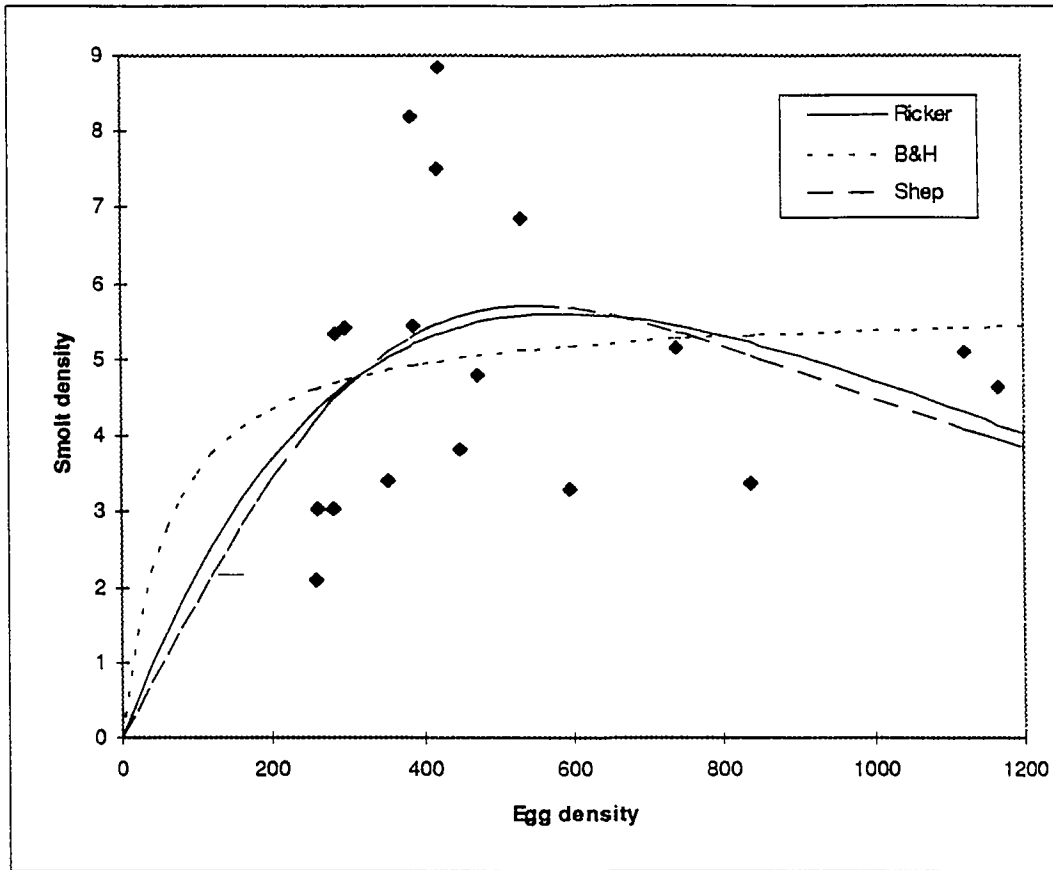


Figure 2.3 Different stock-recruitment curves fitted to data from the River Bush

All of these models explain a very low proportion of the variance (low R^2), thus the variance around the model is not much less than the variance around the mean smolt output (a horizontal line). It is theoretical considerations that have given a model that passes through the point (0,0), not the data.

The three different error structures for the Shepherd model are illustrated in Figure 2.4.

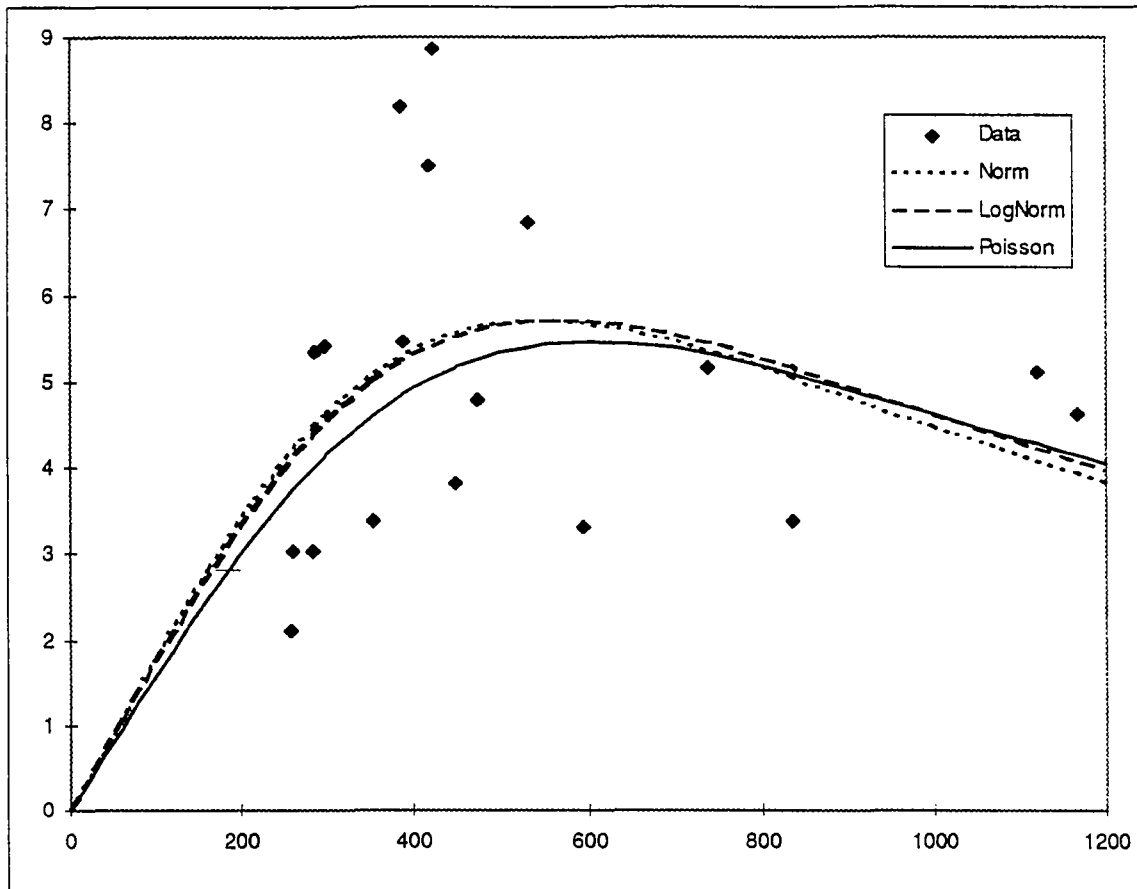


Figure 2.4 Shepherd stock-recruitment curve fitted to data from the River Bush, assuming normal, Poisson and log-normal error structures

The quantity of data, and the magnitude of the error, make it difficult to statistically select the most appropriate model. For example, the Shepherd model (which includes flat-topped and dome-shaped curves) is dome-shaped (i.e. $\lambda > 1$), but the estimate of λ is not significantly different from 1 (flat-topped). Three of the four years that produced high smolt outputs were consecutive (Figure 2.12), perhaps suggesting that this reflects the autocorrelated nature of salmon populations, rather than the existence of a dome-shaped relationship (see Section 2.9).

2.4.3 Estimation of targets for the Bush

The parameter estimates obtained above for the Beverton-Holt and Ricker models, and the equations in Table 2.3, were used to estimate target values for the River Bush, and are shown in Table 2.7. The replacement line ($\phi = 644.64 \text{ eggs.smolt}^{-1}$) was estimated assuming a smolt to adult (homewater) survival of 31.6%, 60% females and a fecundity of 3,400 eggs per female.

Table 2.7 Possible egg deposition targets for the River Bush (eggs 100m⁻² useable nursery habitat, area=41.06 ha)

	p	Beverton- Holt			Ricker		
		Normal	Poisson	Lognormal	Normal	Poisson	Lognormal
Maximum gain		419	451	560	504	518	548
Proportion (p) of replacement level	0.8	2901	2920	2979	1322	1352	1391
	0.6	2176	2190	2234	991	1014	1043
	0.4	1451	1460	1490	661	676	696
	0.2	725	730	745	330	338	348
Proportion (p) of maximum smolt output	1.00	3627	3651	3724	586	606	654
	0.95	887	1001	1390	418	432	466
	0.90	482	554	819	357	369	398
	0.85	319	370	562	312	323	348

The choice of model clearly makes a large difference to the estimate of the target. For the maximum gain target, estimates vary between 419 (Beverton-Holt, Normal) and 560 (Beverton-Holt, LogNormal). Maximum gain targets derived from the Ricker curve are less variable, since the shape of the curve more clearly defines this point.

Targets based on escapement are directly proportional to the value of p selected. The differences between the Beverton-Holt model and the Ricker model are due to the lower value of the replacement level with the dome-shaped curve.

Targets based on smolt output are very sensitive to the value of p selected, and also to the model assumed. This is because if the relationship is assumed to be dome-shaped, the maximum smolts are produced at around 600 eggs/100m⁻², whereas if an asymptotic curve is assumed, the maximum smolts are produced at the replacement level of around 3600 eggs/100m⁻². At p=0.85, the choice of model becomes less critical.

2.4.4 Sampling error

Even if it were possible to select the most appropriate stock-recruitment model, sampling error will still generate uncertainty in the estimate of a spawning target. The parameter estimates in Table 2.4 to Table 2.6 are very uncertain, as reflected in the standard errors, and these uncertainties will be reflected in the confidence intervals around the target estimates. Simulations (5000) were used to estimate the approximate confidence intervals for the maximum gain targets for the Bush using the nine models fitted in Section 2.4.2. The results illustrate the enormous uncertainty in the egg density required for maximum gain (Table 2.8 to Table 2.10). If one is willing to accept the Ricker model as the correct model, then the

confidence intervals vary between about 400 and 800. The upper confidence intervals for the Beverton-Holt and Shepherd models are considerably higher.

Table 2.8 Confidence intervals for the maximum gain target using the Ricker model

		Normal	Poisson	Log Normal
Expected value		504	518	548
Simulation results	Mean	525	537	566
	SE	110	104	120
	SE/Mean	0.209	0.194	0.212
	Lower 95% CL	374	389	402
	Median	505	518	544
	Upper 95% CL	790	799	849

Table 2.9 Confidence intervals for the maximum gain target using the Beverton-Holt model

		Normal	Poisson	Log Normal
Expected value		419	451	560
Simulation results	Mean	681	677	1219
	SE	8862	6215	18633
	SE/Mean	13.00	9.18	15.28
	Lower 95% CL	195	210	294
	Median	325	354	474
	Upper 95% CL	1498	1684	2921

Table 2.10 Confidence intervals for the maximum gain target using the Shepherd model

		Normal	Poisson	Log Normal
Expected value		491	508	535
Simulation results	Mean	731	801	988
	SE	1020	1725	11730
	SE/Mean	1.3955	2.1550	11.8759
	Lower 95% CL	357	378	393
	Median	582	611	639
	Upper 95% CL	1715	1877	1834

It must be stressed that the confidence limits on these target estimates assume that the replacement line is constant from year to year and exactly known. They do not take into account the uncertainties associated with the replacement line, only those associated with the stock-recruitment curve. These confidence limits therefore represent under estimates of the true uncertainties, and this underestimation is probably considerable. It would be possible to improve the confidence limits associated with the targets, but this would require data for the River Bush that were not available.

2.5 Between river variation in stock-recruitment curves

2.5.1 Comparison of adult-smolt data

Methods

In an attempt to distinguish genuine differences in stock recruitment curves from all other sources, stock-recruitment data (known to be available for selected rivers) was requested in order to enable statistical comparisons to be made. Permission to use such data from a number of rivers (see Table 2.11) was originally sought by the NRA. The data was subsequently requested by WRc by means of a simple questionnaire (Appendix A); a completed questionnaire was received only for the River Bush.

Table 2.11 Stock recruitment data from the UK

River	Permission to use data	Type of data	Notes
River Bush, Ireland	Yes	Adult trap; smolt trap; egg deposition	Data received and analysed
River Burishoole, Ireland	No	Adult trap; smolt trap; egg deposition	Data withheld by authors until after publication
Shelligan Burn, Scotland	Yes	Juvenile electrofishing data; emergent fry densities	Permission obtained to re-use published data only
Girnock Burn, Scotland	Yes	Juvenile electrofishing data; adult trap; smolt trap; egg deposition	Permission obtained to re-use published data only

Table 2.12 indicates the range of estimates for each of a series of habitat parameters for Girnock Burn and the River Bush. For the comparison of stock recruitment curves, the total salmonid nursery area was used for the two river systems.

Table 2.12 Estimates of area types within two river systems

Habitat type	Estimate of area in:	
	Girnock Burn	River Bush
Total catchment area	2,800.00 ha	33,700.00 ha
Accessible fluvial area	5.88 ha	84.55 ha
Spawning habitat	0.55 ha	-
Total salmonid nursery area	4.69 ha *	41.06 ha
Grade 'A' nursery area	-	23.38 ha **

*: Taken as the total of Type 1 and Type 1a habitats, as described by Buck and Hay (1984)

***: All conditions necessary for qualification as 'nursery habitat' are idealised, plus stable stone cover present over >50% of the river bed

In view of the lack of available data for the UK, the comparison exercise was repeated for Canadian rivers using (with permission) stock-recruitment data from the ICES publication (Chaput *et al.*, 1993) details of which are listed in Table 2.13.

Table 2.13 Comparison of estimated Beverton-Holt SR parameters (for egg to smolt) and the principal features of the rivers assessed

River system	Latitude	Fluvial area (ha)	Years for which data obtained	Mean smolt production (No.100m ⁻²)	Minimum smolt output (x 10 ³)	Maximum smolt output (x 10 ³)
Gimock Burn ¹	57°00'	5.88	1966-89	4.05	0.621	3.799
River Bush	55°10'	84.55	1974-91	2.41	8.610	36.360
Pollett River ²	46°00'	36.37	1954-60	2.76	4.098	20.674
Big Salmon River	45°25'	46.50	1964-67	4.59	11.900	27.000
Rivière de la Trinité	49°20'	211.19	1980-87	3.21	36.740	103.156
Little Codroy River	47°40'	38.90	1954-60	2.32	5.354	12.490
Conne River ³	47°30'	131.80	1987-88	4.65	52.258	70.368
Western Arm Brook ⁴	51°11'	29.00	1972-86	4.53	6.153	21.973
Rivière Bec-Scie	49°50'	16.46	1984-88	2.31	2.459	4.882
NW Miramichi River ⁵	47°00'	250.00	1950-67	0.95	12.878	51.161

¹: River is a tributary of a larger system (the Aberdeenshire Dee)

²: Based on natural spawning but piscivorous birds actively controlled

³: There is an additional lacustrine area which is known to be used by parr; the fluvial area estimated at only 2.8% of the total wetted area

⁴: There is an additional lacustrine area which is known to be used by parr; the fluvial area estimated at only 1.4% of the total wetted area

⁵: May be subjected to adverse perturbations: industrial development; DDT spraying; mine effluent effects; and logging practices (Chaput *et al.*, 1993)

With the Canadian data, the only common definition of habitat for which estimates of area were available was the total fluvial area.

Generalised Non-linear Modelling was used to fit a Beverton-Holt stock-recruitment curve to the data:

$$R = \frac{1}{a + b/S} + e$$

In the following analysis, the error e is assumed to be either normal or log-normal, so that the importance of choice of error structure can be assessed. In addition, the order of fitting the

parameters a and b may make a difference to the conclusions, and so the models were fitted in both orders.

Results

The results of the comparison exercise between the River Bush and Girnock Burn are shown in Table 2.14. The two orders of fitting are shown; a followed by b (+a, +b) and b followed by a (+b, +a). There are no significant differences between the curves, either in terms of the a or b parameters.

Table 2.14 Analysis of variance for the comparison of stock recruitment curves for the River Bush and Girnock Burn

	Normal					Log Normal				
	d.f.	s.s.	m.s.	v.r.	F pr.	s.s.	m.s.	v.r.	F pr.	
Regression	2	1105.1	552.552	184.55	<.001	101.841	50.9204	351.66	<.001	
+a	1	0.1	0.1	0.03	ns	0.005	0.005	0.03	ns	
+b	1	3	3	1.00	ns	0.179	0.179	1.24	ns	
or										
+b	1	0.3	0.3	0.10	ns	0.07	0.07	0.48	ns	
+a	1	2.8	2.8	0.94	ns	0.114	0.114	0.79	ns	
Residual	37	110.8	2.994			5.357	0.1448			
Total	41	1219	29.732			107.382	2.6191			

The curves for these two data-sets were plotted on the same figure (Figure 2.5). The parameter estimates relating to these two curves are given in Tables 2.15 to 2.18 for a range of scenarios from assuming a common a and b for both curves (Table 2.15) to separate a and b for both curves (Table 2.18). In all cases the models have a relatively small standard error for parameter “a” (corresponding to the asymptote of the curve). Since most of the data falls around the horizontal portion of the curves, this parameter is little different to the mean of the smolt output. Although there is far more uncertainty in the parameter “b” (which corresponds to the rate of increase of the curve) this is not surprising given that there is little data for this part of the curves.

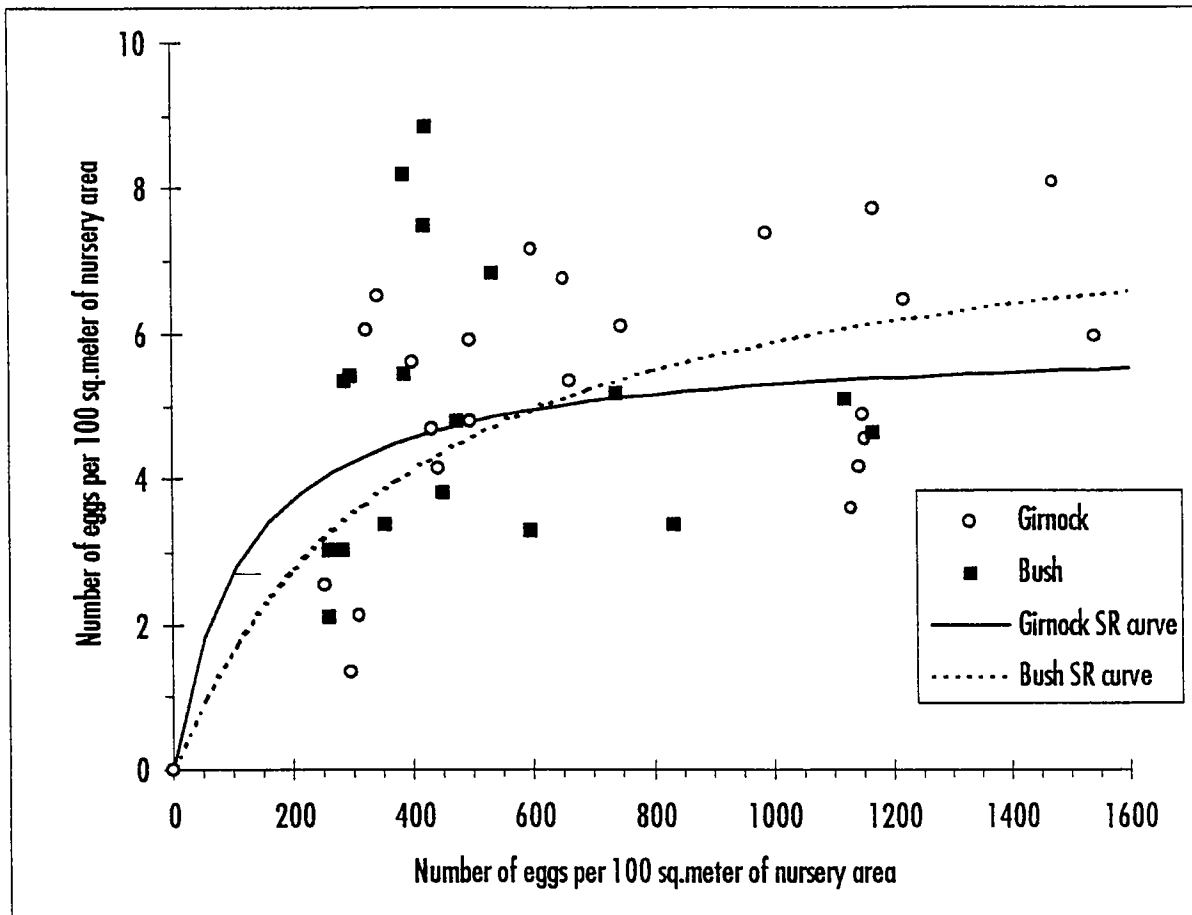


Figure 2.5 Comparison of Beverton-Holt stock-recruitment curves for the River Bush and the Girnock Burn

Table 2.15 Parameter estimates for stock recruitment curve for River Bush and Girnock Burn -combined a and b

	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a	0.1494	0.02	0.139	0.0251
b	22.9	10.8	35.4	12.7

Table 2.16 Parameter estimates for stock recruitment curve for River Bush (2) and Girnock Burn (1) - separate a and constant b

	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a ₁	0.1486	0.0202	0.1399	0.0256
a ₂	0.1524	0.0283	0.1355	0.0343
b	22.5	11.5	35.9	13.5

Table 2.17 Parameter estimates for stock recruitment curve for River Bush (2) and Girnock Burn (1) - constant a and separate b

	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a	0.1484	0.0209	0.1362	0.026
b ₁	25.3	13.8	41.2	16.2
b ₂	21.6	11.1	32.6	13

Table 2.18 Parameter estimates for stock recruitment curve for River Bush (2) and Girnock Burn (1) - separate a and b

	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a ₁	0.1353	0.0241	0.1211	0.0306
a ₂	0.1755	0.0418	0.1684	0.0494
b ₁	32.2	16.2	48.8	18.7
b ₂	11	17.5	20.2	20.4

Whilst there would appear to be little difference in the stock-recruitment relationships in the two rivers (both having an asymptote of around 7 smolts/100m²) any such conclusion is critically dependent on the definition which is used for nursery habitat (Section 2.6). The single curve for both data sets is shown in Figure 2.6.

