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as discerned for an eastern Scottish river**

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Executive Summary

It is widely acknowledged that Atlantic salmon (*Salmo salar*) sub-stocks exist in Scottish rivers. These sub-stocks are associated with diverse life-histories, relating to different environments and pressures. However, there are significant challenges associated with the analysis of populations at the sub-river scale.

This report investigates the potential for assessment of fish populations at a sub-river scale. A sophisticated mathematical model was used to separate salmon from a single river (North Esk, eastern Scotland) into three sub-stocks, based on the number of years the adults have spent at sea (their sea-age) and the month of the year in which the adults return to freshwater to breed (their run-timing).

The model showed that the three proposed sub-stocks were characterised by different trends in abundance over time, and dissimilar patterns of fecundity and recruitment of juveniles. These findings were underpinned by extensive data spanning three decades and were robust to three wide ranging marine mortality scenarios (a process which is poorly understood). However, despite the North Esk being the best studied river in Scotland, detailed examination of the consequent productivity estimates showed that the overall situation was inadequately described by the current combination of data and models.

Nevertheless, the findings illustrate the potential benefits to salmon management of describing a fishery that is composed of disparate sub-stocks in terms of its component parts, rather than assuming a single, common, stock. Attention is also drawn to the challenges and risks of transferring fishery management criteria between well-studied rivers and rivers with less detailed information, where those rivers are characterised by markedly different sub-stock compositions.

Abstract

Modelling an Atlantic salmon (*Salmo salar*) population as three phenotypically homogeneous sub-stocks showed different sub-stock dynamics and time-trends, a finding which was robust to three quite extreme variations of marine-mortality scenarios. A process-centred demographic analysis of a phenotypically mixed population (river North Esk, eastern Scotland) separated the life-cycle into two portions: density-dependent (spawner to smolt), represented by a stock-recruitment relationship; density-independent at sea and in both the estuary and river during

return to spawning sites. Extensive data spanning three decades was judiciously used to parameterise the model for three phenotypically distinct sub-stocks (early-running multi-sea-winter; late-running multi-sea-winter; and one-sea-winter). Quantification of different population parameters was achieved for the putative sub-stocks, illuminating historical population-trends and underlying mechanisms. The approach forms a template for similar model decompositions at other rivers with similar data. Broad implications for salmon management more widely included the enhanced benefits of a process-based life-cycle model that described more phenotypically homogeneous sub-stocks (than a single-stock formulation) for the transport of population parameter values (or derived Biological Reference Points) from well documented (parameter-donor) catchments to data-sparse (parameter-recipient) catchments.

Introduction

Fishery managers frequently treat stocks as if they are homogeneous and fully mixing, an assumption that could have deleterious consequences if untrue. A number of wild Atlantic salmon (*Salmo salar*) stocks are thought to be below full reproductive capacity (ICES 2015), raising concerns from fisheries managers and conservationists (AST 2014). Consequently the need for local monitoring to facilitate management of remaining populations is accordingly very high (Chaput 2012). Achieving successful management is hampered by the species' complex life-cycle, which can vary very locally, within-catchments, and also by ongoing fishery exploitation.

In Scotland the Atlantic salmon fishery contributes in excess of £60m per annum to the rural economy (Riddington *et al.* 2002). Although historically dominated by commercial net fisheries, this contribution comes increasingly from the sporting rod-fishery (Radford and Gibson 2004), to which the larger 'multi-sea-winter' (MSW) fish are of greater value than smaller one-sea-winter fish (grilse, 1SW). These Scottish rod-fisheries (increasingly catch-and-release) benefit substantially from the fact that fresh-run, and thus 'catchable' (Thorley *et al.* 2007; Bacon *et al.* 2011), salmon are available in rivers somewhere in Scotland virtually throughout the year (Youngson *et al.* 2002; Stewart *et al.* 2002). By contrast, many other European countries have runs restricted to just a few months (e.g. May to July in Sweden, June to August in Norway, June to September in Iceland).

Scottish stocks of Atlantic salmon have changed appreciably over the last half century (Youngson *et al.* 2003; Vøllestad *et al.* 2009), with low catches of early-running MSW salmon being viewed with particular concern by fishery managers. Less attention has been focused on grilse, whose stocks and catches seem to have remained more nearly stable or increased, and on late-running MSW fish, whose stocks varied more than grilse (Anon 2009, 2013). Although the ultimate causes of these changes are matters of debate (Vøllestad *et al.* 2009; Bacon *et al.* 2009), the desire to preserve stocks of early-running MSW salmon has led to a number of local, national and international actions aimed at reducing fishery pressures, particularly on early-running MSW fish.

Scottish MSW salmon run throughout the year, but predominantly in the early part of the season, whereas grilse dominate the run in the later months. MSW returners are the main source of individually desirable target fish, but grilse are essential to maintaining numbers of potential target fish in late season. Thus the sea-age composition of catchment stocks is of central interest to Scottish fishery owners.

Early-running salmon on the Scottish east coast are broadly associated with upland spawning habitats, whilst late-run components mainly use lowland ones (eg Laughton and Smith 1992; for a discussion see Bacon *et al.* 2012). Although grilse in the large catchments of eastern Scotland are mainly associated with lowland spawning, a small number, and proportion, of grilse spawners are regularly found in surveys of upland sub-catchments. Such 'upland' and 'lowland' designations probably represent extremes of a continuum, and thus no clear habitat boundaries or spawning zones can be reliably defined.

The aim of this paper is to assess whether treating phenotypically distinguishable *putative* sub-stocks as a single fully-mixing stock might impair appropriate management decisions. We recognise that such phenotypes have both genetic and environmental influences, which are sufficiently complex that current data cannot fully reflect them; hence any modelling will be incomplete. However, we describe a pragmatic way of defining sub-stock phenotypes, which assumes independence of stocks and provides a sharp contrast to the assumption of 'fully-mixing' for single-stock models. Reality probably lies between these extremes, involving complex interactions between stocks (e.g. though: sub-stock mixing; assortative-matings; and heritabilities of phenotypes; all of unknown degrees). Nevertheless we consider it useful to contrast the merits of these different sub-stock paradigms for management purposes, as this highlights the strengths, weaknesses and risks associated with

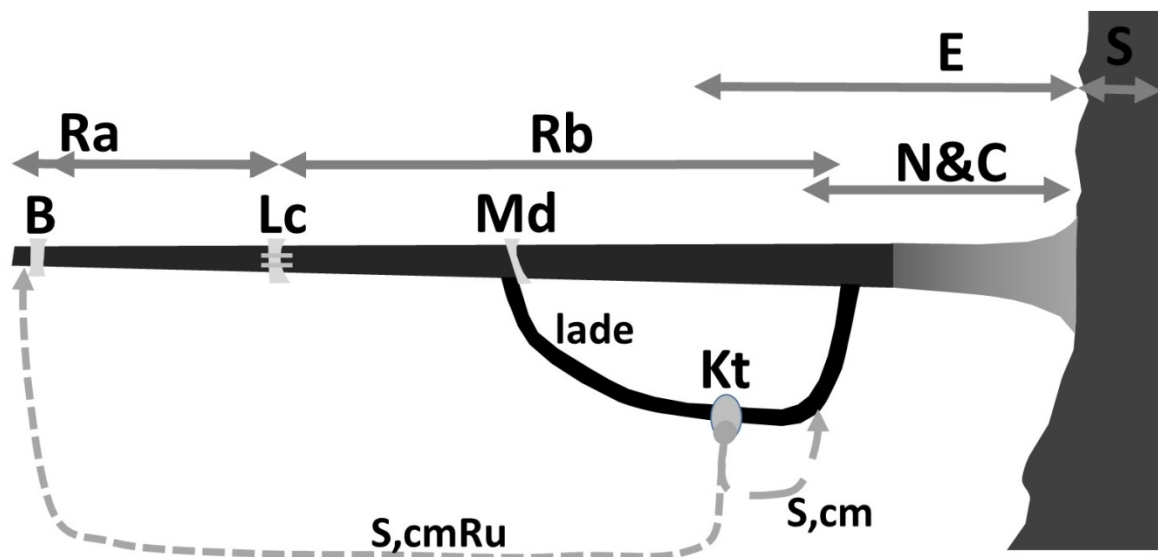
different approaches in the absence of perfect data and models. In order to develop an internally consistent set of demographic descriptions for the phenotypically differentiated sub-stocks (by sea-age and run-timing) which co-exist within many Scottish river catchments, one first needs to quantitatively integrate data from various life-cycle stages. Here we combined data from the monitoring of various salmon life-stages (smolt emigration; fishery removals; adult fish counter) on the intensively studied Scottish river North Esk.