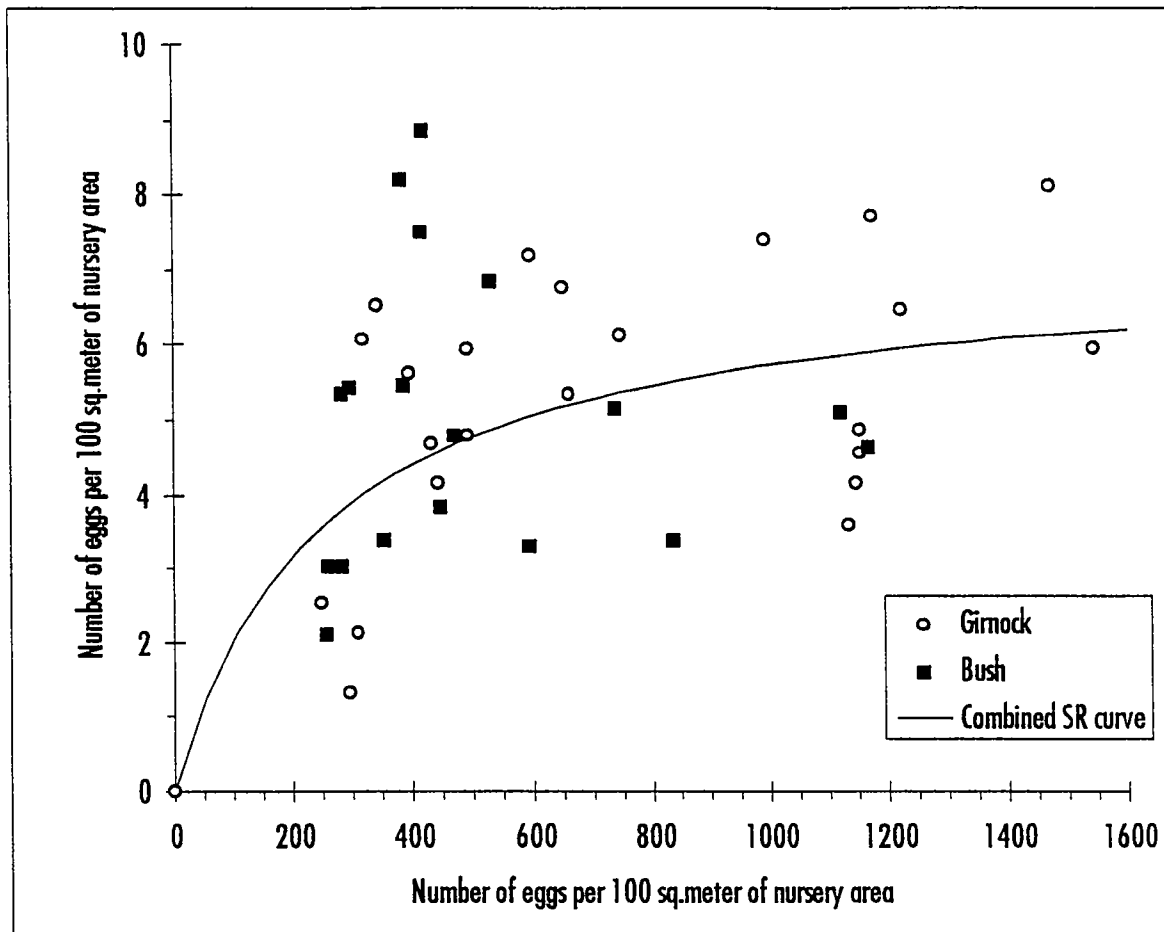


Figure 2.6 A single Beverton-Holt stock-recruitment curve fitted to combined data from the River Bush and the Girnock Burn

The residual variation for the two rivers is very similar (Table 2.19) and not significantly different.

Table 2.19 Residual variation for the stock recruitment curves of the River Bush and Girnock Burn when fitted separately.

	Residual degrees of freedom	Residual Mean Square	
		Normal	Log Normal
Girnock	21	2.445	0.1411
Bush	16	3.714	0.1496

The statistical comparison between the stock recruitment curves for Canadian rivers reveals highly significant differences between them. A difference in either the a parameter or the b parameter adequately describes the difference, and no further significant improvement is gained by fitting individual parameters to each river (Table 2.20).

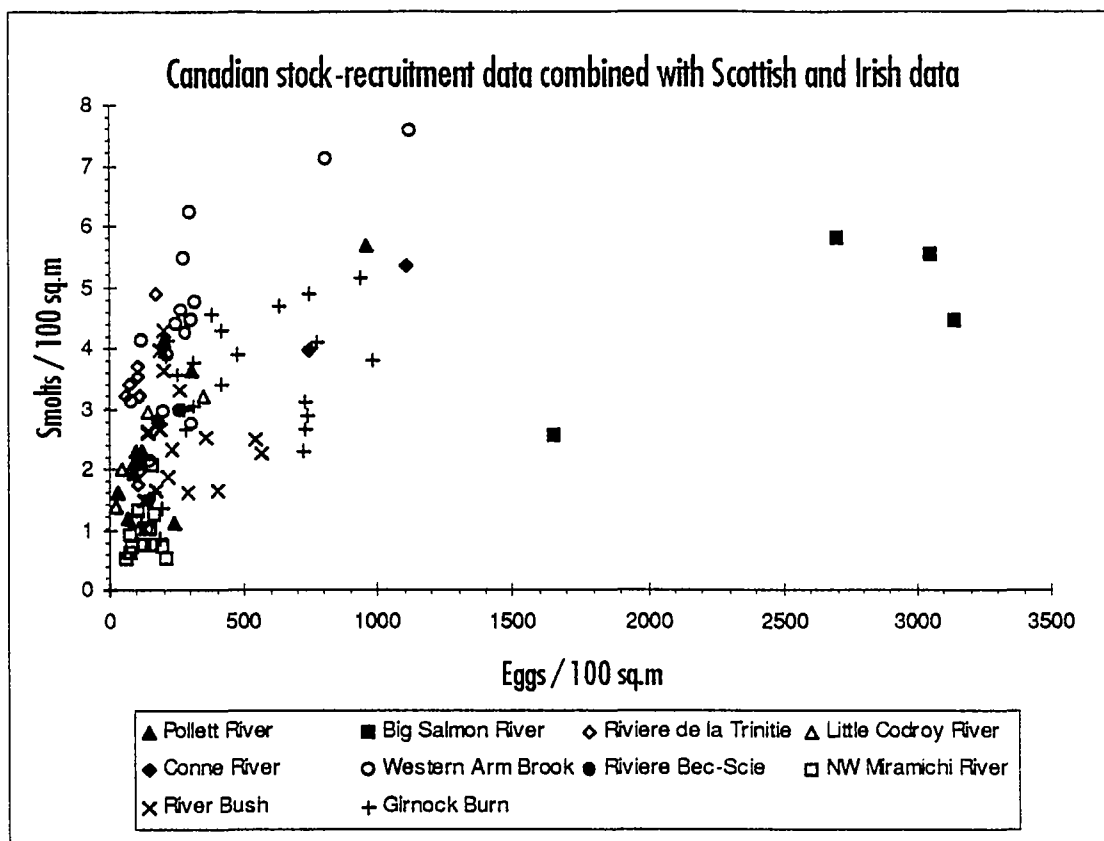


Figure 2.7 Stock-recruitment relationships for Canadian, Scottish and Irish river systems (see text)

Table 2.20 Analysis of variance for the comparison between Canadian stock recruitment curves

	Normal					Log Normal			
	d.f.	s.s.	m.s.	v.r.	F pr.	s.s.	m.s.	v.r.	F pr.
Regression	2	543.70	271.85	417.64	<0.001	46.23	23.12	192.86	<0.0001
+a	6	53.09	8.85	13.59	<0.001	15.07	2.51	20.95	<0.001
+b	6	3.46	0.58	0.89	ns	0.47	0.08	0.65	ns
or									
+b	6	51.61	8.60	13.21	<0.001	14.18	2.36	19.72	<0.0001
+a	6	4.94	0.82	1.26	ns	1.36	0.23	1.88	ns
Residual	44	28.64	0.65			5.27	0.12		
Total	58	628.89	10.84			67.04	1.16		

The parameter estimates are given in Tables 2.21 to 2.24. As for the Bush and Gironck, a range of assumptions from a common a and b through to separate a and b for each river are made.

Table 2.21 Parameter estimates for stock recruitment curve for Canadian rivers - constant a and b

Parameter	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a	0.1252	0.0186	0.1833	0.0494
b	40.03	6	35.61	8.04

Table 2.22 Parameter estimates for stock recruitment curve for Canadian rivers - separate a and constant b

Parameter & river	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a ₁	0.1733	0.027	0.2791	0.056
a ₃	0.0502	0.0414	0.1635	0.0563
a ₄	0.1907	0.0523	0.245	0.0658
a ₅	0.1815	0.0262	0.1984	0.0522
a ₆	0.112	0.0128	0.1613	0.0252
a ₇	0.2388	0.0674	0.329	0.0728
a ₈	0.796	0.232	0.976	0.108
b	28.88	4.13	16.66	4.3

Key to rivers:

- 1 Pollett River
- 3 Rivière de la Trinité
- 4 Little Codroy River
- 5 Conne River
- 6 Western Arm Brook
- 7 Rivière Bec-Scie
- 8 NW Miramichi River

Table 2.23 Parameter estimates for stock recruitment curve for Canadian rivers - constant a and separate b

Parameter & river	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a	0.12	0.0141	0.2045	0.0324
b ₁	49.6	11	27.13	8
b ₃	19.96	3.36	11.76	5.13
b ₄	36.45	7.8500	16.58	5.0200
b ₅	86.8	27.9	16.4	57.9
b ₆	27.21	4.99	10.15	7.94
b ₇	49.2	11.3	35.2	11.6
b ₈	125.3	33.6	106.3	13.4

Table 2.24 Parameter estimates for stock recruitment curve for Canadian rivers - separate a and b

Parameter & river	Normal		Log Normal	
	estimate	s.e.	estimate	s.e.
a ₁	0.1399	0.0353	0.2395	0.0676
a ₃	0.2014	0.0996	0.293	0.143
a ₄	0.2927	0.0855	0.3142	0.0842
a ₅	0.053	0.135	0.053	0.2640
a ₆	0.1064	0.0147	0.129	0.0386
a ₇	0.218	0.193	0.245	0.216
a ₈	0.782	0.647	0.817	0.282
b ₁	42.6	13.9	23.33	9.19
b ₃	11.2	10.4	3.3	13.6
b ₄	11.46	8.91	9.4	5.95
b ₅	149	133	149	246
b ₆	31.25	5.37	25.55	9.88
b ₇	32.5	32.1	29.4	32.1
b ₈	30.7	77.2	35.2	31.5

2.5.2 Comparison of electrofishing data

Methods

It was originally intended to analyse available electrofishing data for the Girnock and Shelligan Burns, with a view to comparing the stock-recruitment characteristics of the juvenile stages. However, a lack of published data for the Shelligan Burn necessarily restricted the analysis to a simple comparison of the 0+ to 1+ survival curves.

Results

The stock recruitment data for the Girnock and Shelligan Burns are presented in Figure 2.8 and Figure 2.9, where the “stock” is represented by the 0+ age-class and the “recruitment” by the 1+ age-class. The range of 0+ densities for the two rivers were very different, with the highest densities on the Girnock Burn being lower than the lowest densities in the Shelligan Burn. The formal analysis of these data and the comparison of parameter estimates for the two data sets was felt to be inappropriate.

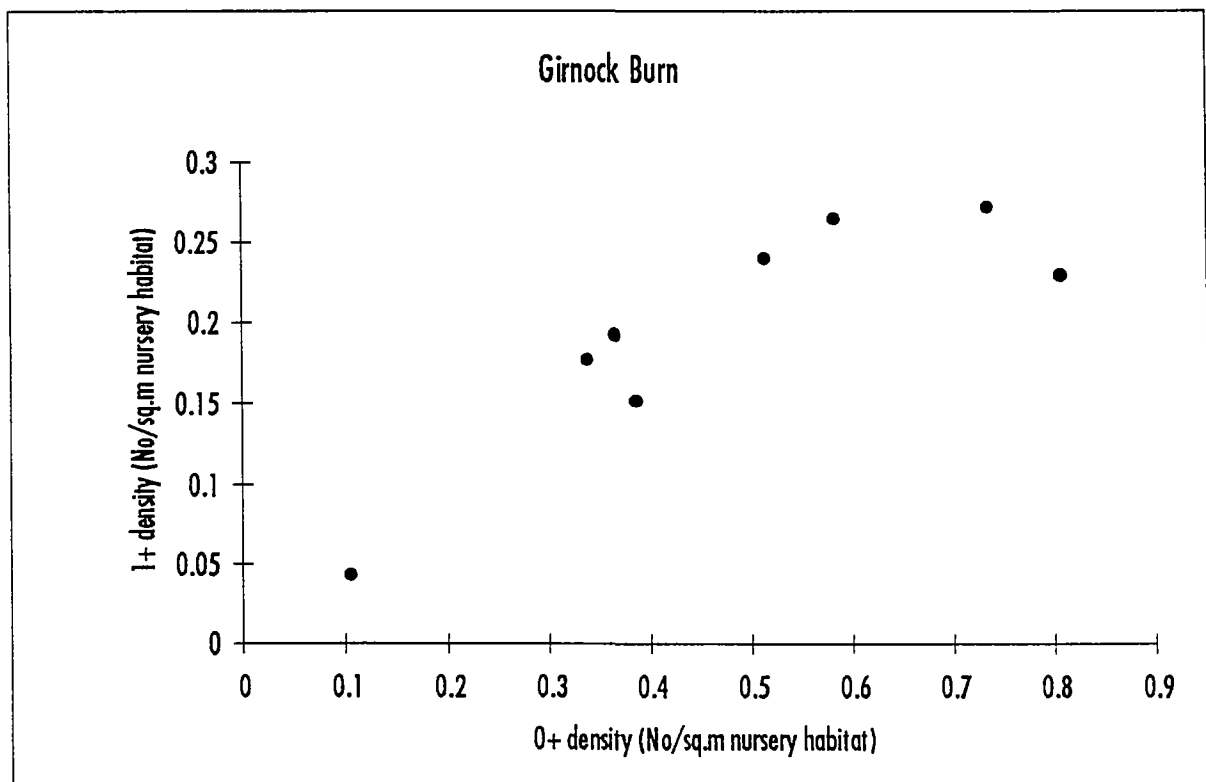


Figure 2.8 Stock-recruitment data (0+ to 1+) for the Girnock Burn

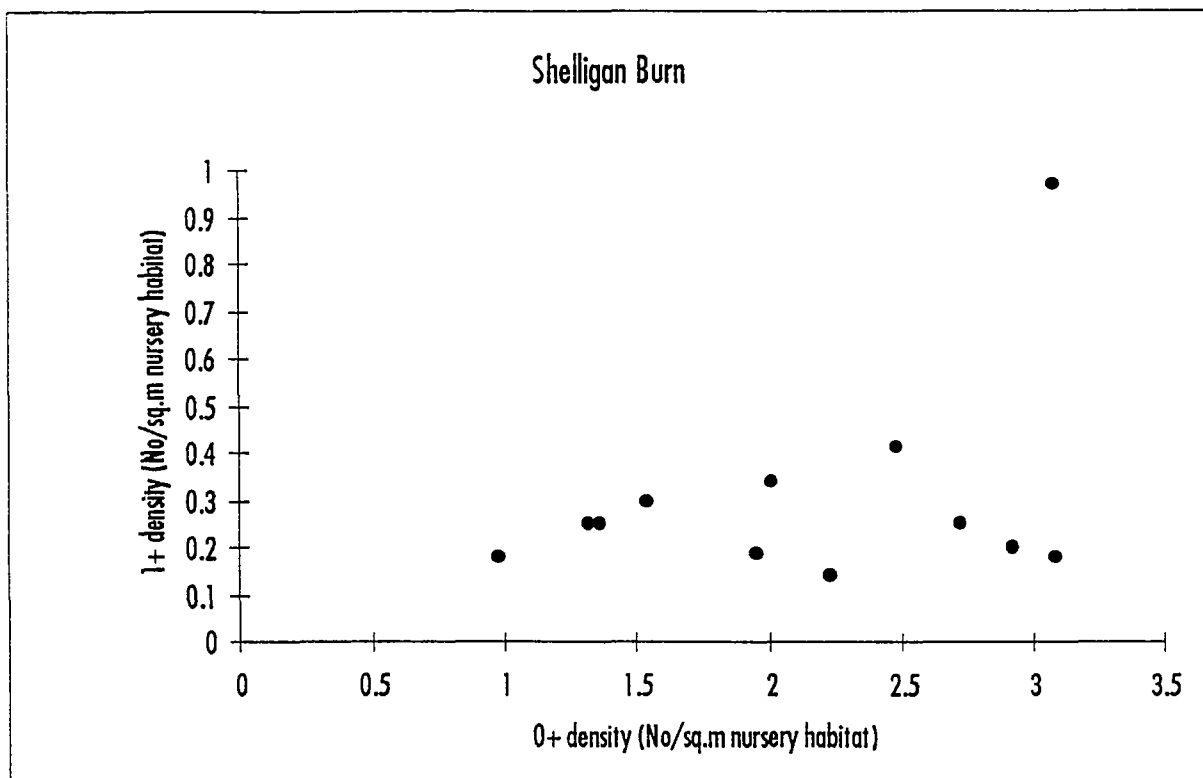


Figure 2.9 Stock-recruitment data (0+ to 1+) for the Shelligan Burn

2.6 Transportation of targets

2.6.1 Adjustment of targets due to differences in the stock-recruitment curve

It is clear from the preceding discussions that defining a spawning target (such as an egg deposition target) requires a knowledge of the stock-recruitment curve and the replacement line. It follows that when transporting a target from a donor river where this information is available (such as the Bush) to a recipient river where it is not, it must either be assumed that the stock-recruitment curve and replacement line in the donor and recipient rivers are identical, or that appropriate adjustments can be made.

Take, for example the maximum gain target of 560 (confidence limits <294, >2921) for the Bush based on the Beverton-Holt stock-recruitment model with log-normal error structure. Assume this target were to be transported to Girnock burn. If it were assumed that the only differences between the two stock-recruitment curves was the asymptote, then from Table 2.16, the asymptotes for the Bush and Girnock are 7.38 ($= 1 / 0.1355$) and 7.15 ($= 1 / 0.1399$) respectively. From Section 2.3 it is seen that a maximum gain target will vary in proportion to this value, and so assuming all else constant (marine survival, age composition, fecundity, shape of stock-recruitment curve), the target for the Girnock Burn would be 543 ($= 560 \times 7.15 / 7.38$). However, the stock-recruitment curves for the Girnock and Bush were not found to be statistically different, and so in practice this adjustment may not be made.

This link between the height of the stock-recruitment curve and spawning target values is employed in Section 4 where habitat models are used to estimate the relative differences in the height of the stock-recruitment curves between rivers.

2.6.2 Definition of stream types and area estimation

When stock-recruitment data are available for a river such as the Bush, the definition of stream types and area estimation is not critical for managing that river since management decisions can be based on data for the total egg deposition and total smolt output. However, the nature of the area which is used when expressing egg deposition and smolt output in density terms is crucial when comparisons are to be made between-systems. In this context, a variety of measures for the area may be employed, based on:

- the total (surface) area of the river system;
- the total area which is accessible to salmon;
- the total area which is used by, or is available to, a specific life-stage (e.g. 'juvenile' or 'nursery' habitat).

Even when the broad definition of habitat is established, the assessment of what constitutes habitat suitable for juveniles, or habitat of a particular quality needs to be defined in an objective way that can be applied to different rivers. In addition to the problems of habitat definition and assessment, areas of stream bed have to be estimated, and this is likely to be subject to large errors.

Consider a system of area A , made up of a number of "sections" of differing access, spawning habitat and nursery habitat. These section may be river reaches or major tributaries, for example, depending on the spatial resolution of available data.

Let each section have a label i , where i is a number between 1 and the n sections defined.

The area of section i (a_i) is given by:

$$a_i = Ap_i$$

where p_i is the proportion of the total stream area occupied by section i .

Let the total stock level entering the river in any particular year be S (measured for example in terms of numbers of adults). The number of adults spawning in section i is given by:

$$s_i = Sq_i$$

where q_i is the proportion of stock spawning in section i .

The density of spawners in section i is therefore given by:

$$\frac{s_i}{a_i} = \frac{Sq_i}{Ap_i}$$

The physical and ecological characteristics of section i will give it a particular stock-recruitment relationship. For simplicity, assume this to be a Beverton-Holt type curve. The number of recruits (r_i , e.g. smolts) per area will be given by:

$$\frac{r_i}{a_i} = \frac{1}{\alpha_i + \frac{a_i \beta_i}{s_i}}$$

where α_i and β_i are the parameters of the Beverton-Holt model.

If this is rewritten in terms of A , S , p_i and q_i we get:

$$r_i = \frac{1}{\frac{\alpha_i}{Ap_i} + \frac{\beta_i}{Sq_i}}$$

The total number of recruits (R , e.g. smolts) produced by the entire system will therefore be:

$$R = \sum_{i=1}^n \frac{1}{\frac{\alpha_i}{Ap_i} + \frac{\beta_i}{Sq_i}}$$

or in terms of density:

$$\frac{R}{A} = \sum_{i=1}^n \frac{1}{\frac{\alpha_i}{p_i} + \frac{\beta_i}{(S/A)q_i}}$$

This assumes that there is no movement of fish between the n sections. If the sections are tributaries, this may be a reasonable assumption to make.

Thus we have the stock-recruitment relationship (relating R to S) for the whole catchment from which the catchment-specific egg deposition target can be derived. This relationship for the whole catchment does not follow the Beverton-Holt model, even though that was the model assumed within each section. The process of aggregating stock-recruitment curves for different reaches with different habitats and spawning densities will result in a different shape relationship for the whole catchment. Even if the stock-recruitment curve in each tributary is dome shaped, the resultant stock-recruitment curve for the catchment may have a far less pronounced dome. For example at high stock levels, spawning may occur in otherwise under-utilised parts of the catchment, compensating for reduced production elsewhere.

If the number of adults (S) entering the system is high such that egg deposition is not limiting juvenile densities in any of the n sections, then:

$$R = A \sum_{i=1}^n p_i \left(\frac{1}{\alpha_i} \right)$$

If a habitat model can predict the density of juveniles when “recruitment” is not limiting (i.e. the asymptote of the stock-recruitment curve, equivalent to $1/\alpha$ - see Section 4.2.4), then the right-hand side of this equation represents the total stream area multiplied by the weighted average of the carrying capacities.

For the Bush, the accessible fluvial area has been categorised into three habitat quality types as shown in Table 2.12. If these are redefined as non-overlapping areas, the highest quality denoted “A” and the poorest “C”, we have the areas for the three habitat types shown in Table 2.25.

Table 2.25 Areas of three grades of stream habitat for the River Bush

Habitat type	Estimate of area (a_i) - (ha)	Proportion (p_i)
Grade “A” nursery area	23.38	0.277
Grade “B” nursery area	17.68	0.209
Grade “C” area	43.49	0.514
Total accessible fluvial area (A)	84.55	1.000

Target estimates for the Bush ignore Grade “C” streams, and so assume that no spawning takes place in them (i.e. $q_C=0$). No data were provided on the assessment of stream habitat on the Bush, or the possible differences between them. However, by definition, the stock-recruitment relationship in Grade A and Grade B habitats are different, and the carrying capacity ($1/\alpha$) in Class A will be higher than in Class B. For illustrative purposes only, assume that the carrying capacity in Class A is twice that for Class B ($2\alpha_A=\alpha_B$), that density independent mortality in Class A and Class B are the same ($\beta_A=\beta_B$), and that spawning occurs at equal densities in the two habitat types. We now have sufficient information to fit the spatially aggregated Beverton-Holt model to data from the Bush. This was undertaken using Genstat, and the results (assuming a Normal error structure) are shown in Table 2.26.

Table 2.26 Parameter estimates for a spatially aggregated Beverton-Holt stock-recruitment model (2 quality classes) fitted to data from the River Bush

Habitat type	Proportion of stream area (p_i)	Proportion of spawners (q_i)	$1/\alpha^*$	β^{**}
Grade "A"	0.277	0.569	7.26	17.3
Grade "B"	0.209	0.431	3.63	17.3
Grade "C"	0.514	0.000 ^{***}	n/a	n/a
Combined A + B	0.486	1.000	5.70	11

(From Table 2.18)

* Carrying capacity ($1/\alpha$) in Grade "A" assumed to be double that in Grade "B"

** Parameter β (density independent mortality) assumed to be the same in both habitat types

*** It is assumed that no spawning takes place in Grade "C" habitat

The new aggregated Beverton-Holt stock-recruitment model can be used to estimate (by iteration) a maximum gain target of 517. As would be expected, this is different to that estimated from a single Beverton-Holt model (419).

If this target were to be transported to an adjacent river system with the same proportions of Class A and B habitat (and unused Class C), with the same stock-recruitment curves and the same replacement line, then the target would remain the same. However, if the proportions of Class A and Class B habitats were different in the adjacent river system, then although the habitat-specific stock-recruitment relationships would be the same, the river-specific stock-recruitment relationship would change, and so would the target as shown in Table 2.27. The fact that the target for a river with all Class B habitat is half that of a river with all Class A habitat is due to the initial (illustrative) assumption that $2\alpha_A = \alpha_B$, and the relationship between carrying capacity and targets discussed above.

Table 2.27 Maximum gain target for rivers with different proportions of Class A and Class B habitat (assuming Class C habitat absent)

p_A	p_B	Maximum gain target	Notes
0.000	1.000	321	
0.250	0.750	411	
0.500	0.500	495	
0.569	0.431	517	Equivalent to ratios estimated on Bush
0.750	0.250	571	
1.000	0.000	642	

2.7 Use of spatial data

Gee *et al.* (1978) looked at data for juvenile salmon from the River Wye, Wales, and constructed stock-recruitment curves and estimated targets from these. There are two fundamental problems with this approach in the context of target setting.

Firstly, data was only available from 0+ summer parr densities through to pre-smolt densities. There was therefore no data for the egg to 0+ summer parr stage of the life cycle, when density dependent regulation is likely to occur. Exponential survival curves were fitted to the data and used to extrapolate back to the early life stages. There are two problems with this alone. Firstly, exponential survival occurs when there are no density-dependent mechanisms operating, and so its use is inappropriate for modelling the density dependent stages of the salmon life cycle (an exponential survival curve generates a linear stock-recruitment curve). Wyatt (1994) showed that density dependent survival was a more appropriate model for at least some of these Wye tributaries. Secondly, when extrapolating, sites with the more rapid exponential mortality will (if extrapolated far enough) appear to have the highest starting density. Thus the observed relationship between (extrapolated) starting density and subsequent survival may be an artefact.

The second problem with the use of the Wye data to derive stock-recruitment curves is that the data represents the “stock” and “recruitment” at a number of sites at one moment in time. If one considers a number of electrofishing sites (say 20), some of these will have good juvenile habitat, others poor juvenile habitat. The stock-recruitment curves for each individual site are likely to be different. The stock-recruitment (0+ to 1+) curves for 20 such sites, ranked in order of 1+ habitat quality are shown in Figure 2.10. The stock recruitment curve for one site is highlighted in a darker colour, and the stock recruitment curve for all the sites combined would be the summation of all the individual curves. If one is prepared to assume that habitat quality (and therefore the site-specific stock-recruitment curve) is identical at all sites, and that stochastic variation operates in a similar manner spatially as well as temporally, then the form of the spatial stock-recruitment curve published by Gee *et al.* (1978) may resemble the true stock recruitment curve.

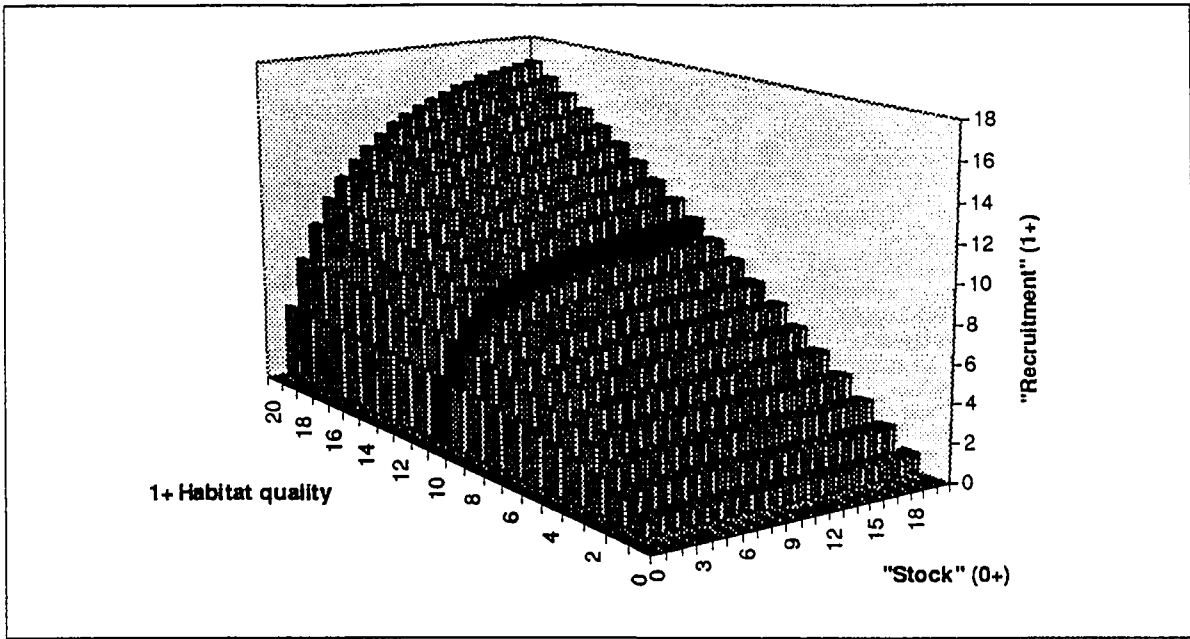


Figure 2.10 Stock-recruitment curves for 20 sites ranked in order of 1+ habitat quality - highlighted data represent the stock recruitment curve for 1 site

In practice, each individual site is likely to have a different stock recruitment curve. In addition, the habitat quality for 1+ and the level of 0+ stock are unlikely to be independent. If one assumes, for example, that sites with high 1+ habitat quality receive a lower 0+ “stock” (habitat requirements for 0+ and 1+ fish are different), then the apparent spatial “stock recruitment” curve is highlighted in Figure 2.11. This one example illustrates that the relationship between stock and recruitment across sites will have a complex relationship to the true temporal stock recruitment curve. Even in this overly simplistic example, a Beverton-Holt-type stock-recruitment curve generates a dome-shaped spatial stock-recruitment relationship.

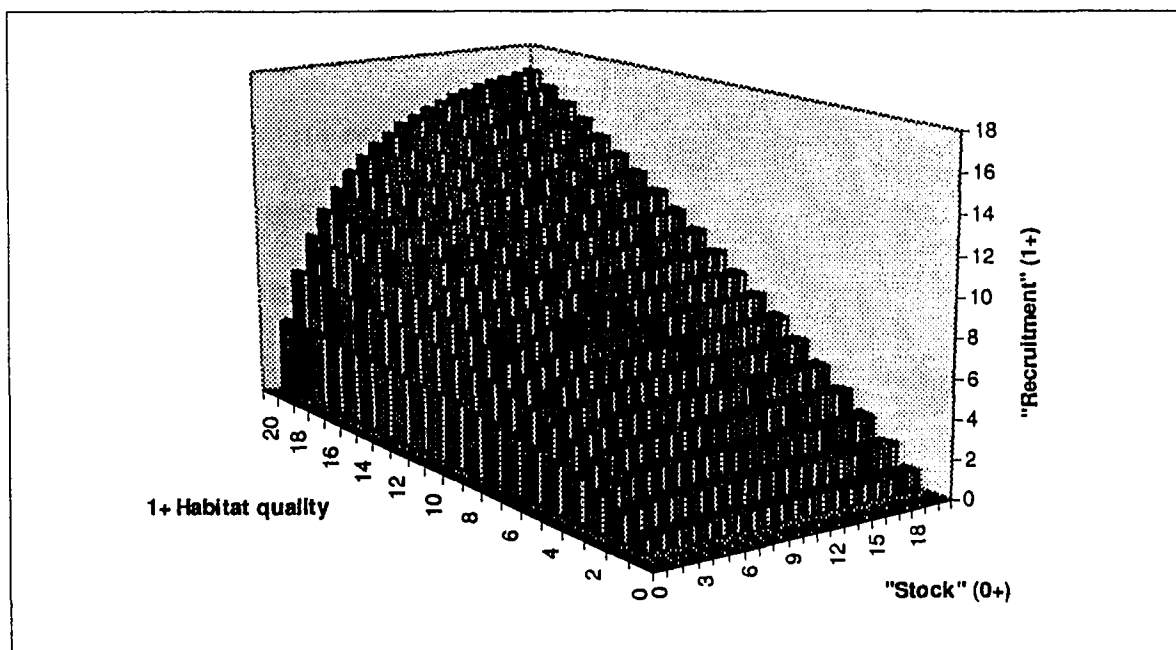


Figure 2.11 Stock-recruitment curves for 20 sites ranked in order of 1+ habitat quality - highlighted data represent one possible interpretation of data collected in only one year (see text for explanation)

2.8 The development of stochastic models

The stock-recruitment curve and the replacement line represent the simplest deterministic model of the salmon life cycle (Section 2.2.3). There are a number of ways in which they may be too simplistic for salmon management. One of these is the need to allow for stochastic variation; whilst it is possible to build safety margins into targets based on the stock-recruitment curve, a more flexible approach is to develop a stochastic model. Other complicating factors include the need for managing the different sea age components of the stock.

One solution is to combine all the information available on a fishery into a stochastic model.

Such models could be developed to any degree of sophistication to reflect the level of understanding for a particular fishery. The combination of more detailed models of the stock recruitment curve, the replacement line, exploitation, and stochastic variation would form the basis of a flexible means of target setting and compliance assessment.

Such a model is illustrated in Appendix C, which is a stochastic version of the deterministic model in Section 2.2.3, with the following refinements:

- the inclusion of net catch (see Model 5, Section 5);
- more refined juvenile model (Section 4.4.2);
- inclusion of different sea ages, and age specific exploitation and fecundity information;
- stochastic variation for freshwater and marine phases.

The purpose is to illustrate how the model might work; no attempt has been made to enter realistic parameter values! The first box requires information on the exploitation, including the number of rods and nets, and for three sea-ages, the relative size of the fishing season and the efficiency of the fishery. The second row of boxes enables information on sea age and smolt age to be entered. The third row of boxes require information on the replacement line for each sea age, and the stock recruitment curve, including estimates of the stochastic variation. The fourth row sets the initial values for the simulation. The two output boxes show the egg deposition (by sea age) and the stock-recruitment curve for a single simulation of 50 years of data. Similar outputs for the replacement line, and trends in rod catch, net catch and run size are available. Running this simulation a large number of times will enable the risks associated with different management activities to be assessed.

Two scenarios are illustrated: an unexploited fishery; and a fishery exploited to maximise gain. As expected, increasing the exploitation moves the fishery towards the left of the stock recruitment curve, but this model allows the affect to be quantified and the risks assessed.

2.9 Compliance assessment and management actions

The way in which compliance with targets is assessed will depend critically on a number of factors:

1. The management response to target failure. Will the response be different if failure is due to:
 - natural drifting of salmon populations (autocorrelation)
 - changes in rod or net exploitation
 - changes in marine survival or sea-age composition (replacement line)
 - changes in freshwater productivity (stock-recruitment curve)?

The final two causes of a change in escapement will be accompanied by a change in the target (see above) i.e. the “goal-posts” of the compliance scheme may be changing. For example, the changes in egg deposition for the River Bush (Figure 2.12) could be interpreted as:

- autocorrelated drift about an equilibrium (target remains constant)
- a shift in the equilibrium position to the right in the late 1980s due to changes in the replacement line (maximum gain target would change)
- a shift in the equilibrium position to the right in the late 1980s due to changes in freshwater exploitation (maximum gain target remains constant)
- a shift in the equilibrium position to the right in the late 1980s due to changes in the stock-recruitment curve (maximum gain target may change)

2. The type of target (e.g. maximum gain) that will be used.

3. The type of compliance scheme:

- Benefit-of-doubt (compliance statistics must be significantly worse than target to fail)
- Fail-safe (compliance statistics must be significantly greater than target to pass)
- Face-value (no account is taken of uncertainty in the compliance statistics)

4. The frequency of assessment

5. The method used to obtain egg deposition data (from rod catch)

6. The method used to transport targets.

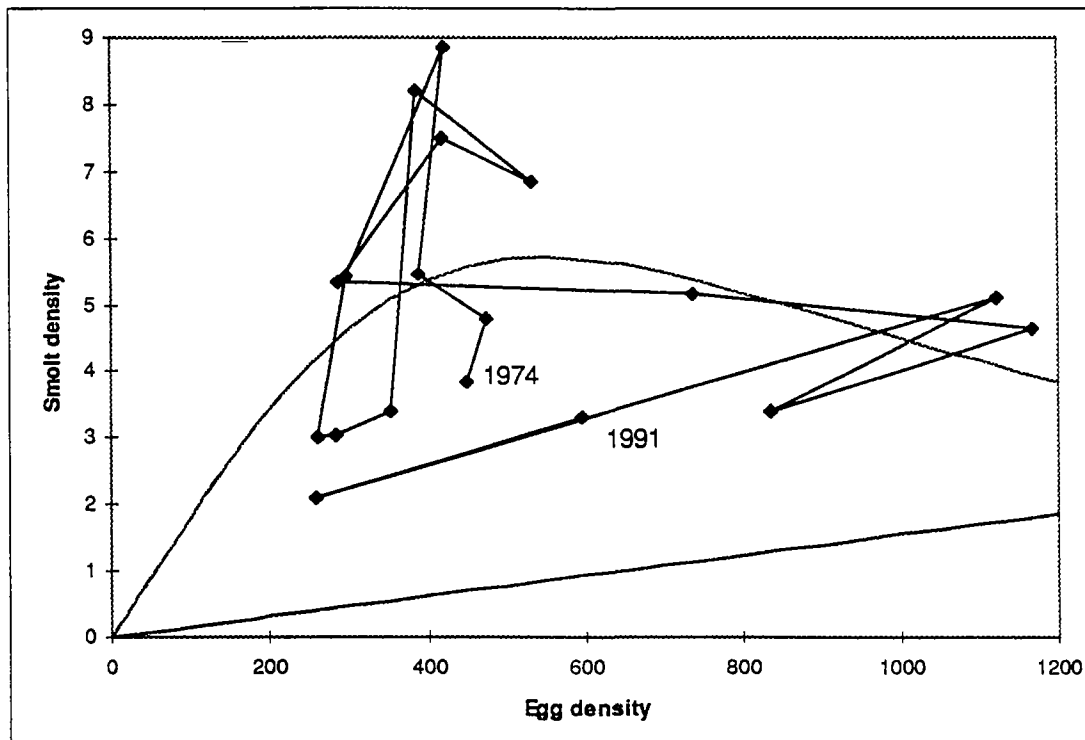


Figure 2.12 Time series of stock-recruitment data for the River Bush, for the period 1974 to 1991. The stock-recruitment curve and replacement line are also shown

Considerable work is still required to resolve some of these issues.

3. AVAILABILITY OF DATA AND FACILITIES FOR THE DEVELOPMENT OF STOCK RECRUITMENT RELATIONSHIPS

3.1 Introduction

The following sections outline the availability of data and facilities within the Agency for the derivation of salmon stock-recruitment relationships. The data were derived from discussions with selected contacts within each of the (former) NRA Regions (see Table 3.1, below). Whilst the following sections indicate the general nature and extent of available information, it is not intended that they should be exhaustive. Consequently, it may be that further facilities or archives of data (for example from R&D work within the Regions) may be available.

Table 3.1 Regional contacts

Region	Contact
(former) Northumbria	Karen Miller
North-West	Miram Aprahamian
(former) South-West	Kelvin Broad
Welsh	Alan Winstone
(former) Yorkshire	Stephen Axford

3.2 Electric fishing surveys (juvenile salmon population estimates)

The following table (Table 3.2, overleaf) outlines the availability of electrofishing data within key regions of the (former) NRA. This listing is restricted to those sites which are able to offer a time series of data over three or more years.

Table 3.2 Extent of available electric fishing data

Region	River / system	Number of sites with time series of data	Number of years or period covered
N'thm & Yorks	Aln - main river	4	≥ 3 years ¹
N'thm & Yorks	Coquet - main river	6	≥ 3 years ¹
N'thm & Yorks	Coquet - tributaries	4	≥ 3 years ¹
N'thm & Yorks	Wansbeck - main river	1	≥ 3 years ¹
N'thm & Yorks	Wansbeck - tributaries	1	≥ 3 years ¹
N'thm & Yorks	North Tyne - main river	6	≥ 3 years ¹
N'thm & Yorks	North Tyne - tributaries ²	2	≥ 3 years ¹
N'thm & Yorks	South Tyne - main river	3	≥ 3 years ¹
N'thm & Yorks	Wear - main river	8	≥ 3 years ¹
N'thm & Yorks	Wear - tributaries	3	≥ 3 years ¹
N'thm & Yorks	Tees - main river	3	≥ 3 years ¹
N'thm & Yorks	Tees - tributaries	5	≥ 3 years ¹
N'thm & Yorks	Esk ⁵	≥4	1979-94
North-West	St John's Beck	6	1987-94
North-West	River Glenderamackin	4	1989-94
North-West	River Caldew		
North-West	River Lune	4	1981-85 & 1988-90
South-Western	Lyd catchment	~25	~10 years
South-Western	Medland Brook ³	4	3 years
South-Western	Hookmoor Brook ³	2	3 years
South-Western	East Okement ³	2	3 years
Welsh ⁴	Clwyd	3	1986-93
Welsh ⁴	Conwy	17	1986-93
Welsh ⁴	Dee	4	1986-94
Welsh ⁴	Dyfi	3	1987-94
Welsh ⁴	Wye	6	1984-94
Welsh ⁴	Teifi	6	1987-94
Welsh ⁴	Tywi	3	1986-94

¹: Sites included refer only to those sites with ≥3 consecutive years of data from the past four years

²: May be additional data for a few (i.e. 4 or 5) sites procured in respect of the Kielder reservoir project

³: Tributaries within the Torridge catchment

⁴: All Welsh sites listed have associated habitat (HABSCORE) data available

⁵: Following an initial catchment-wide survey in 1979, at least 12-14 sites have been surveyed on the River Esk per year; latterly (since 1989) approximately four of these surveys have been fully quantitative; the remainder being semi-quantitative

3.3 Smolt trap data

Table 3.3 outlines the extent of downstream (smolt) trapping facilities throughout the Agency. Such data could be used in conjunction with data from upstream (adult) traps (where such facilities exist - see Section 3.4) to derive relationships between potential egg deposition and smolt output from any given river system. However, in many cases the quality of data collected is inadequate for this purpose and the cost of improvement is likely to be considerable.