Three subsidiary points were also addressed. The first was the potential impact of systematic sea-age reporting bias ('grilse error') in the salmon rod-catch data. The second was the demographic importance of inter-phenotype (sub-stock) breeding, which is known to occur, but whose impact on catchment population dynamics is currently unknown. The third was the impact of a number of changes in fisheries practice and management which have been made during the study period and that had the capacity (or indeed intent) of differentially influencing particular sub-stock components.

Materials and Methods

The River North Esk (Montrose, Angus, Scotland; 56° 42' 33"N, 2° 27' 57" E) is the only river in Scotland where data on adult returns, smolt output, fisheries mortality and on population demography, are collected and available at comparable and large spatial scales (the whole catchment). The North Esk is designated as Scotland's monitored salmon river, providing data to ICES and NASCO, and these detailed population data were used for this investigation. The layout of the various fishery and monitoring operations from the coast, through the estuary and along the river banks are shown schematically in Figure 1.

Figure 1. Diagram of the North Esk estuary showing the main features of the river, fishery and salmon population-study. The North Esk's main-stem is shown as the thick black horizontal line, flowing from the smolt-release bridge (B) down over the Logie salmon-counting weir (Lc), over the Morphie Dyke (MD), on through the estuary (E) and thence to the sea (S). At Morphie Dyke a portion of the river flow is diverted into an old mill-lade (lade), which forms the site of the Kinaber smolt-trapping weir (Kt). After the smolts have been marked a portion (S,cm) are released downstream in the lade to migrate straight to the estuary, and the remaining portion (S,cmRu) are transported a few kilometres upstream prior to release at B (so that their re-capture can estimate the trap-efficiency). The spatial extents of the different fisheries in this stretch of river are indicated for: the estuarine net-and-coble (N&C); the rods below the Logie counter (Rb) and the rods above the Logie counter (Ra, which extend well upriver from the boundary of this diagram). Over 90% of the accessible wetted river area is above Lc, so the calculations enumerate the great majority of the entire breeding population



The local fishery board undertook a small amount of exploratory salmon-stocking during the study, but (given the approach and the low overall effort) that work is not believed to have resulted in any appreciable increases in smolt numbers. Indeed, as the stocked ova were obtained from wild North Esk salmon, studies elsewhere imply that there would likely have been no change or a small decrease (see Young 2013 and Bacon *et al.*, 2015).

Data Sources and Data Processing

Ages of Adult Salmon

Sea-age- and return-date-stratified data on both the numbers and weights of salmon catches, from both the net and coble fisheries within the North Esk estuary and for (groups of) rod-fishery beats (lengths of river owned by particular proprietors) within the North Esk, were available, from records provided by the proprietors and owners of all Scottish salmon fisheries from 1952 to the present day (see <http://www.gov.scot/Topics/marine/Publications/stats/SalmonSeaTroutCatches> [Dec-2014]).

The different sea-age phenotypes of Atlantic salmon are associated with different marine life-histories (see Malcolm *et al.* 2010 for a review). This contention is supported by stable isotope studies demonstrating differences in the marine diet among groups of Atlantic salmon returning to UK rivers (MacKenzie *et al.* 2012), differences in the marine growth performance of Atlantic salmon (Bacon *et al.* 2009) and by observed variations in temporal patterns of Atlantic salmon abundance (Youngson *et al.* 2002).

Scale analysis (Bacon *et al.* 2009; Bacon *et al.* 2011) yields strong confirmation of the high accuracy of the estimated sea-ages reported by the netsmen from their net and coble catches (based on visual assessment of body size). However, the Atlantic salmon sea-ages provided by the rod- and net- data-sets for the North Esk have differing accuracies and, importantly in the case of the rod-fisheries only, bias. A more restricted scale-ageing study of Scottish rod-caught fish (MacLean *et al.* 1996) confirms that rod-angler-reported sea-ages from the rod and line fisheries are appreciably inaccurate (much less accurate than the nets). . Accordingly, in this study, the angler-reported sea-ages for rod-caught salmon were corrected, based on data provided in MacLean *et al.* (1996), to form our default (grilse-error corrected) data-set (details of the correction procedure are given in Supplementary Material, part A).

Adult Counter

In 1980 (the starting date for the present study) a resistivity counter was installed at the Logie weir on the North Esk, some 6 km from the sea and some 1 Km upstream of the Morpie Dyke weir (Fig.1). The weir diverts water into the Kinnaber lade,

which is used to provide estimates of smolt numbers and ages (see below). Over 90% of the wetted river-area available to spawning salmon is above the Logie counter: although a few redds have been recorded between the counter and the head of tide, the great majority of the population is likely to spawn above the Logie counter. The Logie counter provides year-round counts of both upstream and downstream adult salmon movements, and the difference between upstream and downstream counts is used to enumerate total immigration. Sea trout are generally smaller than salmon in this river, and consequently these counts are not appreciably confounded by sea-trout. The counter results show that Atlantic salmon migrate into the North Esk in substantial numbers from February to November.

Commercial In-River Fishery

The net and coble fishery traditionally operated from February to August inclusive and provided scale samples from which the sea- and freshwater-ages of returning adults were obtained. This information was subsequently used to allocate sea-ages to fish passing over the counter (see below). Age estimates outside these months are based on smaller and less comprehensive samples. Since 1999, the start of the netting season has been delayed until May, somewhat altering the representativeness of the net and coble data in recent years.

Estimating numbers of grilse and MSW fish emigrating past counter

The estuarine net and coble fishery is neither age- nor size-selective, (due to the small mesh-size used and its method of deployment) so the salmon escaping this fishery were assumed to contain the same fraction of grilse as the net and coble catch (F_N). If, over some period (say a month), the rod fishery in the part of the river between the estuary and the counter catches a total of T_{RB} fish of whom an (accurately evaluated, scale-read) fraction F_{RB} are grilse, then, provided natural mortality is small compared to fishery mortality, the fraction (F_C) of the grilse in the resistivity counter's total for the same period (T_C) is given by

$$F_C = F_N + \frac{T_{RB}}{T_C} [F_N - F_{RB}] \quad [1]$$

A short derivation of this formula is provided in Supplementary Material, part D. This relationship, using the rod-catch grilse proportion from below the counter (corrected according to the prescription detailed in Supplementary Material, part A) was used to

determine the grilse to MSW ratio in the overall (nett, total flux) monthly population flow measured by the Logie counter.

Estimating Pre-Estuary abundance

The numbers of salmon (by sub-stock) entering the estuary were assumed to be equal to the sums of the catches plus the fish passing the counter (thus any fish spawning below the counter were hence omitted from this pre-estuary abundance (PEA) estimate). Assuming that natural mortality (and, in recent years, mortality associated with catch-and-release by rods) is small relative to direct fishing mortality. If so, then subtraction of the monthly aggregated sea-aged rod kill (i.e. numbers caught, killed and retained, adjusted for grilse-reporting-error) above the Logie counter from the sea-aged nett monthly immigration past the counter yields the sea-age and run-time stratified spawner counts which were one of the key data inputs to this investigation. The other central input was the sea-age and run-time stratified abundance of individuals returning to the estuary (the pre-estuary abundance, hereafter PEA), which was obtained by adding the monthly aggregate sea-age stratified estuarine net and coble catches to the monthly rod kill below, and the monthly aggregated immigration past, the Logie counter. In this study PEA was used to provide more precise single-catchment numbers than 'pre-coastal home-water fishery abundance' (PCHWFA), which is used in national and global assessments, but whose 'coastal catch' sub-components cannot be accurately ascribed back to particular rivers.

Smolt trap and estimates of smolt numbers

Annual smolt number estimates were obtained from the North Esk since the early 1970's. A capture-mark-recapture programme at Kinnaber Mill, close to the tidal limit of the North Esk (Fig.1) operated from late March to June or July, until several days in a row when no smolts were observed (Sheerer 1992). The Kinnaber Mill lade receives a portion of the North Esk flow and typically takes 5% to 10% of total emigrants. Smolts are caught and marked at a total-trap across the Kinnaber Mill lade (the trap is 100% efficient except on the rare occasions it spills). Known proportions of those marked smolts are transported back upriver and the proportion of such released-and-marked fish subsequently re-captured in the lade allows estimation of sampling efficiency and thus total numbers (Shearer 1992; Bjorkstedt 2005). The resulting estimates of total smolt output formed the third input to our

analysis, and were sub-dividable into smolt (freshwater-winter) age-classes by scale-readings from samples of Kinnaber smolts.