Table 3.3 Availability of smolt trapping facilities and data

Region	River	Location	Years recorded	Months of operation
N'thm & Yorks	Coquet	Warkworth ¹	1984-9 ²	May
N'thm & Yorks	- ditto -	- ditto -	1993-present ³	March-June
N'thm & Yorks	Esk		1979-83, 1985, 1991-2, 1994	April-May
N'thm & Yorks	Ure	Mickley	1967-present ⁴	April-May
N'thm & Yorks	Wear	Durham	1984-91 ²	May
N'thm & Yorks	- ditto -	- ditto -	1992-present ³	March-June
North-West	Leven	-	Not yet operational	-
North-West	Kent	-	- ditto -	-
South-Western	Axe	Bottom of system	? 1959-1976 ⁵	-
South-Western	Tamar	Bottom of Wolf system ⁶	1986-1993	-
South-Western	- ditto -	Bottom of Thrushel system ⁶	1986-1993	-
South-Western	Frome	East Burton	1981 ⁷	-
Southern	Test	Romsey	1992-present ⁸	-
Southern	- ditto -	Nursling Mill	- ditto - ⁸	-

¹: Trap believed to be inefficient and size-selective

²: Operated by MAFF

³: Operated by Agency

⁴: Annual to 1981 - subsequently sporadic: available data only likely to cover 1987, 1990 & 1993

⁵: Former MAFF study facility; no longer operable

⁶: Data felt to be unreliable due to frequent 'overtopping' of traps by high river levels

⁷: Fixed eel trap used for smolt capture in 1981. Trap is operable but currently out of service

⁸: Both partial traps, each covering only one of several river channels

Welsh Region have indicated that there are no smolt trapping facilities that may be the source of potentially useful information.

3.4 Adult traps

As discussed above, data from upstream (adult) traps can be used in conjunction with data from downstream (smolt) traps to derive stock recruitment curves, providing that assumptions are made regarding the egg deposition rate of the upstream migrants.

However, with the exception of the trapping facilities on the Tamar system (in the former South-West Region), the upstream traps which are operational within the Agency (see Table 3.4) are not associated with downstream traps.

Table 3.4 Availability of adult trapping facilities and data

Region	River	Location	Years of operation	Notes
North-West	Caldew	Nr Carlisle	1992-94	-
North-West	Lune	Forge Weir, u/s Lancaster	1993-94	-
North-West	Ribble	Waddow Hall	1994	-
South-Western	Tamar	Gunnislake	1989-93	-
South-Western	Tamar system	Bottom of Wolf system ¹	1986-93	-
South-Western	- ditto -	Bottom of Thrushel system ¹	1986-93	-
Southern	Test	Romsey	1995	Only intermittent data ²
Welsh	Tawe	Panteg Weir	1990-94	April to November
Welsh	Taff	Blackweir	1991-94	April to December ³
Welsh	- ditto -	Radyr	1990-94	May/July to December ⁴
Welsh	Dee	Chester Weir	1991-94	All year

¹: Data felt to be unreliable due to frequent 'overtopping' of traps by high river levels

²: Operation severely limited due to weed-cutting activities; trap covers only one of several channels that may be used by ascending fish

³: July to January in 1991; April to November in 1992

⁴: September to December in 1990; May to December in 1991 & 1994; June to December in 1993; July to December in 1992

There are no adult (upstream) traps currently in operation in Northumbria and Yorkshire Region.

3.5 Counter data

Fish counter data may be used in lieu of upstream trapping data to estimate adult stock size. Counter facilities are, or have been, operated on many rivers throughout the regions (see Table 3.5) suggesting that data on potential levels of egg deposition may be derived for a wider range of rivers than could be achieved from upstream trapping data.

Table 3.5 Availability of fish counter facilities and data

Region	River	Location	Period of operation	Notes
N'thm & Yorks	Coquet	Warkworth	Jan.1993-present	Situated within fish pass
N'thm & Yorks	- ditto -	- ditto -	Aug.1993-present	- ditto -
N'thm & Yorks	Wear	Durham	Oct.1994-present	- ditto -
N'thm & Yorks	Main Tyne	Rising Mill	-	Proposed for 1995
N'thm & Yorks	North Tyne	Chollerford	-	Proposed for 1995
N'thm & Yorks	Tees	Tees barrage	-	Not yet operational
N'thm & Yorks	Wear	Framwellgate	-	Present but not operated
North-West	Calder	-	-	-
North-West	Derwent	Yearl	-	-
North-West	Kent	Basinghyll	-	-
North-West	Leven	Backbarrow	-	-
North-West	Lune	Broadrairie	-	-
North-West	- ditto -	Forge Weir	-	-
North-West	Ribble	Waddow Weir	-	-
North-West	- ditto -	Locks Weir	-	-
North-West	- ditto -	-	-	-
North-West	Wyre	Garstang	-	-
South-Western	Tamar	Gunnislake	1993-present	Replaced original upstream trap
South-Western	Fowey	Restormel	-	Not yet operational
Welsh	Afan	-	n/a	Fails to provide accurate counts
Welsh	Conwy	Conwy Falls	1994 - present	-
Welsh	Dee	Manley Hall	1978 - 1991	Non-operational since 1991
Welsh	Usk	-	1989 to 1994	Two months of data missing (1991)
Southern	Arun	Hardham	1995-present	-
Southern	Itchen	Gators Mill	1991-present	Earlier data available but reliable only post-1991
Southern	Ouse	Barcombe	Proposed : not yet installed	-
Southern	Test	Nursling Mill	1991-present	Earlier data available but reliable only post-1991
Southern	- ditto -	Conegar Bridge	1991-present	Earlier data available but reliable only post-1991

3.6 Redd count data

Attempts have been made to estimate the numbers of spawning salmon from redd counts (e.g. Hay, 1987). Such counts may therefore be used as a surrogate for more direct estimates of the number of spawning salmon ascending a system. The availability of redd count data throughout the former NRA is given in Table 3.6.

Table 3.6 Availability of redd count data

Region	River / system	Number of years or period covered	Notes
N'thm & Yorks	Aln	1985-1994	Excl. 1989
N'thm & Yorks	Coquet	1986-1994	Excl. 1988 & 1989
N'thm & Yorks	North Tyne	1980-1994	-
N'thm & Yorks	South Tyne	1980-1994	-
N'thm & Yorks	Tees	1985-1994	Excl. 1986, 1989 & 1990
N'thm & Yorks	Wear	1978-1994	Excl. 1981, 1989 & 1990
North-West	N.Cumbria ¹	1974-85 ⁵	Excl. 1979
North-West	W. & SW.Cumbria ²	1974-92	Excl. 1979, 1984 & 1986
North-West	S.Cumbria & N.Lancs. ³	1974-92	Excl. 1984
North-West	Lancs ⁴	1981-92	Excl. 1984
South-Western	Lyd catchment	~10 years	Ties in with juvenile surveys
Welsh	Wye	1984 to 1994	Additional data available ⁶

¹: **North Cumbria Rivers:** Eden (d/s Eden Groves; d/s Eden Brow; d/s Temple Sowerby & u/s Temple Sowerby); Eamont; Lowther; Irthing; Gelt; Border Esk; Black and White Esk; Liddel; Lyne.

²: **West and South-West Cumbria Rivers:** Ellen; Derwent; Marron; Cocker; Greta; Ehen; Calder; Irt; Bleng; Esk; Mite; Annas.

³: **South Cumbria and North Lancashire Rivers:** Duddon; Crake; Leven; Eae; Winster; Gilpin; Kent (and tribs.); Bela; Keer; Lune; Rawthey; Dee; Greta; Wenning; other Lune tribs.

⁴: **Lancashire Rivers:** Ribble; Hodder; Wyre.

⁵: Some data also available for 1989-91

⁶: Additional data for the period prior to 1984 has been recorded, although it may well be less readily available

Northumbria Region: data collation prior to 1992 is known to have been very inconsistent and has consequently been described as being 'unreliable'. In addition, the introduction in 1992 of a new standard procedure for redd counting means that data obtained by following the new procedure cannot be used for comparison studies with pre-1992 data. It is hoped that the new programme should facilitate the collation of more consistent data, which will ultimately provide reliable information on the status of salmon stocks.

North-West Region: the quality of the redd count data available varies according to the flow conditions prevailing at the time of surveying (high flows and turbid waters making counting difficult or impossible); in addition, the differentiation between salmon and sea-trout redds is not clear.

3.7 Data applications

Recommendations regarding the use of fisheries data derived from the sources outlined above are covered in Section 6.

4. USE OF HABITAT MODELS

4.1 Introduction

The objective of this section is to investigate the use of habitat models to predict site and river specific carrying capacities for juvenile salmonids and evaluate and attempt to develop methods to derive ova deposition optima from these. Section 4.2 discusses how habitat models can be used to predict site-specific carrying capacity, and Section 4.3 considers the role of habitat models in determining the carrying capacity of an entire river system. Section 4.4 exploits the link between habitat models and stock-recruitment curves to discuss deriving spawning targets from habitat models.

4.2 Use of habitat models to predict site-specific carrying capacity

4.2.1 Relationship between S-R and survival

To understand the relationship between carrying capacity and habitat models, it is useful to recognise the relationship between the survival curve and stock-recruitment curve. The stock-recruitment curve represents two points on a survival curve.

Consider, for example, the Beverton-Holt stock-recruitment model:

$$R = \frac{1}{a + b/S}$$

where S is stock,

R is recruitment, and

a and b are parameters.

The equation for a survival curve where the mortality rate at any moment in time is linearly related to the density of fish present is:

$$d_t = \frac{1}{at + 1/d_0}$$

where:

t is the time elapsed from time 0;

d_t is the density present at time t;

d_0 is the density at time 0, and

a is a parameter.

If t is held constant (for example, we are interested only in the density of fish remaining after 2 years from birth), then it can be seen that the relationship between d_t and d_0 follows a Beverton-Holt stock recruitment curve with $b = 1$.

The relationship between the stock recruitment curve and survival curve is also illustrated in Figure 4.1. Survival curves run from back left to front right, with starting densities from 0 to 200 (arbitrary units). Beverton-Holt-type stock-recruitment curves run from front left to back right, covering the range of stock levels 0 to 200. If the stock-recruitment curve is considered early in the life of the fish, it is close to a straight line (which will approximate to 45° if stock and recruits are both presented at the same scale, and the mortality rate is close to zero). As time progresses, the stock recruitment curve develops its characteristic flat top. The same information is given in Figure 4.2, which represents only three points in time.

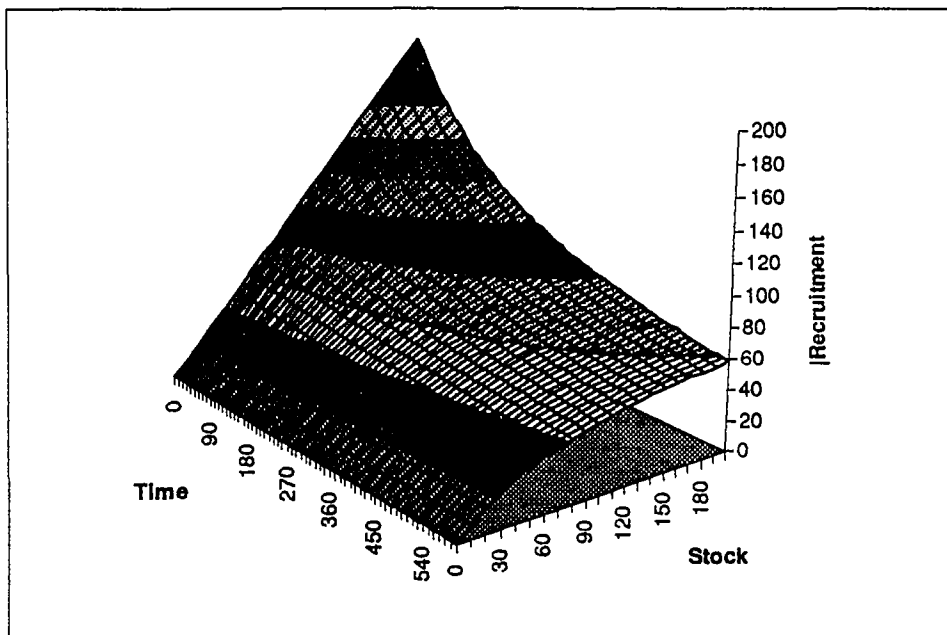


Figure 4.1 Relationship between stock-recruitment curve and survival curve

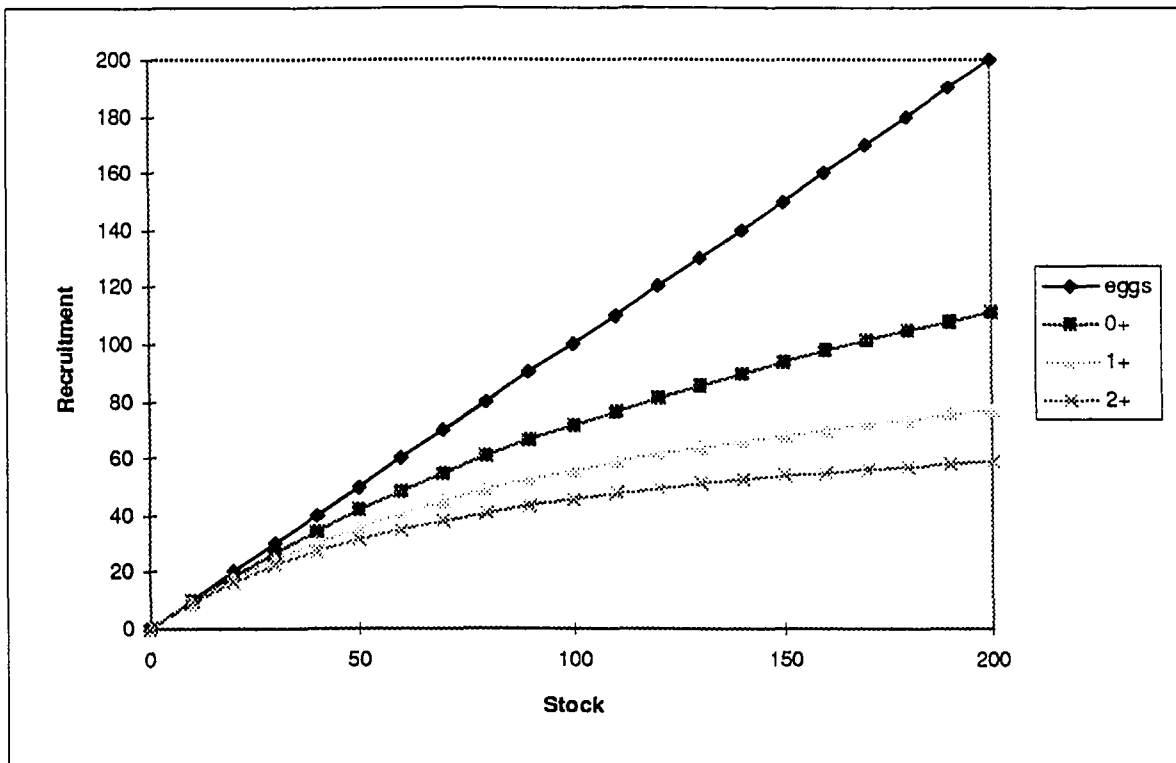


Figure 4.2 Stock-recruitment curves for three stages in the salmon life cycle: egg to 0+; egg to 1+ and egg to 2+

It was stated in Section 2 that stock-recruitment curves based on different life stages are not comparable. Thus it is not possible to simply compare an egg to smolt curve with a summer 0+ to pre-smolt curve. One way to deal with this is to develop a model of survival from egg to smolt, and use the model to extrapolate from one stock-recruitment curve to another.

4.2.2 Definition of carrying capacity

There are a number of possible definitions of carrying capacity, many along the line of “the population density that the environment can support on a continuing, steady-state basis”. One important criterion is whether the definition refers to the existing environment, or the potential of the environment. For example, if a salmonid stream has excellent instream habitat quality, yet the water quality is constraining the population due to anthropogenic influences, then definitions of carrying capacity could relate to the existing environmental conditions, or the conditions that would prevail if the water quality was improved to the extent that it was not limiting. Similar arguments apply to the physical habitat.

Four potential definitions of carrying capacity are shown in Table 4.1. An important difference between an estimate of the carrying capacity defined by a habitat model (such as HABSCORE - Milner *et al.*, 1993) and one obtained from a stock-recruitment curve is that the habitat model predicts the abundance for “pristine” water quality (Definition C) whereas the stock-recruitment curve reflects the current status of the river (Definition A).

Table 4.1 Four possible definitions of carrying capacity

	Existing habitat	Habitat after restoration
Existing water quality	A (S-R Curve)	B
Water quality after restoration	C (HABSCORE)	D

In all of these definitions, it would normally be assumed that recruitment is not limiting, for example, it would be assumed that salmon have access to the site.

4.2.3 Relationship between stock recruitment curve and carrying capacity

The relationship between the carrying capacity and the stock-recruitment curve will depend on what curve is being assumed:

1. **Ricker curve.** For this model, the maximum smolt production occurs at intermediate egg densities; at high egg densities, the river will be below carrying capacity.
2. **Beverton-Holt curve.** This stock-recruitment curve has an asymptote, and at egg deposition levels that generate juvenile densities “close” to the asymptote, egg deposition could be considered not to be limiting.
3. **Cushing curve.** With this curve, juvenile densities continue to rise with increasing egg deposition, although the rate of increase declines. In theory, the smolt output is limited only by the egg density, and so the carrying capacity is difficult to define. Given current understanding of salmonid ecology this is not biologically realistic.

If one considers the Beverton-Holt stock recruitment curve and a population of fish where recruitment is not limiting, then the height of the curve would correspond to the long term average smolt output for the existing environmental conditions. The height of the stock-recruitment curve would therefore correspond to the carrying capacity defined in terms of the mean population level (in terms of smolt output) by A in Table 4.1.

For the Beverton-Holt stock-recruitment curve:

$$R = \frac{1}{a + b/S}$$

as S (Stock) becomes very large (i.e. not limiting) then b/S will become small, and so R (recruits) will become close to 1/a.

4.2.4 Relationship between HABSCORE and carrying capacity

Current HABSCORE models predict the long-term average densities of 0+ and >0+ salmon assuming that recruitment and water quality are not limiting. This is known as the Habitat Quality Score (HQS) and would correspond to definition C of carrying capacity.

4.2.5 Relationship between HABSCORE and the stock-recruitment curve

When calibration sites for HABSCORE were selected, they were chosen such that recruitment was not thought to be limiting. Thus in terms of the stock recruitment curve, calibration sites occurred around the horizontal portion; in Figure 4.3 this is to the right of the vertical dashed line.

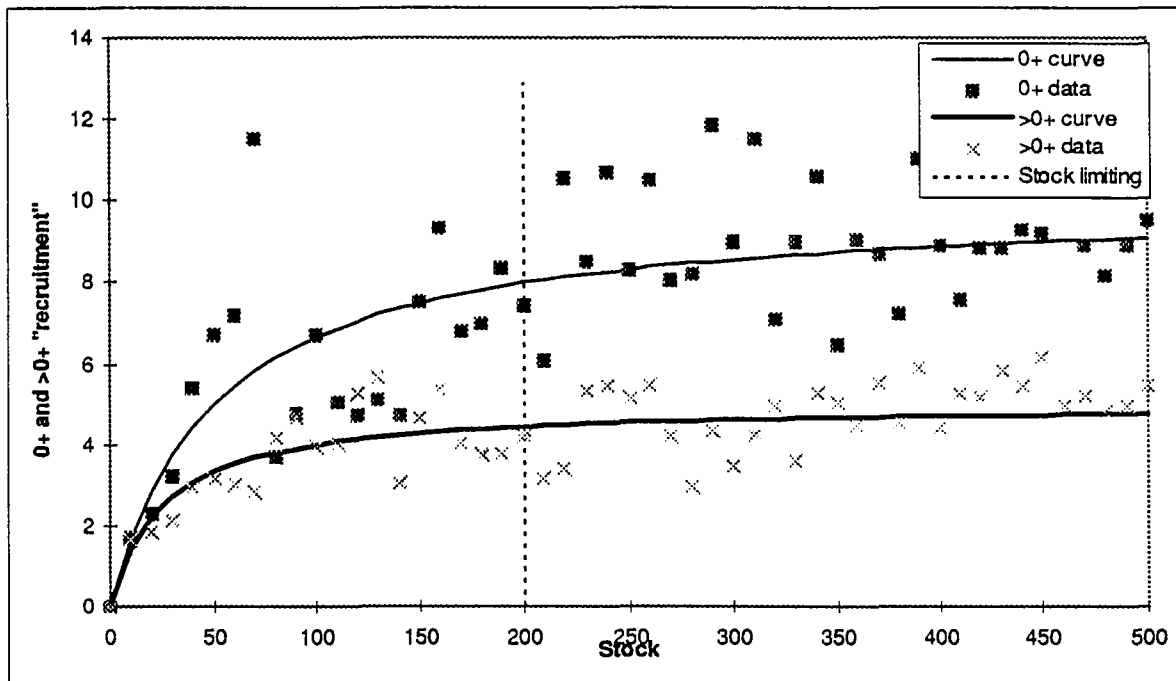


Figure 4.3 Simulated egg to 0+ and egg to >0+ stock recruitment curve for salmon. Sites operating to the right of the dotted line would qualify for inclusion into the HABSCORE calibration exercise

However, HABSCORE predicts the carrying capacity in terms of 0+ and >0+ densities, whereas the asymptote of the stock-recruitment curve is usually expressed as smolt densities. Given that most density dependent mortality occurs early in the life of a juvenile salmon, rivers which have high juvenile (0+, >0+ densities) are likely to have proportionally higher smolt output densities. Thus under conditions where water quality is not limiting, the HQS from HABSCORE (0+, >0+) is likely to be related to the height of the stock-recruitment curve (1/a for a Beverton-Holt curve). If a dome-shaped curve is believed to be operating, then HABSCORE calibration sites may have had egg deposition densities higher than those that produce the maximum smolt production, and were therefore below carrying capacity.

The assumption that recruitment is not limiting is even more complex for the older age classes. Consider a site with poor 0+ habitat but good >0+ habitat. If egg deposition was not limiting 0+ numbers (but habitat was), then the numbers of 0+ may be limiting the number of >0+. Three issues require consideration here:

- the influence of high egg densities on juvenile densities in the HABSCORE calibration sites if a dome-shaped stock-recruitment curve was operating;

- the spatial relationships between habitat types within a catchment, and the degree to which juvenile salmon move within a catchment; and
- the degree to which the presence of poor 0+ habitat may have been limiting >0+ numbers in some of the HABSCORE calibration sites.

The exact interpretation of the outputs of HABSCORE in relation to the stock-recruitment curve are complex and require further consideration (see also Section 4.4). The main features are summarised in Table 4.2.

Table 4.2 Relationship between HQS (HABSCORE) and the height of a stock-recruitment curve

	HQS from habitat model		Height of stock-recruitment curve
Units	Long-term average densities (0+, >0+)	parr	Average smolt output per unit area
Assumptions regarding egg deposition	Not limiting juvenile densities		Not limiting smolt output
Assumptions regarding water quality	Predicts densities that would be present if water quality not limiting.		Based on observed densities and existing water quality

4.3 Use of habitat models to predict river-specific carrying capacity

4.3.1 Introduction

The problems with relating the outputs from HABSCORE to carrying capacity at a single site discussed above also apply to predicting the carrying capacity for a river reach.

Three approaches to estimating carrying capacity for a river system are described in this section:

- by using catchment-specific habitat models (Section 4.3.2);
- by using catchment-specific habitat models to aggregate site-specific habitat models (Section 4.3.3);
- by using catchment-specific habitat models to aggregate survey data (Section 4.3.4).

4.3.2 By using catchment-specific habitat models

To illustrate how catchment-based models could be utilised to predict river-specific carrying capacities, a preliminary methodology is illustrated here. This will also be used in the development of models for rod and net catch (Section 5). The following method utilises HABSCORE data plus additional data from larger Northumbrian rivers (1:50,000), Agency River Habitat Survey (RHS) data (1:625,000) and GIS data (1:250,000).

The steps used are:

- a) Definition of river types and estimation of section lengths;
- b) Habitat modelling using GIS data;
- c) Application of models to river system.

In addition, it was necessary to relate stream orders from 1:50,000 maps to those from 1:250,000 GIS (Appendix F) and to estimate stream widths from 1:250,000 stream orders (Appendix G). These procedures are very approximate, and are only included in this report to illustrate the steps a) to c) below.

Definition of river types and estimation of section lengths

To assess the carrying capacity of a river system, it is necessary to first have some form of description of the catchment in terms of its size and character in relation to the habitat requirements of juvenile salmon. The Agency R&D programme includes a project to “develop and map stream habitats”, and this may provide the basis of techniques relevant to setting and assessing compliance with spawning targets. For this illustrative exercise, the most readily available measure of the size of a river system was from a low-resolution (1:250,000) Geographic Information System (GIS).

The data available for each river reach are shown in Table 4.3, with details of altitude class in Table 4.4. Reach boundaries occur at confluences and altitude class boundaries.

Table 4.3 Data available from GIS

Data	Comments
Stream Order	Strahler, as measured on a 1:250,000 map
Link Number	Shreve, as measured on a 1:250,000 map
Altitude class	Defined in Table 4.2
Cartographic class	Not considered further

Table 4.4 Definition of altitude classes available from GIS

Altitude class	Altitude (m)
1	Sea
2	Below sea level
3	0-50
4	50-100
5	100-150
6	150-200
7	200-300
8	300-400
9	400-500
10	500-600
11	600-700
12	700-800
13	800-900
14	900-1000
15	1000-1100

To illustrate the type of information available, data for the River Dee, North Wales is given (overleaf) in Table 4.5.

Not all of this river would be necessarily be accessible to migratory salmonids. Given the grid references of impassable falls or barriers, it would be possible to recalculate the length or area available for salmonids, however it was not possible to do this within the constraints of this project.

Table 4.5 Total length (m) of river of different stream order and altitude class for the River Dee (900 sections), North Wales

Altitude	Stream order					Total
	1	2	3	4	5	
0-50	75443	85222	24249	11676	2030	198621
50-100	38027	31161	20531	0	0	89718
100-150	32194	29118	2067	17096	0	80474
150-200	55613	9171	2658	9082	0	76524
200-300	96711	43096	769	0	0	140576
300-400	95201	10947	0	0	0	106148
400-500	29484	373	0	0	0	29857
500-600	7280	0	0	0	0	7280
600-700	559	0	0	0	0	559
	430512	209088	50273	37854	2030	729759

Habitat modelling using GIS data

In the extended HABSCORE database (i.e. including Northumbrian large river sites), data was available for the density of 0+ and >0+ salmon. Carrying capacity for this exercise was defined in terms of the >0+ fish.

A simple model relating >0+ salmon densities to altitude and stream order was developed, and the results are shown in Table 4.6 and Table 4.7. It must again be stressed that this model predicts carrying capacity given that water quality is not limiting.

Table 4.6 Model relating >0+ salmon density to altitude and stream order based on HABSCORE data set

	estimate	s.e.	t (212)
Constant	2.052	0.121	16.94
(stream order - 3.37) ²	-0.1877	0.0657	-2.86
altitude - 141.9	0.00598	0.00117	5.13
(altitude - 141.9) ²	-0.0000208	0.0000120	-1.73
stream order - 3.37	0.0742	0.0838	0.89

Table 4.7 Accumulated analysis of variance for model relating >0+ salmon density to altitude and stream order

Change	d.f.	s.s.	m.s.	v.r.	F pr.
+ (stream order - 3.37) ²	1	24.993	24.993	17.68	<.001
+ altitude - 141.9	1	32.773	32.773	23.18	<.001
+ (altitude - 141.9) ²	1	5.131	5.131	3.63	0.058
+ stream order - 3.37	1	1.109	1.109	0.78	0.377
Residual	212	299.698	1.414		
Total	216	363.704	1.684		

Note: Percentage variance accounted for was 16.0%.

Application of models to river system

The models can then be applied to the different combinations of altitude and stream order available from GIS (Table 4.8), and the applied to any river system by multiplying the model outputs by the river size (Table 4.9). All four terms in the model were used to construct these tables.

Table 4.8 Predictions for >0+ salmon densities (100m²) for different altitude classes and stream order

Altitude class	Stream Order					
	1:250,000	1	2	3	4	5
	1:50,000	1.3038	2.5153	3.7268	4.9383	6.1498
0-50		1.1	2.4	2.9	2.1	0.8
50-100		1.8	3.9	4.8	3.4	1.4
100-150		2.7	5.7	7.0	5.0	2.0
150-200		3.6	7.6	9.3	6.6	2.7
200-300		4.5	9.5	11.7	8.2	3.4
300-400		4.2	9.0	11.0	7.8	3.2
400-500		2.6	5.6	6.8	4.8	2.0
500-600		1.1	2.3	2.8	2.0	0.8
600-700		0.3	0.6	0.8	0.5	0.2
700-800		0.1	0.1	0.1	0.1	0.0
800-900		0.0	0.0	0.0	0.0	0.0

Table 4.9 Predictions of >0+ salmon numbers for the River Dee

Altitude class	Stream Order						
	1	2	3	4	5		
0-50	1,744	4,207	3,487	16,161	1,995	27,594	17%
50-100	3,402	6,007	3,580	5,056	-	18,046	11%
100-150	4,700	12,642	2,926	14,151	-	34,418	21%
150-200	8,533	9,092	7,714	6,943	-	32,282	19%
200-300	18,886	8,907	2,610	108	-	30,512	18%
300-400	14,379	5,887	-	-	-	20,266	12%
400-500	3,334	-	-	-	-	3,334	2%
500-600	383	-	-	-	-	383	0%
600-700	24	-	-	-	-	24	0%
700-800	4	-	-	-	-	4	0%
800-900	-	-	-	-	-	-	0%
	55,389	46,741	20,316	42,419	1,995	166,861	
	33%	28%	12%	25%	1%		

There is a large degree of uncertainty in these estimates. Much of this will come from the model that predicts the densities, which could be estimated, but the inaccuracies in estimating stream areas will also be important. Confidence limits for these estimates are not required for the map (below) or the rod catch model (Section 5) and so are not shown here.

By relating this model back to the GIS information, >0+ salmon habitat quality as defined by this model of stream order and altitude can be mapped. A map of the Dee produced in this manner is given as Figure 4.4.

4.4 Derivation of ova deposition optima from habitat models

4.4.1 Introduction

It has been argued in previous sections that the HQS produced by HABSCORE is closely related to the height of the stock-recruitment curve providing:

- smolt output is related to 0+ and >0+ densities; and
- water quality is not limiting the height of the stock-recruitment curve.

It has also been demonstrated that differences in the height of a river-specific stock-recruitment curve (Section 2.6.1) or the relative proportion of habitat types each with its own stock-recruitment curve (Section 2.6.2) can be used to transport targets from one river to another.

It follows that the output from habitat models can be used to adjust targets for differences in carrying capacity (as measured by the model) as they are transported from donor to recipient rivers. Current habitat models tell us nothing about the shape of the stock-recruitment curve (dome / flat-topped) or the rate of ascent of the curve, only the height. Thus when using habitat models to transport a target, it must either be assumed that these components (along with the replacement line) stay constant, or they are also adjusted using recipient-river-specific information.

4.4.2 The relationship between juvenile densities and smolt output

Habitat models such as HABSCORE predict the density of 0+ and >0+ salmon, whereas the y-axis of the stock-recruitment curve from which targets are derived are expressed in terms of smolt output per unit area. To use habitat models to predict the height of the stock-recruitment curve, it is therefore necessary to convert from units of juvenile density to smolt output.

If one considers a stretch of river with uniform habitat, and assumes that the density dependent survival in each year is different, the survival process can be thought of as a chain of stock-recruitment curves. Once again, the Beverton-Holt curve will be used to illustrate the point, but the arguments would equally apply to any stock recruitment model.

Consider the 3 years from egg to final smolt output, and using subscripts $i = 1, 2$ and 3 to denote the three years, the following terms are defined:

p_i	Proportion of individuals smolting after i years
q_i	Proportion of individuals remaining after i years ($= 1 - p_i$)
HQS_i	Habitat Quality Score from habitat model for age class i
b_i	Parameter b of Beverton-Holt stock recruitment curve in year i (≥ 1)
e	Initial egg deposition
s_i	Smolt output in year i

By regarding the output from the stock-recruitment model for the first year as the input to the stock-recruitment curve for the second year, it can be shown that the stock-recruitment curve for any age of smolt (from e to s_i) is:

$$s_i = \frac{1}{a_i + \frac{b_i}{e}}$$

where:

$$a_1 = \frac{1}{p_1 HQS_1}$$

$$a_2 = \frac{1}{p_2 HQS_2} + \frac{b_2}{q_1 p_2 HQS_1}$$

$$a_3 = \frac{1}{p_3 HQS_3} + \frac{b_3}{q_2 p_3 HQS_2} + \frac{b_2 b_3}{q_1 q_2 p_3 HQS_1}$$

$$b_1 = \frac{b_1}{p_1}$$

$$b_2 = \frac{b_1 b_2}{q_1 p_2}$$

$$b_3 = \frac{b_1 b_2 b_3}{q_1 q_2 p_3}$$

These equations describe stock-recruitment curve in terms of the habitat quality for different ages of fish, and offer the potential for deriving ova deposition optima from habitat models.

To illustrate the process using a simple example, assume that all smolts leave the river after 3 years, i.e.

$$p_1=0, q_1=1$$

$$p_2=0, q_2=1$$

$$p_3=1, q_3=0$$

This gives:

$$s_1=0,$$

$$s_2=0$$

and:

$$s_3 = \frac{1}{a_3 + \frac{b_3}{e}}$$

where:

$$a_3 = \frac{1}{HQS_3} + \frac{b_3}{HQS_2} + \frac{b_2 b_3}{HQS_1}$$

and:

$$b_3 = b_1 b_2 b_3 .$$

In terms of targets, we then obtain:

$$\text{Maximum gain} = \frac{\sqrt{b_1 b_2 b_3 \beta} - b_1 b_2 b_3}{\frac{b_2 b_3}{HQS_1} + \frac{b_3}{HQS_2} + \frac{1}{HQS_3}}$$

where β is the replacement value (eggs/smolt), and also:

$$\text{Maximum smolt output} = \frac{1}{\frac{b_2 b_3}{HQS_1} + \frac{b_3}{HQS_2} + \frac{1}{HQS_3}}$$

Using some illustrative values, we obtain a range of smolt outputs and maximum gain targets varying with the habitat quality (Table 4.10 - overleaf).

Table 4.10 Maximum smolt output and egg deposition targets generated from a model of juvenile salmon survival and habitat quality

b_1, b_2, b_3	β	HQS ₁	HQS ₂	HQS ₃	max smolt output	egg deposition target (max gain)
	(eggs/smolt)				(/100m ²)	(/100m ²)
3	1000	200	100	10	8.7	785
3	1000	200	100	5	4.7	499
3	1000	200	50	10	8.0	670
3	1000	200	50	5	4.4	450
3	1000	50	100	10	7.7	443
3	1000	50	100	5	4.3	335
3	1000	50	50	10	7.1	404
3	1000	50	50	5	4.2	312

We therefore have a stock-recruitment model that has aggregated three age-specific models together (egg to 0+, 0+ to 1+ and 1+ to 2+), and utilised the outputs from a habitat model to generate three of the six parameters required. The resulting age-aggregated stock-recruitment model can be used to estimate target egg deposition levels.

This method does not rely solely on habitat models, and requires other information regarding the dynamics of juvenile and adult stages. There are many assumptions and simplifications, and this should be regarded only as an initial attempt at combining habitat models and stock-recruitment curves, and the basis for further development. Some of the issues regarding the interpretation of HQS as a carrying capacity, as is assumed in the above models, were discussed in Section 4.2.4.

The use of age-aggregated stock-recruitment curves (perhaps driven by simple habitat models) discussed in this section, combined with the river-section-aggregated stock-recruitment models discussed in Section 2.6.2 provides the basis for a potentially useful target transportation system.

For such a system to be used as a working methodology would require a habitat inventory for rivers for which targets are going to be set. Habitat description may be qualitative descriptors (“main river”, “good tributary”, “poor tributary” for example), or based on simple habitat models derived from survey-, map- or GIS-derived parameters (Section 3.2). The primary objective for the further development of methodologies that generate egg deposition optima from habitat models should be to produce a workable methodology that can be utilised by Agency staff. Whilst this is likely to be simplistic at first, the assumptions and simplifications being made should be known and the consequences well understood.

5. FACTORS INFLUENCING BETWEEN-RIVER VARIATION IN ROD AND NET CATCH

5.1 Introduction

The objective of this section is to examine factors influencing between-river variation in rod and net catch (e.g. catchment size, chemical productivity, fishing effort) and attempt to develop models to predict expected catch and equivalent ova deposition optima for these.

5.2 Available data

5.2.1 Assessment of productivity

The quadratic model relating >0+ salmon density to altitude and stream order developed in Section 4 was used to give an index (S_i) of the suitability of different stream order and altitude combinations for salmon. For each catchment, estimated salmon density was combined with GIS estimates of river size to give an estimate of the total number of >0+ salmon in the catchment. This was used as an index of the productivity (smolt output) of the catchment.

5.2.2 Rod and net catch data

Changes in the licensing and reminder systems in recent years have resulted in large changes in angler returns. In addition, consistent effort data has not been published nationally until recently. For the purposes of this exercise, the data from 1993 will be analysed for spatial patterns to assess the feasibility of the approach outlined below.

The NRA salmon catch statistics for 1993 are given in Appendix D. The total declared rod catch (R_i) of salmon for the Wye, for example, was 798 ("Table 8"). Of the licences returned, 501 had effort data, reporting 8,565 days of fishing and a catch of 471 salmon ("Table 12"). It was assumed that the catch per unit effort was the same for anglers who declared effort as for those who did not. The total rod effort (r_i) on the Wye was therefore estimated as 14,511 days ($= 798 / 471 \times 8565$). The total net catch (N_i) was obtained from "Table 6" (Appendix D).

5.2.3 River size

The "catchability" of fish is likely to be a function of river size (w_i) at the location of the fishery. A number of possible indices of river size are available from GIS such as the maximum stream order or the total length of river. The latter was used in this exercise.

5.3 Form of model

The relationship between declared catch and run size is complex. Measures of catch or catch per unit effort within-season have been used as indicators of run size through time, however, in this application it is necessary to relate the spatial variation in catch to spawning escapement.

It would have been possible to use an empirical modelling approach. For example, a multiple regression approach could have been used to relate rod catch to river length and rod effort:

$$R = \alpha + \beta_1 l + \beta_2 r$$

where:

l is a measure of river length; and

r is rod effort.

Whilst such a model may have been successful in explaining variation, it would have been more difficult to interpret the model in relation to targets. It is believed that the best approach is to develop a model relating rod and net catch to spatial factors from theoretical considerations and calibrating the model from the data.

5.3.1 Relationship between catch and effort

There are a number of possible models relating catch to effort. The simplest is:

$$R_i = \delta r_i T_i$$

Where:

R_i = rod catch in the i th river

r_i = rod effort in the i th river, measured for example in number of licences, or rod days

T_i = number of salmon entering the river, and

δ = "catchability" of salmon.

This model may be satisfactory where exploitation rates are low, but where exploitation rates are high, it becomes unrealistic since an increase in effort (r_i) could result in the catch (R_i) exceeding the number of salmon present (T_i). A more realistic model in this instance would be:

$$R_i = T_i [1 - \exp(-\alpha r_i)]$$

Where:

α = “catchability” of salmon.

For low exploitation rates, this model behaves in a similar manner to the simple proportional model above. More complex models are available, but many have been developed to model the behaviour of catch and effort through time, rather than between rivers.

5.3.2 Relationship between “catchability” with river size.

When considering the use of rod catch to predict trends within one river, it may be sufficient to assume that the average “catchability” of salmon remains constant between years. One problem with spatial comparisons, however, is that “catchability” is likely to vary with river size. The simplest model is that “catchability” is directly proportional to a measure of river “size” (w_i), such as discharge or width at the location of the rod fishery.

This would modify the model relating catch to effort as follows:

$$R_i = T_i \left[1 - \exp\left(-\frac{\alpha r_i}{w_i}\right) \right]$$

where α is redefined as being relative to the river size (w_i), and would be assumed to be constant between rivers.

A slightly more complex model would assume that “catchability” is proportional to a power of river size, thus:

$$R_i = T_i \left[1 - \exp\left(-\frac{\alpha r_i}{w_i^y}\right) \right] \quad (1)$$

5.3.3 Smolt output

The index of productivity (Section 5.2.1) was derived from a GIS-based catchment model, and represents an index of productivity that assumes water quality and recruitment are not limiting. This will vary with catchment size, and also the productivity as measured by the relative proportion of different river types present in the catchment.

It would be possible to use a life-cycle model that would additionally correct for the reduction in smolt output in heavily exploited rivers. Such a model is considerably more complex, and is discussed further in Section 5.7.

5.3.4 Relationship between number of adults and number of smolts

The average number of adult salmon running up a river will be related to the smolt output (S_i) from the catchment. In the absence of river-specific data, a constant marine mortality has to be assumed.

$$T_i = \beta S_i$$

where:

S_i = index of total smolt output from the catchment; and

β = constant, relating to factors such as marine survival (this is the gradient of the replacement line).

It may be more realistic to assume that β varies according to the (j th) geographical region.

$$T_i = \beta_j S_i \quad (2)$$

where β_j = constant for the j th region.

An elaboration of this model would be to specifically include the declared net catch (N_i):

$$T_i = \beta_j S_i - N_i \quad (3)$$

This assumes that the net catch reported for a particular river represents fish that were destined to enter the rod fishery for that river. It is known that in some rivers, the net fishery exploits fish that are moving around the coast.

5.3.5 The final model

The models for rod and net catch are obtained by combining equations (1) and (3) and can be expressed in a number of ways, for example:

$$\frac{N_i + R_i}{S_i} = \beta_j - \left(\frac{R_i}{S_i} \right) \frac{\exp\left(\frac{-\alpha r_i}{w_i^\gamma}\right)}{1 - \exp\left(\frac{-\alpha r_i}{w_i^\gamma}\right)}$$

$$\frac{R_i}{S_i} = \left(\beta_j - \frac{N_i}{S_i} \right) \left(1 - \exp\left(\frac{-\alpha r_i}{w_i^\gamma}\right) \right)$$

$$\text{Log} R_i = \text{Log}(\beta_j S_i - N_i) + \text{Log} \left(1 - \exp\left(\frac{-\alpha r_i}{w_i^\gamma}\right) \right)$$

In the first two cases, the left-hand-side of the equation is divided by S_i in an attempt to stabilise variances. Logs are used in the third case for the same reason.

Note that in this model there are five variables (R_i , S_i , N_i , r_i and w_i), and at least three unknown parameters (α , β and γ).

5.4 Model calibration

5.4.1 Three parameter model, net catch ignored

The first model to be calibrated did not include net catch directly (i.e. the fish lost to the net fishery would be included in the estimate of β), and included only a single β . The logarithmic form of the model was found to be the most satisfactory:

$$\text{Log}R_i = \text{Log} \left(\left(1 - \exp \left(\frac{-\alpha r_i}{w_i^\gamma} \right) \right) \beta S_i \right) \quad \text{Model 1}$$

The analysis of variance for this model is given in Table 5.1.