Data Analysis

Density-dependent and Density-independent Life-cycle Segments

Many studies have demonstrated that the major density-dependent processes in the life-cycle of Atlantic salmon occur during the freshwater stages (eg Jonsson *et al.* 1998; Gurney *et al.* 2010) and that the demographic processes between emigration to sea as a smolt and return to the spawning grounds as an adult are essentially density-independent (eg Gurney *et al.* 2010).

In this analysis the density-dependent part of North Esk's salmon population life-cycle was regarded as starting with the return of adult spawners to their natal habitat and ending with emigration of their progeny to sea as smolts. For each distinct sub-stock, this part of the life-cycle was characterised by a separate stock recruitment relationship. The available information about the density-independent parts of the life-cycle was heavily concentrated in the segment between return to the estuary and spawning, so this segment of the life-cycle was treated separately from the segment between smolting and return to the estuary (hereafter referred to as 'at sea').

The 'at-sea' portion of the Atlantic salmon life-cycle, while complex, shows no evidence of density-dependence. It is composed of fisheries mortality in both distant water (oceanic) and coastal commercial fisheries and predation mortality in both oceanic and coastal locations. For all of these there is little or no information that can be reliably attribute fish to the North Esk. At-sea survival is also affected by survival and growth processes that are complex, poorly understood and likely to vary in both space and time (eg Eriksson 1994; Friedland 2013; McGurk 1996; Salminen *et al.* 1995). This study required an objective approach to characterise the at-sea mortality of *specific cohorts* (hereafter smolt-year-classes) of sub-stocks (spent differing periods at-sea and having appreciably differing body sizes on return). As we could find no suitable quantitative data for Atlantic salmon that could be generalised to Scottish fish, we here adapted an allometric approach based on McGurk's (1996) results for Pacific salmonids.

The sizes, sea-ages and seasonal return times of Scottish Atlantic salmon vary within seasons and have varied over time (Bacon *et al.* 2009): by the 1970s the

number of three sea-winter (3SW) salmon at the North Esk (and on the eastern coast of Scotland more generally) had declined to near zero. The proportion of previous-spawners is also very low (1.7% on the Scotland east coast generally, Bacon *et al.* 2009) and only 0.9% for the North Esk. Consequently, the sea-age structure was simplified by treating the repeat-spawners and 3+SW salmon as 'MSW' fish, but characterising their periods at sea as if they were 2SW (hereafter 2SW'). Average periods at sea (assuming a median smolt emigration time of May for all smolts and a median monthly return time for each of the proposed sub-stocks based on their scale-read ages and counts) were used for each putative sub-stock, of 16, 22 and 28 months for grilse, early- and late2SW' fish respectively, with associated mean sizes at return of 60, 72.5 and 80 cm fork-length respectively.

Estimating Sub-population Smolt Production and Sea-survival

To partition smolts among phenotypic stocks we denoted the number of individuals of sub-stock i returning to the river in year y by $R_{i,y}$, the total smolt production that year as P_y and defined an (unknown) quantity $\varphi_{i,y}$ to represent the proportion of the year y smolt output who will, if they survive, return to the river as sub-stock i individuals. Finally we denoted the proportion of sub-stock i individuals going to sea as smolts in year y who will survive to form part of the pre-estuary population in year $y + \tau_i$ as $S_{i,y}$ so that

$$R_{i,y+\tau_i} = \varphi_{i,y} S_{i,y} P_y \quad (2)$$

As The $\varphi_{i,y}$ (proportions i of the year y smolt production), must sum to one over all sub-stocks, for each year. Hence we know that for each and every year y

$$\sum_{all\ i} \varphi_{i,y} \equiv \sum_{all\ i} \left[\frac{R_{i,y+\tau_i}}{S_{i,y} P_y} \right] = 1 \quad (3)$$

Equation (3) is little use, because it contains as many unknowns as there are sub-stocks. However, if, for each sub-stock i , we can relate each $S_{i,y}$ to a single year-class-dependent constant, ε_y , so that

$$S_{i,y} = \mathcal{S}_i(\varepsilon_y) \quad (4)$$

then equation (3) becomes

$$\sum_{all\ i} \varphi_{i,y} \equiv \sum_{all\ i} \left[\frac{R_{i,y+\tau_i}}{\mathcal{S}_i(\varepsilon_y)P_y} \right] = 1 \quad (5)$$

which, for each year in which total smolt output P_y and subsequent pre-estuary numbers $\{R_{i,y+\tau_i}\}$ are known, can be solved for the single unknown ε_y . Although few variants of equation (5) have closed-form solutions, its general case is readily treated numerically (we used *optimise* from the R package, R Dev. Team, 2011).

Once we know ε_y , we can calculate the proportional survival from smolt to returner ($S_{i,y}$) of sub-stock i individuals emigrating to sea in year y from equation (4) and the number ($p_{i,y}$) of such individuals from,

$$p_{i,y} = \varphi_{i,y}P_y = \frac{R_{i,y+\tau_i}}{S_{i,y}} \quad (6)$$

The time-series of smolt to PEA survivals calculated from this process for any given sub-stock are related by a non-linear transformation defined by our assumption about \mathcal{S}_i , to those for other sub-stocks whose smolts form part of the undifferentiated smolt-output observations.

Modelling Smolt to Pre-estuary Survival

One needs an explicit definition of the function $\mathcal{S}_i(\varepsilon_y)$ to model smolt to pre-estuary survival. However, a number of plausible alternatives exist, given the paucity of data to test such models.

A simple formulation for smolt to pre-estuary survival, which we called the *uniform risk-rate (UR) model*, assumes that all individuals (of whatever sub-stock) who emigrate in year y are subject to the same *per-capita, per-unit-time* mortality rate while at sea. In this formulation, if sub-stock i individuals spend m_i months at sea, then ε_y is the at-sea mortality rate for individuals emigrating in year y and set

$$S_{i,y} = \mathcal{S}_i(\varepsilon_y) = \exp[-\varepsilon_y m_i] \quad (7)$$

A potentially much more realistic formulation can be found in the work of McGurk (1996) who examined the marine-mortality of a number of species of Pacific salmon, and concluded that the marine survival (s) of a species whose individuals go to sea at weight W_0 and return to spawn at weight W_s can be well described by

$$s = \exp\left[-\frac{\alpha_m}{\beta_m} (W_s^{\beta_m} - W_0^{\beta_m})\right] \quad (8)$$

Although the values that McGurk obtained for his parameters α_m and β_m varied considerably between species, the form seemed highly robust, so we shall postulate that the allometry parameter (β_m) remains constant over time for a given sub-stock, and identify the ratio (α_m/β_m) with our sub-stock independent smolt-year parameter ε_y . Hence we write

$$\mathcal{S}_i(\varepsilon_y) = \exp[-\varepsilon_y W_i] \quad \text{where} \quad W_i \equiv W_{si}^{\beta_m} - W_0^{\beta_m} \quad (9)$$

In this formulation, W_0 represents the sub-stock independent smolt weight and W_{si} represents the spawning weight of sub-stock i individuals.

We examined two variants of this allometric model, which were differentiated by the value chosen for the allometry parameter β_m . Our *default allometric mortality (DAM)* model used the value of β_m found by McGurk as most suitable for a composite dataset encompassing all five species of Pacific salmon covered by his study, namely $\beta_m = -0.37$. As an alternative quite extreme case, but which McGurk (1996) argued was also well supported, we examined a *uniform survival (US)* model, in which all sub-stocks have the same smolt to pre-estuary survival (N.B. this implies considerably different marine-mortality risk-rates), which we achieved by setting $\beta_m = 0$

Estimating Stock Recruitment Relationships

Relating stock and recruits

For each of the sub-stock decompositions, the data described above either provides directly, or allows one to infer, yearly time-series of both spawning stocks and their subsequent smolt outputs. To use these data as the basis of a stock-recruitment relation requires one to associate spawning stock in one year with recruitment (smolt output) at some later time - a process which is materially complicated by individual to individual variability in time taken to develop from ova to smolt.

The actual freshwater age distributions of cohorts of North Esk smolts going to sea is well established from large samples of smolt scales obtained from Kinnaber lade (for details see Todd *et al.* 2012). The smolt-age distribution at the North Esk (which is rather typical of east-coast Scottish fish (Bacon *et al.* 2011)) has changed slightly over the duration of our study period (Todd *et al.* 2012), and the annual age-stratified estimates (i.e. including the trend, its annual fluctuations and any recording errors) were hence used here, with one simplification; to maximise data-points (by reducing data-loss from ‘end-effects’¹) consequent on collating smolt contributions over four freshwater-emigrant age-classes, from S1s to S4s), the smolt-ages considered were amalgamated into S2’s and S3’s (S2’=S1+S2; S3’= S3+S4), ignoring the small average contributions of S1s and S4s (6.9% and 0.5% respectively).

To determine the total smolt output ($O_{i,y}$) associated with the year y spawning stock for a particular sub-stock ($A_{i,y}$), we define $\psi_{d,y}$ as the (sub-stock independent but calendar year dependent) proportion of the yearly smolt production ($p_{i,y}$) which smolt in the d^{th} year after ova deposition and thus see that

$$O_{i,y} = \sum_{d=1}^{\infty} \psi_d p_{i,y+d} \quad [10]$$

¹ If one has X calendar years of spawner-production data, this can only be modelled in full (to calculate the production of their ova) once (a) their oldest-aged smolts and (b) the oldest-sea-aged adults of those smolts, have all returned. Thus data is lost from the end of the time-series of X spawner-production years until those census results have been collated. To increase our sample size, X , we here ignore the rare extremes of smolt-ages (4,5) and sea-ages (3 or older). The data loss is reduced if the more extreme age-classes are amalgamated.

Bayesian estimation of a stochastic stock-recruitment relation

Standard Bayesian methods were used to determine the parameters of a stochastic representation of the spawning stock to smolt production relationship (Gurney *et al.* 2010 B); see the Discussion section for an explanation of why an ova-to-smolt relationship was not used instead. The expected relationship between stock (A) and recruits (O) is here represented by a conventional Beverton-Holt (BH; Beverton and Holt, 1957) curve:

$$O \in \{O\} = \frac{O_{max}A}{A + H} \quad [11]$$

where O_{max} represents the maximum possible output (recruitment, here smolts) and H represents the spawner population needed to produce an expected recruitment of half the maximum. A further assumption made when setting up the model was that actual output values were Negative Binomially distributed around the expected value with a shape factor θ , which is approximately the inverse of the square of the coefficient of variation.

The maximum number of smolts produced per individual spawning fish was defined as:

$$\beta \equiv \frac{O_{max}}{H} = F B_o L_{os} \quad [12]$$

β can subsequently be decomposed into the product of the proportion of the spawning population which is female (F), the ova fecundity of the females (B_o) and the ova to smolt survival (L_{os}); see Supplementary Material, part I, for an illustration of how, and why this is useful.

As the life-history stages characterized by this adult-to-smolt stock recruitment relation are highly density-dependent, we used the prior-knowledge prescription of Gurney *et al.* (2010 B) to estimate initial informative 'control priors' to define the prior parameter distribution from which the Markov-Chain Monte-Carlo process calculated a posterior distribution, representing the sum of knowledge provided by our new data and the prior. If the data do not show the saturation implied by the informative prior, then the estimated curve will be more saturated than if estimated with an uninformative prior, and the precision of the parameter estimates will be a little *impaired* (see Gurney *et al.* (2010 B) for details).

The resulting posterior distributions provide estimates of both the most plausible values for the model parameters (O_{max} , H , θ), the most probable expected stock recruitment relation (ESR) and their credibility limits. After some experimentation, it was found that this process explored the posterior distribution rather efficiently, and that using a burn-in of 10^4 iterations, followed by a MCMC sequence of 2×10^4 iterations produced results which scarcely differed from those produced by an MCMC sequence a factor of 10 longer.

Changes in Fisheries Practice During the Study Period

A number of changes in fisheries practices occurred during the study period. Those which might be expected to generate changes in parameters reported in this paper include: reductions and subsequent phasing out of the distant-water fisheries in West Greenland (1971-1993) and the introduction (1978) and subsequent decline (ca. 1981-1992) of the Faroes fishery; change of the 'Morphie Dyke' net and coble fishery in the lower North Esk to a rod fishery in 1991; delayed start to the estuarine net-fishery season from mid-Feb to 1st April in 2000, and to 1st May in 2005; the gradual introduction of catch-and-release practices in the rod-fishery from the late 1990s (records kept since 1994) and, particularly, from 2001 onwards.

The first of these changes should alter the marine survival from smolt to pre-estuary adult (PEA) for sub-stocks visiting the fishery areas, while the remaining three will change the proportion of *pre-estuary adults who survive to spawn*. The listed management changes should all produce enduring rather than transient parameter alterations, so our strategy for detecting such effects in the presence of strong year-to-year variability was to look for alterations in the decadal smoothed mean values of the parameter concerned.

Evaluation Criteria

The adult time-series data, both pre-fishery and spawner numbers, are contrasted between the single- and sub-stock-scenario results to assess whether the resulting time-trends differed. Those direct adult count data were particularly reliable. In contrast, enumeration of the smolt numbers derived from much less direct and more variable estimates. Comparison of smolt production was accordingly made as follows. An index of smolt productivity, per female per putative sub-stock, i (and thus independent of sub-stock size), was obtained from the appropriate sub-stock's SR curve by estimating β (eqn. 12). We then took ratios, for different pairs of the β_i sub-

stocks, to assess whether one stock was relatively more productive than another². However, as the sub-stocks differed in average female body-sizes, and fecundity is size dependent, those SR derived productivity ratios were then themselves divided by body-length predicted fecundity ratios for the same pair of sub-stocks. The procedure resulted in a sub-stock comparison index whose expectation is 1.00 if the SR derived ratio and size-expectation ratio are identical. The size-expectations were calculated from North Esk results reported in Bacon *et al.* (2012). Expectations are here presented for two ova-productivity criteria (total ova volume and total ova numbers), with the ova numbers being calculated both from the standard (historic, upland) equation and also with an egg-number adjustment for their actual upland/lowland breeding locale, where appropriate; the full calculations are explained and illustrated in Supplementary Material, part E.

Results

The North Esk Population as a Single Entity

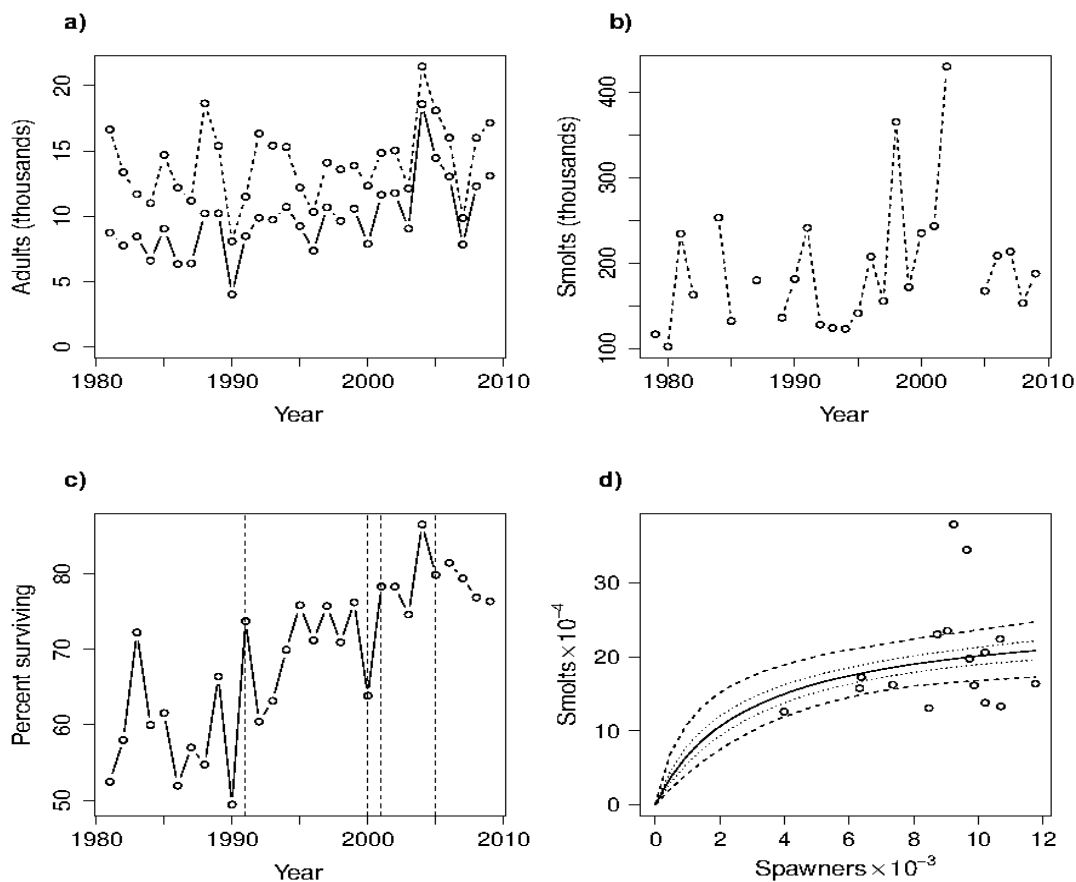
The aggregated totals (over all sea age classes) of pre-estuary adults and spawner numbers changed slowly over the study period (Fig. 2a), with the latter slowly approaching the former (as emphasised by the proportion of PEA surviving to spawn, Fig. 2.c). Total smolt-production was highly variable, with a slight overall increase (Fig. 2.b).