Table 5.1 Analysis of variance for the three parameter model, net catch ignored

	d.f.	s.s.	m.s.	v.r.	Fpr.
Regression	3	1032.33	344.1084	486.63	<.001
Residual	49	34.65	0.7071		
Total	52	1066.97	20.5187		

The percentage variance accounted for was 69.2%, and the standard error of observations was estimated to be 0.841.

The estimates of α and β had very high standard errors (Table 5.2), and they are therefore very unreliable. The estimate of γ is somewhat better.

Table 5.2 Estimates of parameters for the three parameter model, net catch ignored

	estimate	s.e.
α	0.34	1.03
β	0.044	0.112
γ	0.761	0.128

In addition to the high standard errors, the estimates of parameters α and β have a very high negative correlation (Table 5.3). This means that from the catch statistics alone, it is difficult to distinguish between a high α (high catchability) with low β (small run size), or a low α (low catchability) with a high β (large run size). The γ parameter is relatively independent of α and β .

Table 5.3 Correlations between parameter estimates for the three parameter model, net catch ignored

	α	β	γ
α	1.000		
β	-0.877	1.000	
γ	0.477	0.001	1.000

5.4.2 Two parameter model, net catch ignored

The second model fitted assumed that γ had a known value of 0.761. This value was obtained from Model 1.

$$LogR_i = Log\left(\left(1 - \exp\left(\frac{-\alpha r_i}{w_i^{0.761}}\right)\right)\beta S_i\right) \quad \text{Model 2}$$

The parameter estimates and fit of the model were similar to the previous model (Tables 5.4 to 5.6).

Table 5.4 Analysis of variance for the two parameter model, net catch ignored

	d.f.	s.s.	m.s.	v.r.	Fpr.
Regression	2	1032.33	516.1626	744.85	<.001
Residual	50	34.65	0.6930		
Total	52	1066.97	20.5187		

The percentage variance accounted for was 69.8%, and the standard error of observations was estimated to be 0.832.

Table 5.5 Estimates of parameters for the two parameter model, net catch ignored

	estimate	s.e.
α	0.338	0.898
β	0.044	0.109

Table 5.6 Correlations between parameter estimates for the two parameter model, net catch ignored

	α	β
α	1.000	
β	-0.999	1.000

5.4.3 Four parameter model, net catch ignored

The model was refined by fitting individual values of β for each of the three regions as discussed in Section 5.3.4 (South West, North West and Northumbrian).

$$\text{Log}R_i = \text{Log} \left(\left(1 - \exp \left(\frac{-\alpha r_i}{w_i^{0.761}} \right) \right) \beta_j S_i \right), j = 1, \dots, 3 \quad \text{Model 3}$$

The addition of the (region x β) interaction term, allowing β to vary between the three regions, gives a highly significant improvement to the model (Table 5.7).

Table 5.7 Analysis of variance for the four parameter model, net catch ignored

	d.f.	s.s.	m.s.	v.r.	Fpr.
Regression (α, β)	2	1032.33	516.1626	744.85	<0.001
+ Interaction ($\beta_1, \beta_2, \beta_3$)	2	11.89	5.945	12.54	<0.001
Residual	48	22.76	0.4742		
Total	52	1066.97	20.5187		

The percentage variance accounted for was 79.3%, and the standard error of observations was estimated to be 0.689, and the plot of observed against expected rod catch is shown in Figure 5.1.

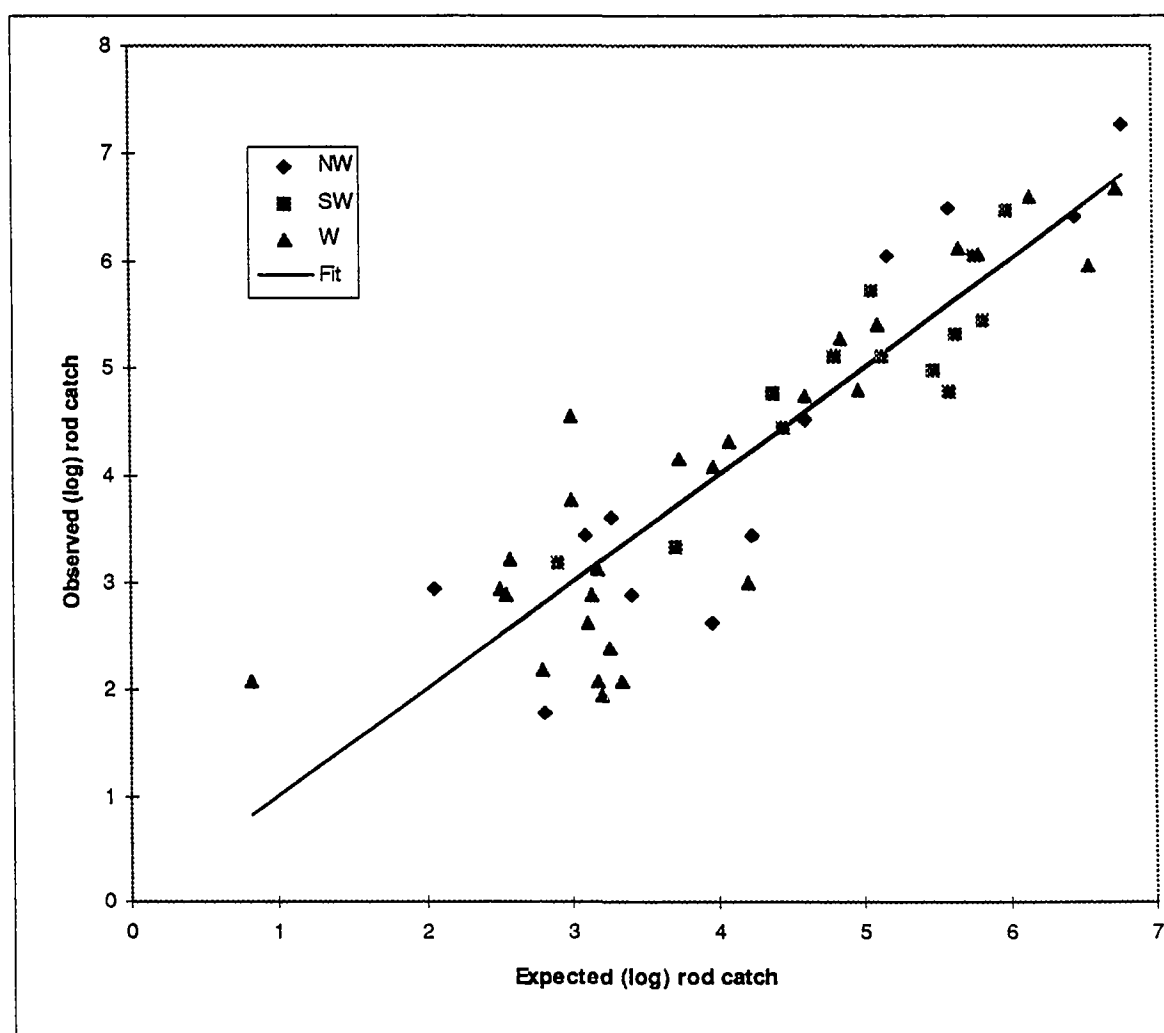


Figure 5.1 Plot of observed against expected rod catch for Model 3

The standard error of the estimates, and the correlations were very high (Tables 5.8 and 5.9).

Table 5.8 Estimates of parameters for the four parameter model, net catch ignored

	estimate	s.e.
α	0.469	0.767
β_1 (North West)	0.0374	0.0560
β_2 (South West)	0.067	0.101
β_3 (Welsh)	0.0213	0.0322

Table 5.9 Correlations between parameter estimates for the four parameter model, net catch ignored

	α	β_1	β_2	β_3
α	1.000			
β_1	-0.991	1.000		
β_2	-0.992	0.983	1.000	
β_3	-0.996	0.988	0.988	1.000

5.4.4 Two parameter model, with net catch

If it can be assumed that the reported net catch for a river corresponds to fish that were attempting to enter that river, then net catch can be included in the model.

$$\text{Log}R_i = \text{Log}(\beta_j S_i - N_i) + \text{Log}\left(1 - \exp\left(\frac{-\alpha r_i}{w_i^{0.761}}\right)\right) \quad \text{Model 4}$$

Attempts to fit this model using the Genstat non-linear model fitting routines were unsuccessful. This was due to the net catch, N_i , in a few rivers being similar to, or exceeding, the value of $\beta_j S_i$. These rivers prevented the fitting process from converging.

In an attempt to produce a possible model that included net catch, a manual trial and error fitting process using least squares was attempted. Values of β_j were picked to minimise the residual sum of squares, and the value of α was obtained from Genstat. The process was repeated until values of α and β_j were stable.

The analysis of variance and parameter estimates for this model are given in Tables 5.10 and 5.11.

Table 5.10 Analysis of variance for the one parameter model, including net catch

	d.f.	s.s.	m.s.	v.r.	Fpr.
Regression	1	1038.71	1038.7104	1874.29	<.001
Residual	51	28.26	0.5542		
Total	52	1066.97	20.5187		

The percentage variance accounted for 75.8, and the standard error of observations was estimated to be 0.744.

Table 5.11 Parameter estimate for the model including net catch

	estimate	s.e.
α	0.3032	0.0331
β_1 (North West)	0.071	-
β_2 (South West)	0.13	-
β_3 (Welsh)	0.031	-

5.4.5 Comparison with rivers of known run size

Given the high correlation between the estimates of α and β , it was desirable to check the estimates against rivers where the run size can be estimated independently of rod catch, using counters or traps. Data for the run size (T_i) of six rivers in 1993 were obtained, and using Models 2 and 3, estimates of α and β were obtained (Table 5.12).

Table 5.12 Estimates of α and β from rivers with “known” run size

River	T_i	S_i	N_i	R_i	r_i	w_i	β	β	α	
							Mod.3	Mod. 2	Mod.2	
Lune	8,300	70,348	2,969	1,434	17,124	426,885	0.1602	0.1180	0.2133	
Kent	1,500	15,632	104	422	4,939	102,034	0.1026	0.0960	0.4335	
Leven	560	16,197	14	31	1,958	125,403	0.0354	0.0346	0.2205	
Mean							0.0994	0.0829		
Tamar	3,519	47,423	1,544	428	3,792	352,694	0.1068	0.0742	0.5696	
Usk	5,197	163,595	1,226	735	7,271	550,875	0.0393	0.0318	0.4904	
Dee	9,757	105,349	1,157	455	8,522	729,759	0.1036	0.0926	0.1623	
Mean							0.0715	0.0415		
							Mean	0.0913	0.0745	0.3483
							SD	0.0471	0.0349	0.1706
							CV	0.5158	0.4687	0.4899

In general, there is reasonable correspondence between the estimate of α and β from the rod catch models, and estimates obtained from rivers with traps or counters. The average estimate of α from these 6 rivers was 0.3483, similar to that obtained from Models 1 and 2 (0.338), but somewhat less than for Model 3 (0.469). The average estimate of β was 0.0745 (Equation 2); somewhat higher than that from Models 1 and 2 (0.044).

5.5 Derivation of targets

The purpose of producing a model to explain the spatial variation in rod catch was to attempt to derive targets from the model for rivers with no counting or trapping facilities. The probability being that run and catch may be related to river size in a predictable way and that deviations (residuals) from such a model may reflect river performance.

To understand the relationship between residuals and river performance, it is necessary to understand the sources of residual variation in the model. Errors and assumptions concerning the variables are likely to be important, for example, the net catch for a particular river may represent fish that would not have entered that river, the assessment of habitat quality based on simple models is very approximate and takes no account of water quality, inaccessible areas or the contribution of lakes. Stochastic variation will also generate deviations from the model, since the model has been calibrated on data from only one year. More sophisticated models

and modelling techniques, utilising river-specific data from a number of years would help to reduce all of the above errors.

A further likely cause of residual variation is the assumption that the parameters of the model α and β_j are constant. If, for example, α is low for a particular river due to flow conditions, then the rod catch may be lower than predicted by the model. If on the other hand β_j is low for a particular river due to high marine mortality, then the number of returning fish and the rod catch will again be lower than predicted by the model. The influence of α and β_j on the size of the residual about the model is summarised in Table 5.13.

Table 5.13 Influence of α and β on the size of the residual about the model

		α (catchability)		
		Low	Average	High
β (run size)	Low	--	-	0
	Average	-	0	+
	High	0	+	++

The models (e.g. Model 3 or 4) can be used to correct for factors such as effort, main river size, total stream area, productivity and net catch. Salmon rivers can then be classified according to (corrected) rod catch (Table 5.14); this was achieved by ranking the rivers, and subdividing then into five equal classes. The Wye, for example, had the second highest rod catch in 1993 (Class A), but when the size, productivity, angling effort and net catch are taken into account, the Wye had a far lower rod catch than expected (Class D). In contrast, the Artro had one of the lowest rod catches (Class E), but when the characteristics of the river are taken into account, it had the second highest rod catch (Class A).

Table 5.14 Classification of salmon rivers according to declared rod catch in 1993 - Class A contains the highest rod catch and Class E the lowest.

	Uncorrected	Corrected for effort, river size and output (Model 3).	Corrected for effort, river size and output, and net catch (Model 4).
Class A	Lune (NW)	Ogwen (W)	Ogwen (W)
	Wye (W)	Artro (W)	Artro (W)
	Usk (W)	Derwent (NW)	Lune (NW)
	Derwent (NW)	Duddon (NW)	Dee (W)
	Exe (SW)	Kent (NW)	Nevern (W)
	Ribble (NW)	Taff (W)	Taff (W)
	Dee (W)	Camel (SW)	Tavy (SW)
	Teifi (W)	Nevern (W)	Duddon (NW)
	Tamar (SW)	Exe (SW)	Usk (W)
	Kent (NW)	Lune (NW)	Kent (NW)
Class B	Tywi (W)	Dee (W)	Derwent (NW)
	Camel (SW)	Usk (W)	Camel (SW)
	Taw (SW)	Llyfni (W)	Conwy (W)
	Dyfi (W)	Conwy (W)	Taf (W)
	Fowey (SW)	Taf (W)	Llyfni (W)
	Conwy (W)	Lyn (SW)	Glaslyn (W)
	Torrige (SW)	Glaslyn (W)	E+W Cleddau (W)
	Tavy (SW)	Irt (NW)	Lynher (SW)
	Teign (SW)	Esk (NW)	Dyfi (W)
	Clwyd (W)	Tavy (SW)	Teifi (W)
Class C	Dart (SW)	Dyfi (W)	Tamar (SW)
	Lyn (SW)	Tamar (SW)	Exe (SW)
	Mawddach (W)	Avon (SW)	Lyn (SW)
	Ogwen (W)	Teifi (W)	Ogmore (W)
	Ehen (NW)	E+W Cleddau (W)	Esk (NW)
	Lynher (SW)	Mawddach (W)	Irt (NW)
	E+W Cleddau (W)	Ogmore (W)	Mawddach (W)
	Taf (W)	Lynher (SW)	Clwyd (W)
	Ogmore (W)	Torrige (SW)	Avon (SW)
	Taff (W)	Dwryrd (W)	Dwryrd (W)
Class D	Esk (NW)	Ribble (NW)	Wye (W)
	Irt (NW)	Wye (W)	Rheidol (W)
	Leven (NW)	Ehen (NW)	Torrige (SW)
	Plym (SW)	Clwyd (W)	Ribble (NW)
	Nevern (W)	Rheidol (W)	Teign (SW)
	Avon (SW)	Fowey (SW)	Ehen (NW)
	Dwryrd (W)	Taw (SW)	Neath (W)
	Tawe (W)	Plym (SW)	Fowey (SW)
	Duddon (NW)	Neath (W)	Dwyfawr (W)
	Llyfni (W)	Teign (SW)	Tywi (W)
Class E	Wyre (NW)	Wyre (NW)	Taw (SW)
	Glaslyn (W)	Tywi (W)	Plym (SW)
	Rheidol (W)	Dwyfawr (W)	Wyre (NW)
	Calder (NW)	Leven (NW)	Aeron (W)
	Neath (W)	Dart (SW)	Dart (SW)
	Aeron (W)	Aeron (W)	Leven (NW)
	Dwyfawr (W)	Ellen (NW)	Dysinni (W)
	Artro (W)	Dysinni (W)	Tawe (W)
	Dysinni (W)	Tawe (W)	Loughor (W)
	Loughor (W)	Afan (W)	Afan (W)
	Afan (W)	Loughor (W)	Ellen (NW)
	Ellen (NW)	Calder (NW)	Calder (NW)

5.6 Use of rod catch to assess compliance

If one considers the escapement rather than the rod catch, the influence of α and β on the escapement is summarised in Table 5.15. Thus if salmon in a particular river are more catchable than average, all other factors being constant, then the exploitation will be higher, and the escapement lower. If, on the other hand, the run size is relatively low, all other factors being constant, then escapement will also be low.

Table 5.15 Influence of α and β on escapement

		α (catchability)		
		Low	Average	High
β (run size)	Low	0	-	--
	Average	+	0	-
	High	++	+	0

A comparison of Tables 5.13 and 5.15 reveals that no conclusions can be drawn about the escapement in a particular river from the residuals of the models fitted above. A high relative rod catch may be generated by either a high catchability or a high run size (Table 5.13), which would result in a low or high escapement respectively (Table 5.15).

Considering this more formally, it is possible to obtain two estimators for escapement (E) expressed as a proportion of the smolt output (S) from the above models.

$$\frac{E_i}{S_i} = \left(\frac{R_i}{S_i} \right) \frac{\exp\left(-\frac{\alpha r_i}{w_i^\gamma}\right)}{1 - \exp\left(-\frac{\alpha r_i}{w_i^\gamma}\right)}$$

or alternatively:

$$\frac{E_i}{S_i} = \beta_i - \frac{N_i + R_i}{S_i}$$

The ratio on the left-hand side of these equations can be regarded as the position of a particular river along the x-axis (stock) of a stock-recruitment curve. The first equation keeps α constant, whereas the second keeps β constant. Rivers with a rod catch above the line would therefore have a high estimate of escapement using the first equation, but a low estimate of escapement using the second equation.

5.7 Refinements to model

It was noted in Section 5.3.3 that the models above assumed that smolt production was proportional to stream area and productivity, but that the reduced smolt output in over-exploited fisheries had been ignored. A more realistic model would assume that the smolt output declines in rivers where exploitation is high. A possible model (derived by relating the sub-models in Section 5.3, and assuming a Beverton-Holt stock-recruitment curve) would be:

$$R_i = \frac{S_i}{2}(1 - \lambda^{U_i}) \left[\phi_j - \frac{N_i}{S_i} - \frac{\beta}{\lambda^{U_i}} + \sqrt{\left(\frac{N_i}{S_i} + \frac{\beta}{\lambda^{U_i}} - \phi_j \right)^2 - \frac{4\beta N_i}{S_i \lambda^{U_i}}} \right] \quad \text{Model 5}$$

where:

R_i = the rod catch in the i th river;

S_i = maximum potential smolt output from the i th river;

U_i = rod effort in i th river;

N_i = net catch in i th river;

λ = parameter relating to catchability of fish;

ϕ_j = parameter relating to marine survival (replacement line) in the j th region;

β = parameter of the Beverton-Holt stock-recruitment curve.

If $\beta=0$ (i.e. the stock-recruitment is a horizontal line, and escapement never limits smolt production), then the model becomes:

$$R = (1 - \lambda^{U_i})(\phi_j S_i - N_i)$$

which is equivalent to Model 4 in Section 5.4.4.

If net catch (N) is zero, then the model becomes:

$$R_i = S_i (1 - \lambda^{U_i}) \left(\phi_j - \frac{\beta}{\lambda^{U_i}} \right)$$

which is equivalent to the life-cycle model in Section 2.2.3. Model 5 thus provides a link between the theory outlined in Section 2 with the models fitted to the 1993 catch statistics above.

Initial attempts to fit Model 5 revealed problems with correlations between the parameters (see Section 5.4.1). However, the inclusion of the stock-recruitment curve into the rod catch model is likely to be a worthwhile refinement, and further work is required.

5.8 Assessment of salmon fishery performance in the Environment Agency, Welsh Region

There are close parallels between the models developed here, and the methods employed by the Welsh Region of the Agency (then the NRA) to assess salmon fishery performance (Environment Agency, 1996). The Agency model was of the form:

$$\frac{E}{A} = f(R, U, A)$$

where:

E = egg deposition;

A = area of useable nursery grounds;

R = rod catch;

U = exploitation rate, where:

$$U = f(r, l)$$

where:

r = rod effort;

l = size of fishery.

One of the estimators for escapement above is of the form:

$$\frac{E}{A} = f(R, r, l, A)$$

where the area A is measured in terms of a habitat quality-weighted index (S).

The models are therefore similar in terms of the quantity being estimated on the left-hand side, and many of the variables used on the right-hand side. They are different in terms of the form of the model, the variables used, the estimated or assumed values of parameters, and the assumption and approximations made.

The process of setting spawning targets from a stock-recruitment curve and replacement line, and assessing spawning escapement from rod catch is summarised in Table 5.16. When a river fails a target under the Agency procedure, the cause may be one of three types. Firstly, the target may have been over-estimated due to over-estimation of marine survival, average fecundity or freshwater productivity. For example, if the freshwater productivity (carrying capacity) declines relative to that assumed from the River Bush, the true maximum gain target for the altered stock-recruitment curve will decline, as will the rod catch (Section 2.3). A target failure will be triggered by the Agency procedure because the estimated target will remain high relative to the declining escapement. The targets set by the Agency therefore represent values that are conditional on the reference conditions of freshwater productivity and marine survival assumed when the target was set.