All of the fishery management actions (with the possible exception of catch-and-release (C&R), which took some years to become established), might be expected to produce an observable co-incident increase in the proportion of the pre-estuary population (PEA) which survives to spawn. However, only the 1991 change in the fishing method used at Morphie Dyke seemed to have been large and sudden enough to produce an immediate change that was big enough to be distinguished from year to year variability (Fig. 2.c).

² None of the sub-stocks had SR data particularly close to the origin, so none had data points near the origin exerting particularly strong leverage on the SR estimates of β . So all estimates of β should be similarly (un)affected by data near the origin, and hence their relative ratios robust to that (widespread) deficiency.

Figure 2. Demography of the North Esk salmon population viewed as a single entity, deduced using grilse-error corrected rod-capture data.

Frame a) shows numbers of adults returning to the estuary (PEA - dashed) and adult spawners (solid). Frame b) shows total smolt production. Frame c) shows percentage survival of pre-estuary individuals to spawn. Vertical dashed lines show management actions : 1991 - Morphy Dyke nets replaced by rods; 2000 - Net season delayed to 1st April; 2001 - rod caught MSW's released; 2005 - Net season delayed until 1st May. Frame d) shows the BH spawner to smolt stock recruitment relation. Points are data re-interpreted using equation 6. Solid line shows the median expected stock-recruitment relation, and the dashed and dotted lines show the 95% and 50% credibility limits. Note that frame (d) contains several fewer data-points than frames a-c. This is both because gaps in the annual smolt estimation record (frame b) prevent correct smolt totals being assigned back to birth-cohorts either side of the gap (according to number of age classes crossing the gap) and also because adults spawning from 2004 onwards do not have offspring returning as 2SW fish by the end of the data-series (needed to provide smolt sub-stock composition via equation 6, and here omitted for consistency with the sub-stock results of Fig.4 below).



Modal SR parameter values (posterior BH estimates) from the grilse-error corrected datasets showed slight differences from those derived from data *not* corrected for grilse-error, but the discrepancies were very small compared to the widths of their 95% credibility regions (Table 1 and Fig. 2d). The corresponding results for 'uncorrected' data are in Supplementary Material, part B. The estimated modal value of $\theta = 11.89$ implied that, with stochastic model predictions at a given stock level, the yearly recruit numbers will vary around their expected mean value (at that stock) with a CV of 29%.

Table 1. Posterior parameter distribution for the North Esk 1980-2004 spawner to smolt data regarding the system as comprising a single stock, and using a Beverton Holt Estimated Stock-Recruitment (ESR) curve with a control prior and using data corrected for grilse error. First two columns show the pair of parameters O_{max} , H , defining the BH SR curve-shape. The third column, θ , represents the negative binomial error distribution factor. The next two columns are biologically informative values derived from the former three columns. The fourth column shows the (approx) modal coefficient of error variation implied by θ (see Gurney *et al.* (2010), equation 2). The fifth column shows maximum individual productivity, β , (equation 8). The top line of each pair shows the mode and the lower line shows the upper and lower 95% credibility limits. See Supplement part B for the like results using un-corrected data (rod-catch data stratified using angler-reported sea-ages).

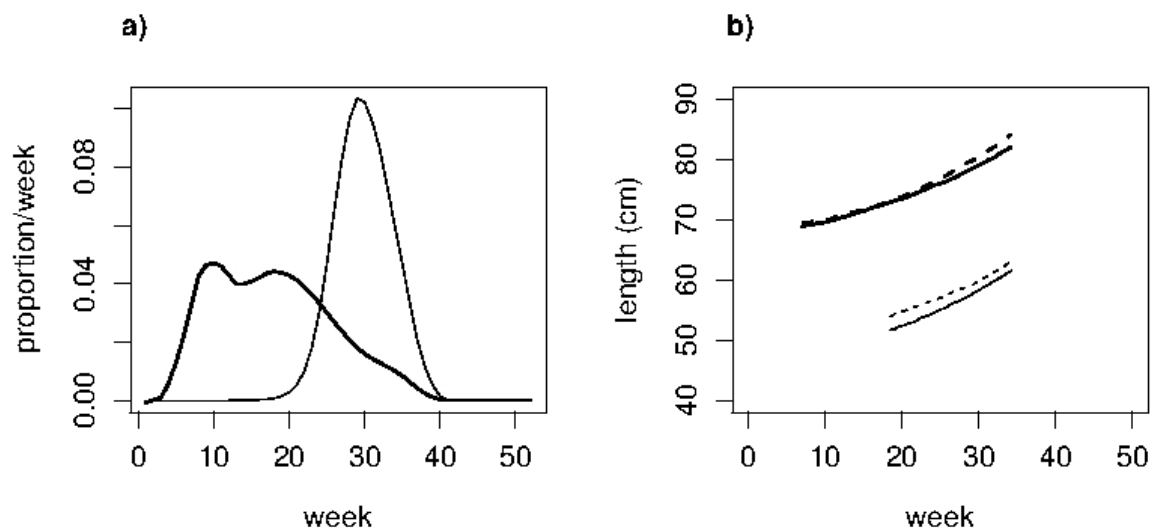
Parameters defining the BH SR curve		Estimated error		Derived biological param.s	
				CV(%)	β
O_{max}	H	θ		$\approx 1/\theta$	$\approx O_{max}/H$
Mode	mode	mode		mode	mode
2.5% 97.5%	2.5% 97.5%	2.5% 97.5%		2.5% 97.5%	2.5% 97.5%
Data Corrected for grilse error					
24.80 × 10⁴	2.232 × 10³	8.08		35%	111
20.00 × 10 ⁴ 36.71 × 10 ⁴	0.978 × 10 ³ 7.154 × 10 ³	3.85 17.09		51% 24%	51 204

Sub-stocks Partitioned by Sea-age and Run-time

The full 12 month difference in time spent at sea between the earliest returning adults from a given smolt-year-class (grilse) and the latest (late-running multi-sea winter fish), Fig. 3a, would prevent a simple mortality calculation (as a per-capita per unit time mortality rate) even for the total data-set. Although the smoothed distributions shown in Fig. 3a suggest that the recorded grilse run was uni-modal and confined to weeks 22-40, the MSW distribution was evidently both much broader and more complex, with fish running abundantly from weeks 5-25, and then declining gradually until week 40. Around week 20 to 21 was a convenient date on which to separate early- and late-running MSW components.

Figure 3. Smoothed within-year patterns of Atlantic salmon returns.

a) Proportion of total North Esk net & coble catches of multi-sea-winter (heavy line) and grilse (light line) made each week. b) Expected body-lengths of two sea-winter (heavy lines) and grilse (light lines) females arriving at the Scottish coast against week of arrival, with individuals who smolted at river age 1 being shown by a solid line and those smolting at river age 3 by a dashed line. Both frames are compiled from a compendium of data obtained over the period 1967-2003. Frame a) is smoothed using R-routine *supsmu* with default parameters. Frame b) is computed and redrawn from a GAM model of the characteristics of Atlantic salmon returning to the Scottish coast (see Bacon *et al.* 2009 for its justification).



Although it may have been desirable to similarly separate earlier and later running grilse, as was done for MSW fish, Fig. 3 indicated that any attempt to do so for grilse on or around week 21, would place the separator on the steepest portion of the grilse run-time distribution: it would thus yield results which were sensitively dependent on the overall choice of separation date, and also on any inter-annual variations in the actual return-date distributions. Unpublished attempts to separate smolts into adult-return phenotypes based on smolt characteristics (smolt-size, smolt-timing or smolt freshwater-age) were extremely unsuccessful. This study accordingly subdivided the modelled population into three sub-stocks: early-run MSW (fish running before June 1st); late-run MSW (on or after June 1st); and all grilse. This choice of three components also matched existing, pragmatic, management practices (i.e. the separation of early and late MSW fish and grilse), whose 01-June separation date was accordingly adopted.

A Sub-stock Structured View of the North Esk Population

Sub-stock productivity

Although the sub-stock results for early MSW fish closely resembled those for the single stock (Fig. 4.a vs Fig. 2.a), with spawner numbers approaching the pre-estuary numbers as the study period progressed (thus indicating increasing proportional escapement), results for both late MSW fish (Fig. 4.d) and grilse (Fig. 4.g) exhibited much weaker overall temporal trends and a lesser degree of convergence between PEA and spawner numbers. Furthermore, annual fluctuations for both sets of MSW fish were higher towards the start and end of the study period, whereas grilse showed bigger annual variations near the middle.

The Bayesian-estimated BH SR curves showed reasonably narrow credibility regions, with a few outlying points (Fig. 4.c,f,i). Note that those SR relationships were less similar than at first appears, due to factors of three and five difference in the maxima of their vertical and horizontal axes (necessary to clearly show details of the SR curves and the distribution of data-points around them). Ideally, a rigorous comparison of the SR curves would be performed using fish *densities* rather than numbers. Unfortunately this was not possible because the sub-catchment areas utilised by the different sub-stocks were unknown. The tabulated SR parameter values and 95% credibility regions (Table 2, Fig.4) showed that the uncertainties around the sub-stocks' SR estimates were quite large compared to the differences between them. Given the inability to re-scale to a common density, a useful

comparison was achieved by examining the 95% credibility estimates of β (smolts-per-female at low densities, Table 2).

The stock recruitment relationships obtained for both the early2SW' and the grilse sub-stocks broadly approximated the single stock results. Rather similar asymptotic numbers of smolts (60,000 vs 100,000) were produced by twice as many grilse of about half the body-mass of the early2SW's. The estimated noise parameters (θ) for these two relations, which imply CVs of 36% and 35% respectively, were closely comparable with the CV of 35% implied by the value of θ obtained using the same procedure on the aggregated (single-stock) data-set.

Figure 4. Demography of the North Esk salmon population viewed as three distinct sub-stocks (Early MSW, Late MSW and all grilse) derived using grilse-error corrected rod-capture data and the default allometric marine-mortality model (DAM). Note the use of different vertical scales between frames of the same type, needed to clearly illustrate the trends and the variation about those trends. Frames a), d) and g) show the yearly time-series of pre-estuary (dashed) and spawner (solid) numbers. Frames b), e) and h) shows a yearly time-series of sub-stock smolt production, estimated via the default allometric marine-mortality model (DAM). Frames c), f) and i) show the inferred sub-stock BH stock-recruitment relations (hundreds of adults, thousands of smolts); note the differing horizontal (stock) scales needed to show detail of the SR curves, their credibility regions and the data-point distributions around the relationships. The points are smolt data re-interpreted using equation 6 for annually varying smolt-age compositions truncated to two smolt age-classes, S2 & S3. The solid line shows the median expected stock-recruitment relation, and the dashed and dotted lines respectively show the 95% and 50% credibility limits

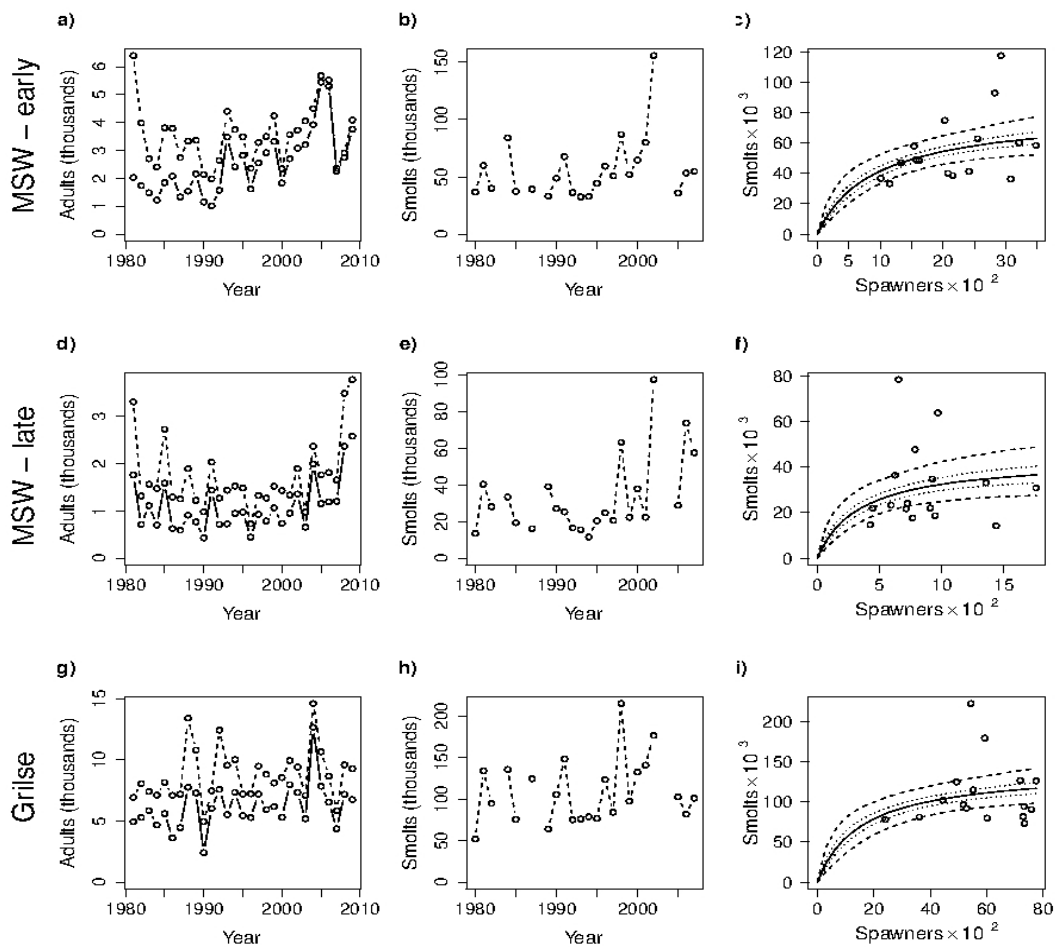


Table 2. Posterior parameter distribution for the North Esk 1980-2004 spawner to smolt data regarding the system as comprising three sub-stocks using the default allometric marine mortality model (DAM) and Beverton Holt ESRs with control priors. First two columns show the pair of parameters O_{max} , H , defining the BH SR curve-shape. The third column, θ , represents the negative binomial error distribution factor. The next two columns are biologically informative values derived from the former three columns. The fourth column shows the (approx) modal coefficient of error variation implied by θ (see Gurney *et al.* (2010) equation 2). The fifth column shows maximum individual productivity, β , (equation 8). The top line of each pair shows the mode and lower line shows the upper and lower 95% credibility limits. The upper section of the table shows results for the default (grilse-error corrected) data, while the lower section shows results without grilse-error correction.

Sub-stock	O_{max}		H		θ		CV(%)		β	
	mode	mode	mode	mode	mode	mode	$\approx 1/\sqrt{\text{mode}}$	$= O_{max}/H$	mode	mode
	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%				
<u>Data Corrected for grilse error</u>										
MSW early	7.52×10 ⁴		785		7.64		36%		95.8	
	5.95×10 ⁴	11.8×10 ⁴	330	2242	3.78	16.8	51%	24%	53	180
MSW late	4.11×10 ⁴		261		3.26		55%		157	
	3.13×10 ⁴	6.87×10 ⁴	125	874	1.65	6.78	77%	38%	78	250
Grilse	13.72×10 ⁴		1313		7.96		35%		104	
	11.1×10 ⁴	19.4×10 ⁴	585	3961	3.92	17.1	51%	24%	49	190

The SR results for the late2SW' sub-stock appeared much less similar to the others. First, the maximum expected recruitment (O_{max}) was a much lower proportion of the asymptotic values for early2SW' and grilse (55% and 30% respectively). Secondly, the half-saturation spawner stock was an even smaller proportion (20%) than that expected by comparison with the (approximately co-located) grilse population. Finally, the noise parameter had an appreciably higher value, with a CV of 55%.