Secondly, the estimate of egg deposition may be underestimated. The estimation of egg deposition rates includes a number of parameters that are difficult to estimate in some rivers. These include the total stream area, and the rod exploitation rate.

Finally, if the target and performance are correctly estimated, then a target failure will be triggered by over-exploitation by the combined coastal, net and rod fisheries.

Table 5.16 Some possible causes of a maximum gain target “failure”

Reason for failure	Possible responsible parameters
Failure relative to reference conditions (target over-estimated).	<ul style="list-style-type: none"> • Marine survival over-estimated when target set. • Average fecundity over-estimated when target set. • Freshwater productivity over-estimated when target set.
Escapement/area under-estimated	<ul style="list-style-type: none"> • Stream area over-estimated. • Rod exploitation over-estimated. • Average fecundity under-estimated.
Failure relative to actual maximum gain	<ul style="list-style-type: none"> • High coastal exploitation. • High estuarine net exploitation. • High rod exploitation (must be known).

Based on the discussion in this section, the following observations are made regarding the Agency methodology:

- The assessment of useable area is critically important. The stream inventories project may improve the estimation procedure.
- The assessment of habitat types and quality in Agency rivers relative to the River Bush is critical for the transportation of targets. The link between the Agency methodology and the methodology used on the Bush is unclear.
- The estimation of escapement relies heavily on an estimate of the rod exploitation. The rod exploitation rate, however, is only known within broad limits for many rivers, and represents a major potential source of error in the procedure.

- In rivers where the rod exploitation rate is unknown, it is assumed to be constant. A systematic decline in rod catch in such rivers would be interpreted as a decline in escapement. A decline in rod catch could however be generated by a reduction in the exploitation rate (and increase in escapement) illustrating the uncertainty in assessing escapement from rod catches in rivers where little is known about exploitation rates.
- There is no allowance for uncertainty in parameter estimates or stochastic variation in stocks. A preliminary simulation (details not presented here) reveals that the confidence interval around the estimate of E/A is likely to be enormous.
- There is now allowance for the uncertainty in the target value estimated from the Bush.
- Assessment of compliance takes a “face value” approach, indeed it has to given that uncertainty in performance estimation is ignored. However, the Agency have recently taken steps to develop a “benefit-of-doubt” (or “fail-safe”) approach to compliance assessment would be more appropriate to salmon management.
- Angling exploitation is likely to be a function of the “catchability” of fish, the river width and flow conditions, and the size of the population (as used in the models in Section 5.3). The Agency should seek to redefine its current model (which predicts exploitation rate from fishing effort and fishery size) to incorporate these factors.
- The methodology takes no account of environmental variables in the assessment of escapement from catch (e.g. flow).
- For the foreseeable future, rod and net catch will remain the only available information on run size, and the only means of assessing egg deposition. Whilst compliance assessment from rod catch data will always be an inexact science, improved methodologies should become available on completion of the Agency R&D project “Catch statistics as a measure of fish stock size”.

6. CONCLUSIONS AND RECOMMENDATIONS

6.1 Setting targets

6.1.1 Fitting stock-recruitment curves

- The stock-recruitment model fitted to data has considerable implications for the estimation of targets. However, river-specific stock-recruitment data is rarely good enough to determine which stock-recruitment model is appropriate. *It is recommended that extreme care is exercised when estimating targets from stock-recruitment data; the implications of fitting different models should be assessed.*
- The methods of fitting a stock-recruitment curve also has implications for the estimation of a target. *It is recommended that the implications (if any) of different fitting method should also be assessed.*

6.1.2 Comparing stock-recruitment curves

- Many attempts at deriving stock recruitment targets have been based on different forms of the stock-recruitment curve, different fitting methods and different life stages. *It is recommended that comparisons between targets are only made where these factors are constant.*
- The methods used in this report for comparing stock recruitment curves allow any model to be fitted with a range of assumptions about the stochastic variation. Statistical comparison of individual parameters, and estimation of the magnitude of stochastic error were also performed. *It is recommended that the methods illustrated in this report are used for comparing stock-recruitment curves.*

6.1.3 Type of target

- The way in which targets will be used to initiate management action within the Agency is presently unclear. *It is recommended that the types of targets that are used for salmon management are chosen with regard to the management action that would be initiated by target failure.*
- The Agency is currently considering maximum gain as an appropriate target for salmon management. Managing a fishery to a maximum gain target will entail controlling exploitation to maximise the catch, regardless of any impacts (marine or freshwater) acting on the fishery. *It is recommended the Agency consider a target-based management plan which includes appropriate consideration of stock conservation in terms of protecting escapement or smolt output.*

- The choice of the type of target will determine the appropriate methodology for transportation. *It is recommended that the type of target and the associated management response is determined in advance of the development of transportation methodologies (see below).*

6.1.4 Derivation of targets

- *For use in target setting, a stock recruitment curve should include all density-dependent life stages (this would typically be an egg - smolt stock recruitment curve), and should be derived for the entire river system.*
- The Agency intend to use the data from the River Bush to obtain a spawning target which will be transported to other rivers in England and Wales. This study demonstrated the large uncertainties associated with target estimates from the Bush. *It is recommended that the uncertainties associated with the current Bush target are considered further, allowing for uncertainties in the replacement line. (Budget estimate £10k).*
- The targets for the Bush were developed by utilising data on total egg deposition and smolt output. However, other data is likely to be available for the Bush (particularly relating to the estimation of the replacement line) which could be used to improve the estimates of target values. *It is recommended that the possibility of improving the target estimates for the Bush by utilising additional information is given further consideration.*
- The use of techniques such as HABSCORE provide a target against which juvenile performance can be compared, and should be regarded as complementary to the assessment of ova deposition targets. *It is recommended that HABSCORE is used to assess the performance of juvenile populations.*
- *It is not recommended that spatial models of rod or net catch are used to set targets for salmon fisheries.*

6.1.5 Transportation

- This study has shown that the target value for a river is directly proportional to “height” of the stock-recruitment curve (carrying capacity), provided that density independent mortality remains constant. Information on the carrying capacity of a river can be obtained from habitat models. *It is recommended that the use of habitat models (or other measures of freshwater carrying capacity) are considered as a basis for transporting targets between rivers.*
- *It is recommended that GIS-driven habitat models are used to transport data from the Bush to UK rivers. The development of a methodology using low resolution GIS (1:250,000) should be considered as an interim measure before the Agency Stream Inventory project (new start) is complete. (Budget estimate £12k).*

- *It is recommended that one of the objectives of the Stream Inventory project should be to develop a robust platform (using GIS data and habitat measurement) for transporting targets. This is likely to require the development of models of habitat suitability for juvenile salmonids that work at a lower resolution (e.g. catchment specific) than HABSCORE (see also recommendations from HABSCORE project).*
- *It is recommended that juvenile survey data (Section 3.2) is used to calibrate national habitat models developed as part of the River Fisheries Habitat Inventory project.*
- *It is recommended that data available from smolt trapping (Section 3.3) is used to assess smolt production rates and is used to calibrate national habitat models developed as part of the River Fisheries Habitat Inventory project.*
- *Targets based on the replacement line (e.g. maximum gain) will vary according to river-specific marine survival, sea-age composition and fecundity. It is recommended that correction for the replacement line is undertaken when transporting targets.*

6.1.6 Stochastic considerations

- *The stock recruitment and replacement line represent a deterministic model of the life cycle of a salmon. Setting targets based on these alone ignores the strong stochastic element that influences population dynamics. It is recommended that target setting considers the stochastic element in all stages of the life cycle of a salmon, that is, both the stock recruitment and the replacement line.*

6.1.7 Sea trout

- *This project has not assessed the interactions between salmon and sea trout. Interactions in the freshwater phase are likely, although the magnitude and mechanisms are poorly understood. In addition, management activities for one species (fishing season, net limitations) will affect the other. Since the primary purpose for setting targets is to determine appropriate management action, it is recommended that the ultimate aim of the Agency should be to develop systems for target setting, compliance assessment and management response for both salmon and sea trout together.*
- *It is recommended that HABSCORE data and models are used to assess the magnitude of detectable interaction between salmon and sea trout (after habitat correction). (Budget estimate £1k for initial investigation).*
- *It is recommended that long-term catch statistics are used to establish the combined spawning escapement from salmon and sea trout in relation to stream areas. (Budget estimate £20k).*

6.1.8 Lifecycle model

- The need to include consideration of factors such as stochastic variation and sea age in target setting and compliance assessment (see above) would suggest that more complex life-cycle models are required for target setting and management decision making. ***It is recommend that the Agency R&D project on modelling the salmon populations of the Dee should include an assessment of the use of such models for target setting. (Budget estimate for initial review and scoping, £16k).***

6.2 Compliance assessment

6.2.1 Area estimation

- The assessment of habitat types is potentially a major source of error when setting targets and assessing compliance. ***The Agency R&D project on stream inventories should specifically attempt to resolve the problem of stream area estimation and habitat assessment on a catchment scale in the context of fishery performance targets.***

6.2.2 Estimation of escapement from rod catch

- Rod catch data is likely to remain the only source of information on run size for many rivers. However, there are a number of areas in which the current methodology could be improved (inclusion of environmental variable, treatment of exploitation). ***It is recommended that the current methods using by the Agency for assessing compliance with targets from rod catch data are refined in the light of the catch statistics R&D project, and the findings of this project.***
- ***To support the development of a model relating rod catch to escapement, it is recommended that long-term data from Agency rivers where trapping or counting facilities have been operating downstream of rod fisheries are utilised for calibration.***

6.2.3 Estimation of compliance from juvenile data

- The response of the juvenile populations to a declining ova deposition will be determined by the shape of the stock-recruitment curve and the position of the fishery on the curve. For many fisheries, a detectable decline in juvenile abundance may only occur after a dramatic decline in ova deposition. In addition, an ova deposition well in excess of a target will not be detected by juvenile surveys. ***It is therefore not recommended that juvenile surveys are used to estimate ova deposition.***

- Juvenile surveys will detect impacts on salmon populations within the freshwater phase (such as habitat degradation or water quality problems) well before a decline in adult stocks. A well designed juvenile monitoring programme will also give information on where in a catchment management actions should be prioritised. In addition, juvenile surveys will detect when and where recruitment may be limiting the juvenile salmon population. *It is therefore recommended that juvenile monitoring programmes are an essential part of salmon management, and should be used to assess fishery performance in conjunction with estimating ova deposition from adult run size.*

6.2.4 Compliance scheme

- A decline in rod catch may be caused by a number of factors such as autocorrelated drift, a decline in marine survival, a decline in freshwater production, a decline in rod or net exploitation (for rivers passing maximum gain target), or an increase in rod or net exploitation (for rivers failing maximum gain target). *It is recommended that a standard methodology is developed to identify the possible causes of an observed rod catch decline and compliance failure (see Table 5.16). Additional evidence would come from environmental variables (e.g. flow, water quality), behaviour of adjacent fisheries, juvenile surveys, marine, coastal and estuarine fisheries.*
- *To assist with the development of the above methodology, it is recommended that a comprehensive assessment of national catch statistics is undertaken to identify common trends between rivers (develop river classification), between rod and net fisheries on the same river, and between salmon and sea trout. This should have the specific objective of guiding management response to changes in catch statistics of rivers where traps or counters are absent.*
- The management response by the Agency to a target failure is likely to be different depending on the likely cause (see above). The proposed management response to target failure will determine the rationale behind the setting of targets in the Agency and the compliance scheme adopted. *It is recommended that the issues of how target failure will be incorporated into Agency salmon management policies are resolved at the earliest opportunity.*

- The statistical assessment of compliance in salmon populations is complicated by the natural long-term drifting of abundance levels. ***It is recommended that a compliance scheme is developed that allows for the autocorrelation observed in salmon populations (Budget estimate £4k).***

6.2.5 Use of traps and counters

- ***It is recommended that where facilities exist to monitor adult run size (traps, Section 3.4 and counters , Section 3.5), that the data generated is used to estimate egg deposition and to assess compliance.***

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APPENDIX A DATA COLLATION QUESTIONNAIRE

1. Introduction

This questionnaire has been designed to obtain information on stock-recruitment relationships in different river systems. Information is required on the nature of the river system, and on how stock and recruitment estimates have been obtained, in order to enable statistical comparisons to be performed.

2. Details of river system

2.1 Catchment size & spawning area

Where stock or recruitment estimate have been obtained from trapping, please give estimates of the area upstream of trapping facilities. This should be the area used to estimate egg deposition / unit area. In addition, please supply estimates of the different types of fluvial habitat present within the catchment (for example, the area of spawning habitat; the area of 'Grade A' spawning habitat; the area of nursery habitat; etc.). State the units of measurement (i.e. m², ha, etc.) for each estimate given.

Parameter	Habitat type *	Estimate
Total catchment area		
Wetted surface area - lacustrine		
Wetted surface area - fluvial, by habitat type:		
Wetted surface area - fluvial, total		
Average dry-weather flow (mean & range)		
Other measures (specify)		

2.4 *Water chemistry*

Please supply the following information on the water chemistry of the catchment, stating the units where appropriate:

Parameter:	Mean	Minimum	Maximum
[Ca]			
[Mg]			
pH			
Conductivity			
Temperature			

2.5 *Other species*

Please list other species present in spawning areas.

--

... continuation sheet for electrofishing data:

Date fished	Age class:						Area
	0+	1+	2+	3+			

4. Publications

What are the most recent publications that give further background information for this data? Please send reprints if available.

Author(s) & year	Title & journal reference

APPENDIX B EXAMPLE OF GENSTAT CODE TO COMPARE STOCK-RECRUITMENT CURVES

```
open 'srcomp.prm'; ch=2; file=in; width=400
vari stock, recr
factor [lev!=(1,2)] river
factor [lev!=(0,1)] girn
factor [lev!=(0,1)] bush
read [ch=2;setn=y;layout=s] stock, recr, river, girn, bush
MODEL recr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b;\
lower=0, 0;\
upper=1, 100;\
init=.14, 35
EXPRESSION REC; VALUE=!E(Fitted=1/(a+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL recr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a1, a2, b;\
lower=0, 0, 0;\
upper=1, 1, 100;\
init=.1211, .1685, 35
EXPRESSION REC; VALUE=!E(Fitted=1/((girn*a1+bush*a2)\
+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL recr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b1, b2;\
lower=0, 0, 0;\
upper=1, 100, 100;\
init=.139, 48.8, 20.2
EXPRESSION REC; VALUE=!E(Fitted=1/(a\
+(girn*b1+bush*b2)/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL recr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a1, a2, b1, b2;\
lower=0, 0, 0, 0;\
upper=1, 1, 100, 100;\
init=.1211, .1685, 48.8, 20.2
EXPRESSION REC; VALUE=!E(Fitted=1/((girn*a1+bush*a2)\
```

```

+(girn*b1+bush*b2)/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
calc lrecr=log(recr)
MODEL lrecr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b;\
lower=0, 0;\
upper=1, 100;\
init=.14, 35
EXPRESSION REC; VALUE=!E(Fitted=log(1)-log(a+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL lrecr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a1, a2, b;\
lower=0, 0, 0;\
upper=1, 1, 100;\
init=.1211, .1685, 35
EXPRESSION REC; VALUE=!E(Fitted=log(1)-log((girn*a1+bush*a2)\
+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL lrecr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b1, b2;\
lower=0, 0, 0;\
upper=1, 100, 100;\
init=.139, 48.8, 20.2
EXPRESSION REC; VALUE=!E(Fitted=log(1)-log(a\
+(girn*b1+bush*b2)/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL lrecr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a1, a2, b1, b2;\
lower=0, 0, 0, 0;\
upper=1, 1, 100, 100;\
init=.1211, .1685, 48.8, 20.2
EXPRESSION REC; VALUE=!E(Fitted=log(1)-log((girn*a1+bush*a2)\
+(girn*b1+bush*b2)/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
Restrict recr, lrecr; cond = girn.eq.1
MODEL recr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b;\
lower=0, 0;\
upper=1, 100;\
init=.14, 35

```



```

EXPRESSION REC; VALUE=!E(Fitted=1/(a+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL lrecr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b;\
lower=0, 0;\
upper=1, 100;\
init=.14, 35
EXPRESSION REC; VALUE=!E(Fitted=log(1)-log(a+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
Restrict recr, lrecr; cond = bush.eq.1
MODEL recr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b;\
lower=0, 0;\
upper=1, 100;\
init=.14, 35
EXPRESSION REC; VALUE=!E(Fitted=1/(a+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL lrecr; FITTED=Fitted
RCYCLE [MAXCYCLE=50] a, b;\
lower=0, 0;\
upper=1, 100;\
init=.14, 35
EXPRESSION REC; VALUE=!E(Fitted=log(1)-log(a+b/stock))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
stop

```

-

-

**APPENDIX C OUTPUTS FROM SALMON LIFE-CYCLE
MODEL**

Exploitation				
		1sw	2sw	3sw
Nets	0			
Rods	0			
net %season		0.8	0.9	1
rod %season		0.7	0.8	0.9
net p catch		0.07	0.06	0.05
rod p catch		0.01	0.01	0.01

Sea age				
smolt O	smolt I			
	1sw	2sw	3sw	
1sw	0.33	0.33	0.33	
2sw	0.33	0.33	0.33	
3sw	0.33	0.33	0.33	
Tot	1.00	1.00	1.00	

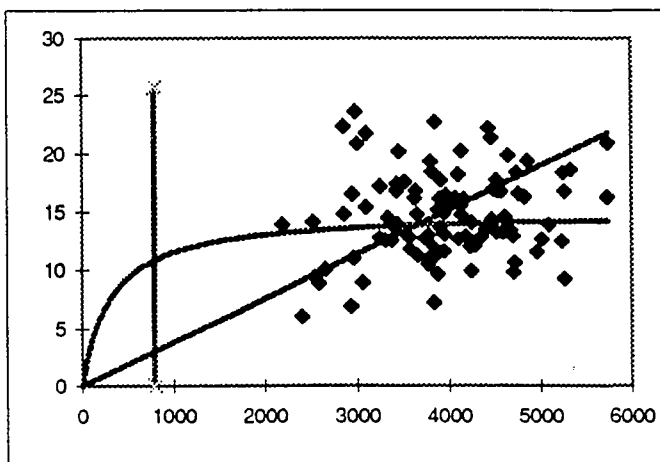
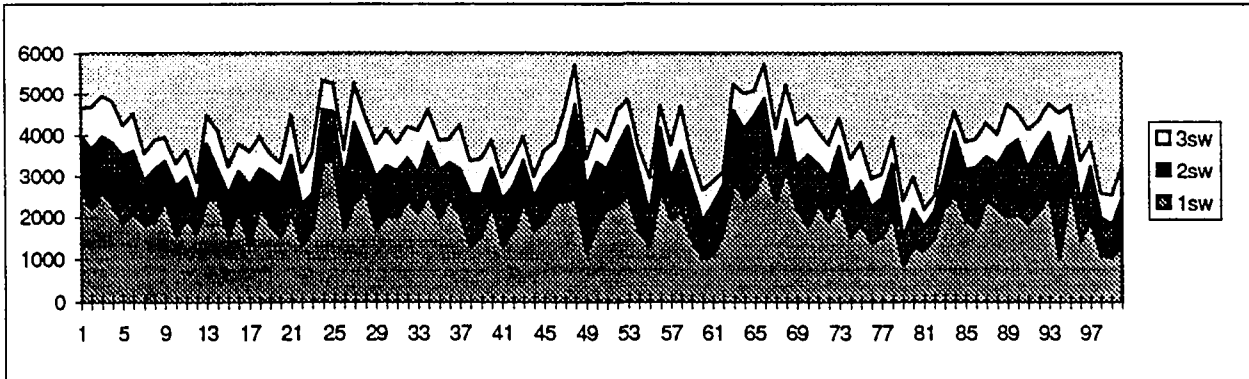
Smolt age				
	S1	S2	S3	Tot
	0.2	0.5	0.3	1

Replacement line				
		1sw	2sw	3sw
smolt -> adult		0.04	0.02	0.01
adult -> egg		10000	12000	15000
error	0.2			

S-R curve	
max smolts	15
max eggs/smolts	20
error	0.3

Initial run size				
number	1sw	2sw	3sw	tot
1500	0.333	0.333	0.333	0.999

Area
10000



Exploitation				
		1sw	2sw	3sw
Nets	15			
Rods	100			
net %season		0.8	0.9	1
rod %season		0.7	0.8	0.9
net p catch		0.07	0.06	0.05
rod p catch		0.01	0.01	0.01

Sea age				
		smolt_l		
smolt_0		1sw	2sw	3sw
1sw	0.33	0.33	0.33	0.33
2sw	0.33	0.33	0.33	0.33
3sw	0.33	0.33	0.33	0.33
Tot	1.00	1.00	1.00	1.00

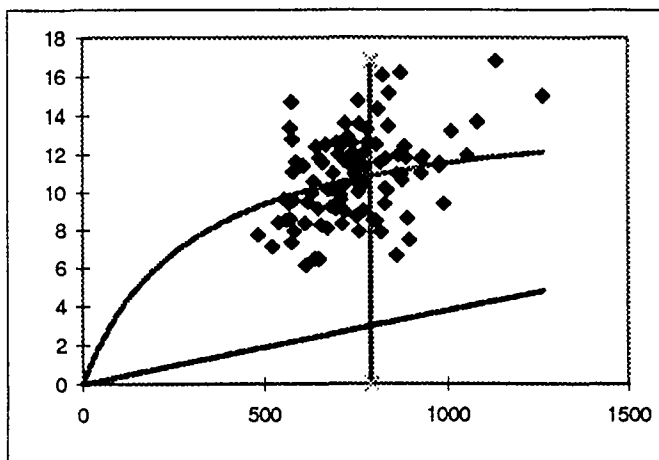
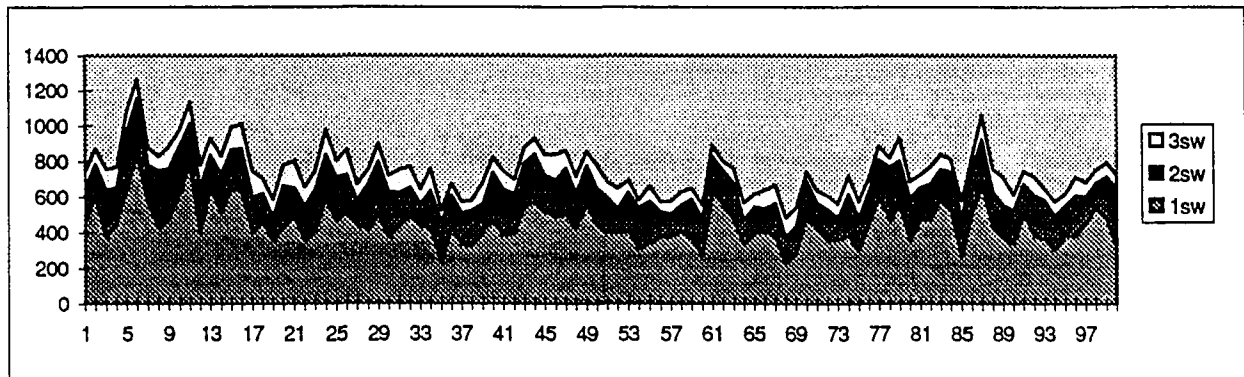
Smolt age				
	S1	S2	S3	Tot
	0.2	0.5	0.3	1

Replacement line				
		1sw	2sw	3sw
smolt -> adult		0.04	0.02	0.01
adult -> egg		10000	12000	15000
error	0.2			

S-R curve	
max smolts	15
max eggs/smolts	20
error	0.2

Initial run size				
number	1sw	2sw	3sw	tot
1500	0.333	0.333	0.333	0.999

Area
10000



**APPENDIX D AGENCY REPORTED ROD AND NET
CATCH DATA FOR 1993**

Table 12 Reported rod effort data for salmon and migratory trout by principal rivers - 1993 season.