An approximate expectation of the relative productivities of female grilse and lateMSW fish (via their average body-weights), suggests that lateMSW ova fecundity should be about 2.4 times that of grilse. So if their offspring approximately co-locate with those of the grilse, and developed at the same rate with the same survival, then their individual smolt productivity should be about 154. This value was extremely close to the modal value of $\beta = O_{max}/H = 157$ estimated via our MCMC determination of the model's parameters (Table 2). However, a similar comparison of the β values between early2SW' and grilse showed a large discrepancy, of a *factor* of two. Similar fecundity-ratio anomalies occurred between different sub-stocks for the other marine-mortality models (see *Productivity Implications...*).

Mortality Rates, Management Actions and Decadal Trends

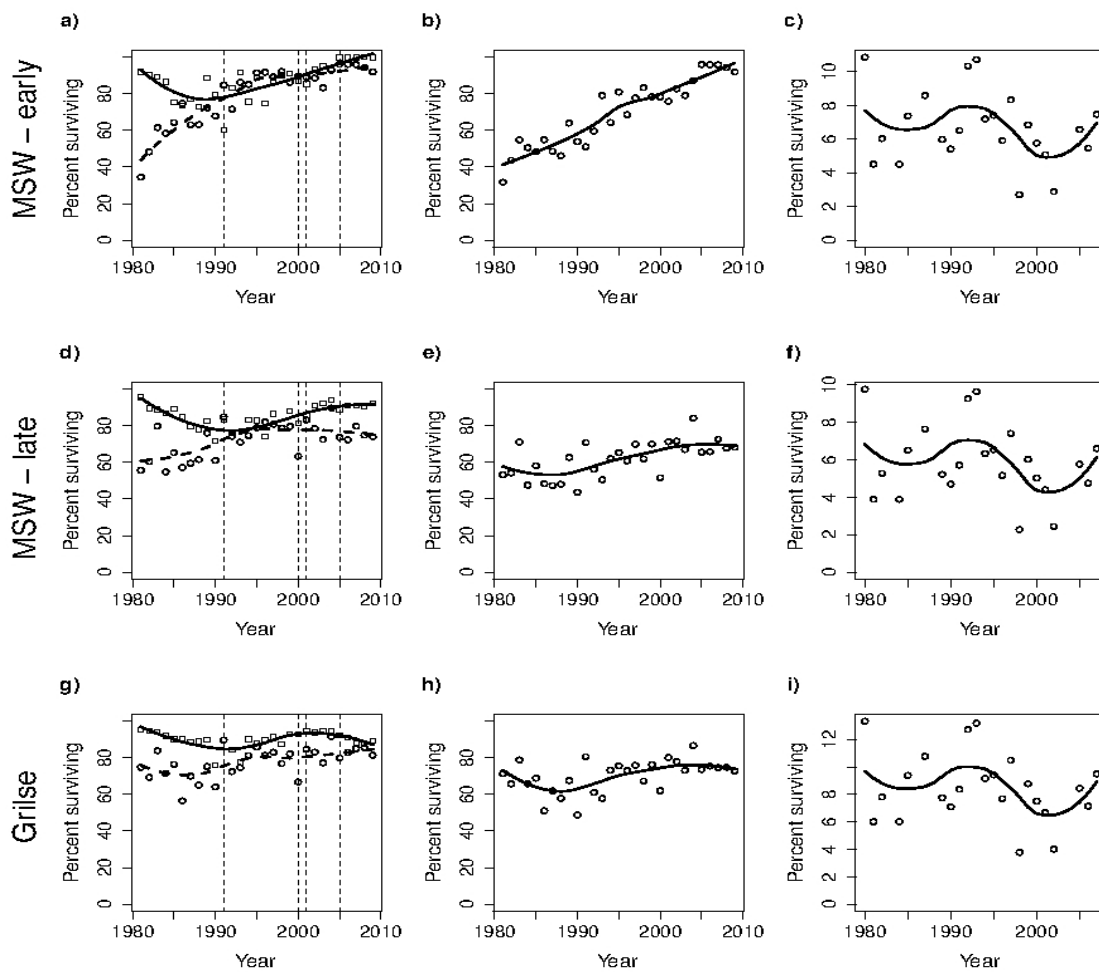
The magnitude and pattern of PEA escapement (i.e. the proportion of pre-estuary returning adults who potentially survive to spawn) differed appreciably between early2SW' fish and the two later-running sub-stocks. For early2SW' fish PEA survival increased more or less smoothly from only 40% in 1980 to nearly 90% in the late 2000's (Fig. 5.b). By contrast both late-run 2SW' fish and grilse showed about the same 60% escapement in the late 2000's as they showed in 1980 (Fig. 5.e,h respectively). In both cases the smoothed escapement dropped a little during the late 1980's and then showed a rise between 1990 and 2005, before dropping back to a value close to that in 1982.

The key driver of the multi-decadal change in PEA escapement for early-run 2SW' salmon was a steady increase in the proportion of fish surviving the estuary nets (Fig. 5.a), leading to a smoothed estuarine net-fishery survival which rose from 40% in 1980 to nearly 90% in 2008. EarlyMSW survival from the estuarine net-fishery thus increased appreciably over the decade 1980 to 1990, *prior* to the removal of the Morpie Dyke nets in 1991, and actually at a similar rate to the increase in net-survival between 1991 and 2000. These changes may well have resulted from economic pressures altering effort by the net-fishery. By the times of the two management-agreements that delayed the opening-dates to the netting-season

(2001, 2005), survival from the nets was already some 90% for early2SW', and, although net-survival continued to rise after 2001, it perforce increased more slowly (being already so close to 100%). Over the same period early2SW survival from the rod-fishery, which was over 90% in 1982, initially decreased to less than 80% in the late 1980's, before rising steadily to virtually 100% following the introduction of catch-and-release in 2005.

For grilse, the smoothed estuarine net-fishery survival changed much less, from roughly 75% to about 80% over the same three decades of the study, while the rod fishery survival, which was over 90% in 1982 dropped a little, to just above 80% by 1990, where after it rose almost to its 1982 value around 2003 before falling back to close on 80% by 2009 (Fig.5.g).

Figure 5. Decadal trends in the density independent parts of the life-cycle of three North Esk sub-stocks, derived using grilse-error corrected rod-capture data and the default allometric marine-mortality model (DAM). Frames a), d) and g) show the component processes of the overall pre-estuary to spawner survival shown in frames b), e), and h). For these frames (a,b, d,e, g,h) 'year' is the year the adults returned (and succumbed to/ survived the fishery, and spawned or not). Frames c), f) and i) show the smolt to pre-estuary survival: here (frames c,f,i) 'year' means the year of common smolting; note the slightly different scales for survival, used to show detail, across frames c,f,i. All frames show yearly values (points) and a smoothed trend (line) obtained by loess smoothing using R routine *loess* with default parameters. Frames a), d) and g, show the percentage of the pre-estuary numbers surviving the estuarine (net) fishery (circles with dashed line) and the percentage of those survivors who also survive the rod fishery (squares with solid line). Vertical dashed lines show dates of management interventions: 1991: Morphy Dyke nets moved to rods, 2000: net season delayed until April 1st, 2001: MSW rod-caught fish released, 2005: net season delayed until May 1st



The estuarine net-fishery survival of late-run 2SW' fish showed a similar pattern to grilse, which run the river at much the same time. Survival increased from only 60% in 1981 to nearly 75% by the mid-1990s, followed by a plateau to the early 2000s, with some suggestion of a small decrease thereafter (to 2009) (Fig.5.d). The rod survival for the late2SW' sub-stock also showed similar changes to the grilse sub-stock, decreasing from over 90% in 1981 to c. 75% in the early 1990s, rising thereafter to apparently plateau at some 95% around 2005 (Fig.5.d).

At-sea survivals showed two roughly decadal-period fluctuations during the study (Fig.5.c,f,i). As each of the three values is exponentially related to the smolt-year-classes' estimated overall survivals (equation 8), which is the same for all sub-stocks, the *pattern* of variation was necessarily the same for all sub-stocks; namely wide variability around a common, but quite flat, overall trend. The smoothed trends showed survival in 2005 being almost identical to that in the early 1980s, with a small drop centred on 1985 and a rather larger drop centred on 2000. However, the survival drop in the early 1980s (Fig.5) was heavily influenced by a single, very high, estimated survival for the 1980 smolting cohort. With the exception of the 1980 estimate, the pattern of survival would be quite consistent with a trend of declining oceanic fishery mortality, and thus increased survival, between 1980 and 1990. Due to its 1980 outlier, this particular data-set was thus equivocal about whether the magnitude of any changes in marine survival were co-incident with the regulation of the oceanic fisheries in West Greenland (1980) or Faroes (1990) (see Discussion, Marine Fisheries, below). However, it is important to note that in this analysis the marine mortalities were assumed independent of sea-age class (except in so far as sea-age is correlated to body-size or period at sea), whereas the marine fisheries were known to have affected only those sea-age classes which were exposed to the fisheries concerned, (primarily the MSW in the case of West Greenland). Hence the absence of an observable effect in a parameter which subsumes at-sea predation mortality with non-estuarine coastal fisheries mortality and distant-water fisheries mortality does not constitute strong evidence in either direction.