NPA Region	River	Number of returns with effort data	Number of days fished	Number of days fished per return	Number of salmon and pike recorded	Catch per license day	Number of migratory trout recorded	Catch per license day	
Northumbria	All	12	240	20.75	2	0.01	5	0.02	
	Coquet	214	8180	28.82	199	0.09	766	0.04	
	Tyne	586	6624	18.48	707	0.07	623	0.06	
	Wear	182	4867	27.24	84	0.08	364	0.08	
	Tees	56	838	15.24	11	0.01	1	0.00	
	Total	1043	21798	20.84	1013	0.06	1180	0.06	
Yorkshire	Uk	88	861	10.81	12	0.01	144	0.16	
	Clus	3	33	11.00	1	0.03	8	0.08	
	Others	11	82	7.45	0	0.00	3	0.04	
	Total	102	1088	18.46	13	0.01	147	0.14	
Thames	Thames	3	98	23.00	1	0.01	1	0.01	
Southern	Trent	21	228	10.86	19	0.09	22	0.19	
	Itchen	23	186	8.48	8	0.03	41	0.21	
	Beaulieu	1	24	24.00	6	0.23	6	0.06	
	Others	18	387	19.83	0	0.00	0	0.00	
	Total	63	665	12.78	33	0.04	69	0.12	
Wessex	Avon	114	1886	17.42	18	0.01	173	0.09	
	Stour	2	16	7.99	0	0.00	8	0.08	
	Piddle	18	282	20.28	2	0.01	18	0.09	
	Frome	81	1878	17.88	48	0.06	18	0.01	
	Total	187	3282	17.56	68	0.02	202	0.08	
	South West	Ass	23	364	15.83	2	0.01	108	0.29
Oar		28	88	4.98	5	0.08	28	0.27	
Es		216	2676	11.96	373	0.14	51	0.02	
Taun		146	1878	12.94	75	0.04	488	0.26	
Dart		143	1486	10.39	48	0.03	242	0.16	
Avon		28	328	18.08	16	0.06	81	0.18	
Erme		28	286	13.38	2	0.01	82	0.31	
Yealm		2	13	6.58	1	0.08	10	0.77	
Phyn		36	883	18.51	22	0.03	198	0.29	
Tiny		54	1153	21.26	86	0.06	182	0.14	
Tarner		202	2216	10.97	268	0.11	183	0.08	
Lynher		41	568	13.81	22	0.04	182	0.28	
Loss		2	43	21.50	0	0.00	15	0.58	
Fowey		138	2283	17.33	101	0.04	337	0.16	
Comel		188	2281	15.78	181	0.07	488	0.21	
Taw		183	1968	10.88	108	0.06	348	0.18	
Tarridge		178	1718	9.68	134	0.08	241	0.14	
Lyn		48	474	9.87	68	0.14	83	0.19	
Others		7	88	12.88	0	0.00	18	0.18	
Total		1848	28478	12.42	1484	0.07	3272	0.19	
Severn-Trent		Severn	378	8983	23.88	172	0.02	4	0.00
Wales	Wye	881	8886	17.18	471	0.06	18	0.00	
	Uk	247	4878	18.84	473	0.19	18	0.08	
	Taf	18	281	26.08	32	0.08	116	0.32	
	Rhymer	8	132	22.08	2	0.02	28	0.22	
	Ogmore	114	2881	25.18	43	0.03	388	0.11	
	Alan	14	387	28.38	2	0.01	87	0.17	
	Narth	48	878	24.48	12	0.01	182	0.16	
	Tawe	86	1983	26.83	8	0.09	68	0.03	
	Laughar	48	888	18.12	4	0.08	117	0.13	
	Tywi	848	12888	18.88	208	0.02	1813	0.15	
	Taf	88	1178	17.28	32	0.03	73	0.06	
	E-W/Gladesu	58	1048	18.07	41	0.04	288	0.26	
	Neveim	58	832	16.84	17	0.02	248	0.38	
	Taf	333	5874	17.84	228	0.04	826	0.14	
	Aaron	18	584	38.88	6	0.01	362	0.43	
	Rhodes	28	583	20.18	14	0.02	128	0.22	
	Dyfi	247	2811	11.38	108	0.04	688	0.21	
	Ogwynn	58	1141	22.82	8	0.01	173	0.16	
	Mawddach	233	3387	14.84	54	0.02	348	0.16	
	Arfa	18	173	10.81	8	0.06	47	0.27	
	Deryfel	18	134	7.44	2	0.01	82	0.39	
	Glwynn	36	781	20.83	13	0.02	168	0.21	
	Owyflaw	38	861	18.88	5	0.01	183	0.26	
	Llyth	28	547	18.84	10	0.02	188	0.33	
	Chryfel	7	51	7.28	5	0.10	4	0.08	
	Seirak	58	878	18.84	24	0.02	48	0.06	
	Ogwen	26	278	11.08	27	0.18	8	0.02	
	Cerwy	143	2386	16.13	108	0.06	73	0.03	
	Chwy	208	2828	13.88	88	0.02	313	0.11	
	Dee	434	8288	14.41	334	0.06	73	0.01	
	Others	82	1348	18.44	8	0.08	338	0.24	
	Total	3882	88641	17.14	2388	0.04	7884	0.11	
	North West	Ribble	888	9888	14.14	483	0.04	381	0.04
		Colver	8	148	24.87	2	0.01	0	0.00
		Wyre	38	428	10.88	6	0.01	44	0.18
		Lune	887	10843	12.51	888	0.08	838	0.08
		Kare	238	3138	13.24	287	0.08	333	0.11
		Laven	86	1074	11.21	17	0.02	27	0.03
Duddon		48	281	5.83	10	0.06	38	0.16	
Esik		17	278	18.88	18	0.07	10	0.04	
R		58	1083	18.88	28	0.03	28	0.02	
Evan		108	2088	18.71	48	0.08	88	0.03	
Derwent		248	4211	18.88	508	0.12	232	0.08	
Eilan		28	846	23.04	6	0.01	4	0.01	
Eden		888	14778	24.42	888	0.07	273	0.02	
Esik (Bolder)		128	1138	8.48	88	0.08	282	0.22	
Others		88	1108	12.28	8	0.01	54	0.08	
Total		3238	58814	18.88	3383	0.07	2872	0.08	
England and Wales		18846	173881	18.48	8488	0.06	14818	0.08	

Note: Effort data is reported for both salmon and migratory trout and is not recorded.
The table only includes returns upon which the number of days fished was reported.
Some returns contained data for less or more rivers.

APPENDIX E EXAMPLE OF GENSTAT CODE TO FIT ROD CATCH MODEL

```
open 'edmod.prn'; ch=2; file=in; width=400
vari number, smolt, net, rod, effort, width, link, nw, sw, w
read [ch=2;setn=y;layout=s] number, smolt, net, rod, effort,\
width, link, nw, sw, w
calc lrod = log(rod)
calc nexp=net*100/smolt
calc y=rod/smolt
MODEL lrod; FITTED=Fitted
RCYCLE [MAXCYCLE=100] a, b, c;\
lower=.00001, 0.00001, .33;\
upper=10000, .99999, 3;\
init=1, .001, 1
EXPRESSION REC; VALUE=!E(Fitted=log(1-exp(-a*effort/(width**c)))\
+log(b*smolt))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
calc twidth=width**0.761
MODEL lrod; FITTED=Fitted
RCYCLE [MAXCYCLE=100] a, b;\
lower=.00001, 0.00001;\
upper=10000, .99999;\
init=.34, .044
EXPRESSION REC; VALUE=!E(Fitted=log((1-exp(-a*effort/twidth))*b*smolt))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
MODEL lrod; FITTED=Fitted
RCYCLE [MAXCYCLE=100] a, b1, b2, b3;\
lower=0.00001, 0.00001, 0.00001, 0.00001;\
upper=10000, 0.99999, 0.99999, 0.99999;\
init=0.34, 0.044, 0.044, 0.044
EXPRESSION REC; VALUE=!E(Fitted=log((1-exp(-a*effort/twidth))\
*(b1*nw*smolt+b2*sw*smolt+b3*w*smolt)))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
restrict lrod; cond=(number.ne.47).or.(number.ne.31)
MODEL lrod; FITTED=Fitted
RCYCLE [MAXCYCLE=100] a;\
lower=.000001;\
```

```
upper=100000;\
init=0.4
EXPRESSION REC; VALUE=!E(Fitted=log((1-exp(-a*effort/twidth))\
*(nw*(.071*smolt-net)+sw*(.13*smolt-net)+w*(.031*smolt-net))))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
```

```
MODEL lrod; FITTED=Fitted
RCYCLE [MAXCYCLE=100] a, b1, b2, b3;\
lower=0.00001, 0.00001, 0.00001, 0.00001;\
upper=10000, 0.99999, 0.99999, 0.99999;\
init=0.3032, 0.071, 0.13, 0.031
EXPRESSION REC; VALUE=!E(Fitted=log((1-exp(-a*effort/twidth))\
*(nw*(b1*smolt-net)+sw*(b2*smolt-net)+w*(b3*smolt-net))))
FITNONLINEAR [PRINT=m,s,e,c; CALC=REC; fprob=y; SELIN=y]
stop
```

APPENDIX F RELATIONSHIP BETWEEN STREAM ORDERS FROM DIFFERENT MAP SCALES

Available information on the relationship between stream order and juvenile salmon abundance is based on the HABSCORE data set, which measured stream order on a scale of 1:50,000. It was therefore necessary to convert from stream order on a 1:50,000 scale to stream order on a 1:250,000 scale. It must be stressed that the method used, and outlined below, is very approximate, and used only for illustrative purposes.

The first step was to relate stream order (1:50,000) from the HABSCORE data set, to stream order (1:625,000) from the Agency River Habitat Survey (RHS) data set. This was done via the common measurement of stream width. The relationship between stream order and stream width for the two map scales are given in Figures 4.4 and 4.5.

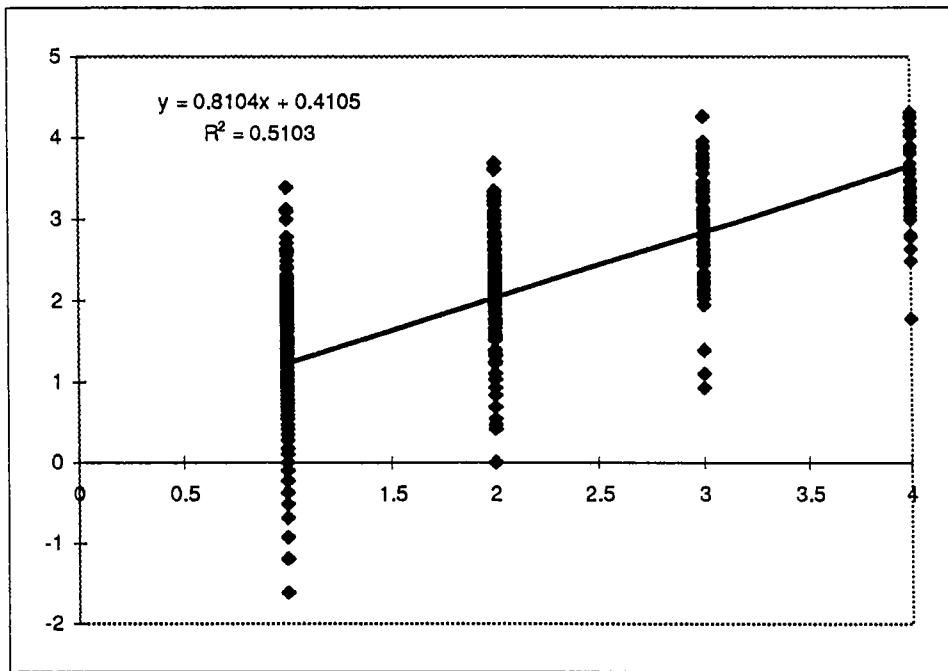


Figure F.1 Relationship between (log) stream width and stream order (1:625,000)

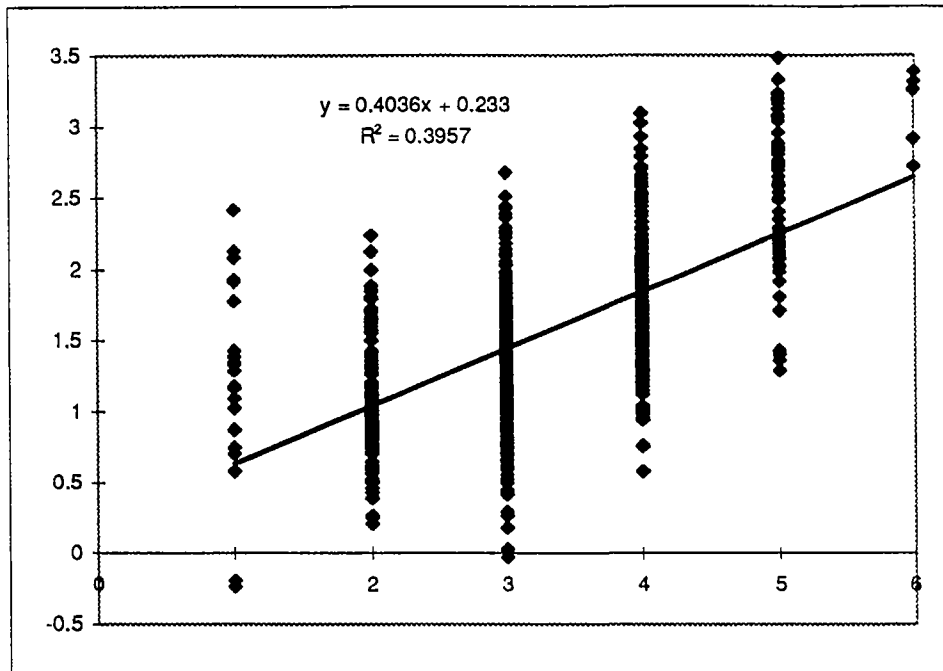


Figure F.2 Relationship between (log) stream width and stream order (1:50,000)

By relating the two graphs, we obtain the relationship:

$$S_{625} = 0.498 S_{50} - 0.2191$$

where:

S_{625} is the stream order at 1:625,000; and

S_{50} is the stream order at 1:50,000.

By assuming a proportional change in width and stream order with map scale, i.e.

$$S_{50} = (575 / 375) S_{250} - (200 / 375) S_{625}$$

we obtain the relationship:

$$S_{50} = 1.2115 S_{250} + 0.0923$$

which is given in tabular form in Table 4.5.

Table F.1 Approximate relationship between stream order (1:250,000) and stream order (1:50,000)

S_{250}	S_{50}
1	1.3
2	2.5
3	3.7
4	4.9
5	6.1

-

-

APPENDIX G RELATIONSHIP BETWEEN STREAM ORDER AND WETTED WIDTH

To convert the river lengths into areas, it was necessary to estimate stream widths. The most readily available data was from the HABSCORE dataset, with additional sites from larger Northumbrian rivers. A simple quadratic model was developed to relate width to stream order and altitude (Table G.1 and G.2). It must be stressed that this model is used here only as an approximate method for demonstration purposes only.

Table G.1 Model relating stream width to altitude and stream order

	estimate	s.e.	t (434)
Constant	1.5177	0.0304	49.97
alt-141.9	-0.000357	0.000291	-1.23
order-3.37	0.4314	0.0230	18.73
(order-3.37) ²	0.1013	0.0182	5.56

Table G.2 Accumulated analysis of variance for model relating stream width to altitude and stream order

Change	d.f.	s.s.	m.s.	v.r.	Fpr.
+ alt-141.9	1	3.7227	3.7227	15.39	<.001
+ order-3.37	1	90.5870	90.5870	374.41	<.001
+ (order-3.37) ²	1	7.4675	7.4675	30.86	<.001
Residual	434	105.0036	0.2419		
Total	437	206.7808	0.4732		

Note: Percentage variance accounted for 48.9.

The outputs from the model are tabulated in Table G.3.

Table G.3 Predicted stream width (m) for altitude and stream order classes

Altitude class	1:250,000 scale 1:50,000 scale	Stream order				
		1	2	3	4	5
0-50		3.0	3.5	5.6	11.9	34.3
50-100		2.9	3.5	5.5	11.7	33.7
100-150		2.9	3.4	5.4	11.5	33.1
150-200		2.8	3.3	5.3	11.3	32.5
200-300		2.8	3.2	5.2	11.0	31.7
300-400		2.7	3.1	5.0	10.6	30.6
400-500		2.6	3.0	4.8	10.3	29.5
500-600		2.5	2.9	4.6	9.9	28.4
600-700		2.4	2.8	4.5	9.5	27.4
700-800		2.3	2.7	4.3	9.2	26.5
800-900		2.2	2.6	4.2	8.9	25.6

**APPENDIX H DATA USED TO CALIBRATE THE ROD
CATCH MODEL (SECTION 5)**

River name	Region	S	N	R	r	w
River Calder	North-west	19984	0	14	1036	106309
River Derwent	North-west	34547	0	664	5570	208383
River Duddon	North-west	3286	25	19	382	32269
River Ehen	North-west	9271	0	92	3922	81252
River Ellen	North-west	5172	0	6	645	43323
River Esk	North-west	47129	0	37	555	366026
River Irt	North-west	4938	0	31	1136	56851
River Kent	North-west	15632	104	422	4939	102034
River Leven	North-west	16197	14	31	1958	125403
River Lune	North-west	70348	2969	1434	17124	426885
River Ribble	North-west	42602	205	608	14633	263379
River Wyre	North-west	10672	0	18	1278	124817
River Avon	South-west	4447	0	24	512	50571
River Camel	South-west	8996	148	307	4388	107126
River Dart	South-west	25107	520	119	3606	174748
River Exe	South-west	63867	714	642	4432	486882
River Fowey	South-west	12890	125	203	4528	80089
River Lyn	South-west	15028	27	118	847	68711
River Lynher	South-west	5198	317	85	2156	46920
River Plym	South-west	5927	0	28	869	49239
River Tamar	South-west	47423	1544	428	3792	352694
River Tavy	South-west	7102	485	166	2815	63021
River Taw	South-west	48341	0	232	4271	395379
River Teign	South-west	21938	977	147	3683	171681
River Torridge	South-west	39141	0	167	2142	310462
E+W Cleddau	Welsh	27674	51	76	1943	148065
River Aeron	Welsh	11764	0	11	1285	82655
River Afan	Welsh	6542	0	7	1390	42909
River Artro	Welsh	3000	0	8	173	25341
River Clwyd	Welsh	46609	238	122	5213	326742
River Conwy	Welsh	49061	51	195	4125	304976
River Dee	Welsh	105349	1157	455	8522	729759
River Dwyfawr	Welsh	6464	4	9	1172	60021
River Dwyryd	Welsh	8221	0	23	1541	69923
River Dyfi	Welsh	56889	28	222	5778	404179
River Dysinni	Welsh	9479	1	8	1521	85144
River Glaslyn	Welsh	7311	2	18	971	78634
River Llyfni	Welsh	3319	0	19	1039	29802
River Loughor	Welsh	10090	0	8	1776	89821
River Mawddach	Welsh	10015	1	115	7213	79581
River Neath	Welsh	12620	0	14	1139	95149
River Nevern	Welsh	2784	19	25	1224	25779
River Ogmore	Welsh	9711	0	59	3926	97556
River Ogwen	Welsh	8425	69	95	968	51001
River Rheidol	Welsh	22711	0	18	750	117661
River Taf	Welsh	21964	13	64	2350	220506
River Taff	Welsh	44319	0	43	485	194143
River Tawe	Welsh	12595	0	20	4229	111871
River Teifi	Welsh	75697	120	433	11345	545038
River Tywi	Welsh	95480	135	388	22613	599773
River Usk	Welsh	163595	1226	735	7271	550875
River Wye	Welsh	382217	6	798	14511	1965158