Comparisons Across Data-sets and Models

The estimates of the demographic process parameters for early2SW' and grilse were rather insensitive to grilse-error correction, as were estimates of estuary-net survival for late2SW'. The major differences were in both the (large) magnitude and temporal variation of the rod-survival estimates for late-running 2SW' fish. The like results to Table 2 and Fig.5 for 'uncorrected' data are given in Supplementary Material part C.

Productivity Implications Contrasted Across Marine-mortality Models

If the present sub-stock models represented the real processes well, then their sub-stock productivity ratios (β s from Table 2) should have been close to the same productivity ratios discerned from the typical sizes of females for each sub-stock, but they were not. Table 3 shows that whatever mortality model was used to estimate productivity, the resulting expectation ratio for at least one sub-stock comparison was unbelievably large (for all three alternative productivity metrics). Detailed results for the other two marine-mortality models are illustrated and tabulated in Supplementary Material, parts F and G respectively.

In evolutionary and competitive terms, even just a 10% initial (to smolt-stage) production difference would be a huge (dis-)advantage to a sub-stock (eg Haldane 1924), yet over half (14/27) the tabulated values differed by more than 50%, and that seven differed by *factors* of between two to four or more (Table 3). Those larger discrepancies frequently involve the lateMSW/grilse comparison, which would be unaffected by the ova-size differences between river-zones (Bacon *et al.* 2012). Even the best fitting of the marine-mortality models (default allometric, DAM) produced unbelievable production ratios (for all three fecundity metrics) for grilse/earlyMSW. Plausible resolution of this problem might well be found from hypothetical inter-breeding and heritability modules. As an example, the SR curve that would result from the simple amalgamation of lateMSW with grilse was calculated (Supplementary Material, part E, Fig.E.1.d).

Table 3. The table gives a comparative productivity index, calculated between different pairs of sub-stocks, such that identical productivity estimates via both estimation routes would always produce an index value of 1.00. The rows show the different pairs of sub-stocks compared. Blocks of three columns show results calculated for three different marine mortality models. Within these triplet-blocks, individual columns show the index as calculated for different productivity metrics (calculated from Bacon *et al.* 2012 for typically-sized females per sub-stock). Shading and italic/bold font differences (see key) emphasise that none of the marine mortality models produce productivity estimates that are reasonably close to those expected (from female salmon of typical sizes and productivities for the same sub-stocks) across all sub-stock comparisons. Productivity metrics for typically-sized females per sub-stock are: Ova Vol.=total volume of all ova produced per female; Upl.Ova#s=total numbers of ova produced per female in ‘upland’ river zones (as normally used); Adj.Ova#s= numbers of ova produced per female adjusting for the up-/low-land spawning situations). MSW means Multi-Sea-Winter. See text for further explanation and Supplement part D for details of the calculation of the index values.

Standardised production ratios for three mortality models and three female production metrics

Sub-stock comparisons	Blocks are different models of Marine Mortality								
	Constant monthly Rate			Allometric, B>0			Allometric, B=0		
	Ova Vol.	Upl. Ola#s	Adj. Ola#s	Ova Vol.	Upl. Ola#s	Adj. Ola#s	Ova Vol.	Upl. Ola#s	Adj. Ola#s
Sub-stocks ratios	1	1	1	1	1	1	1	1	1
Early MSW / early MSW	1.74	1.87	1.29	1.21	1.30	0.90	1.02	1.10	0.76
Late MSW / early MSW	1.03	0.89	1.12	1.95	1.70	2.14	4.14	3.59	4.53
Grilse / early MSW	1.69	2.09	2.09	0.62	0.77	0.77	0.25	0.31	0.31
Late MSW / Grilse									

Shadings denote ratios not within the given ranges

Shading key

Range	Magnitude description
0.5~1.5	±50%
0.5~2	Factor of 2
0.25~4	Factor of 4

Discussion

The modelling approach presented here relied on extending well-established protocols for whole-river salmon population assessments (eg Chaput 2012; Crozier *et al.* 2003a; Potter *et al.* 2003) to a more detailed sub-catchment and sub-stock level, and separating density-independent marine-mortality from density-dependent processes in freshwaters (Jonsson *et al.* 1998). Our results provide strong evidence that sub-stock structure affected productivities and trends in abundance at the North Esk. In general, if such sub-stock dynamics are not considered, the 'overall' population dynamics may be misunderstood, which might impair the estimation of reliable Biological Reference-Points (BRPs). Additional data (see below) are needed to parameterise better models.

Single-stock catchment models assume either: that there are no sub-components (-stocks) with different population parameters (including mortality regimes); and/or (as an approximation) that the proportions of any sub-components are constant over time (so that any small biases are constant). However, international salmon management (ICES 2014) reports regional populations' statuses by the stock types MSW and grilse (having different oceanic feeding zones). Furthermore, Scottish salmon status assessments have treated earlyMSW (conveniently separable by return-date alone) differently for over twenty-five years (Youngson 2002). Our present findings add to the view that abundance trends and population parameters (especially fecundity aspects) potentially also differ between lateMSW and grilse populations at the North Esk. Failure to account for such differences could potentially have deleterious consequences for weaker within-river stocks. Given the ova-fecundity differences reported by Bacon *et al.* (2012) and de Eyto *et al.* (2015), there is now greater cause for concern that population parameter, and/or population composition, differences within and between catchments may matter appreciably.

Single-river BRPs are commonly applied to other sites because of the significant challenges involved in developing within-river stock-specific BRPs (Crozier *et al.* 2003b). Our analysis is the first attempt to quantify whether sub-stock differences could affect reference points, and it strongly suggested they do. Interestingly our analysis (Fig2a, Fig4a) shows that in the North Esk, the estimated single-stock trend in abundance was, perhaps fortuitously, rather similar to the trend of the earlyMSW component that was the managers' main focus. However it was not similar to our inferred trends for lateMSW salmon or grilse. Furthermore, there is no reason to

believe that such similarity between single-stock trend and earlyMSW trends would apply at other sites.

The model presented here is a paradigm for Atlantic salmon populations that contain phenotypically diverse sub-stocks. It was parameterised for large east-coast Scottish catchments, using practicable, intensive, large-scale monitoring data, supplemented by a simple, *generalised* spatial-structure for sea-age and run-time distributions within such a (Scottish) catchment. The key findings of large differences in the population dynamics between different within-river sub-stocks were robust to quite extreme variations in the marine-mortality sub-models. They showed two important differences between the putative sub-stocks. First, that trends and annual/decadal fluctuations in returning adult numbers differed appreciably between sub-stocks over time. Secondly, the relative fecundities of putative sub-stocks (as deduced from SR analyses) were strongly affected by details of the (presently somewhat unrealistic) marine-mortality models. In short, it was both desirable and possible to decompose the North Esk's Atlantic Salmon stock into sub-stocks: however, detailed examination of the consequent productivity estimates showed the overall situation was inadequately described by the current *combination* of data and models.

Long-term Trends in Population Dynamics

Survival at Sea

An accurate assessment of marine-mortality is required to model sub-stock population dynamics of Atlantic salmon ('return-rates', *sensu* Chaput 2012). This paper inferred marine survivals indirectly from sub-process models of: (i) smolt-allocation between sub-stocks; and (ii) relative marine-mortalities, based on return-sizes or periods spent at sea (which are themselves correlated to size and so also loosely correlated with survival). Both these present process-models were imperfect: the sub-stock phenotypes are unlikely to be completely genetically heritable; the degrees of sub-stock mixing and assortative-matings are unknown; and the fishes' periods at sea and return-sizes are only loosely correlated with survival. But our finding that estimated sub-stock trends and parameters still differed, given any one of three widely differing variants of the marine-mortality sub-model, was persuasive evidence that the sub-stock structuring is indeed important.

Speculation about the effects of alternative marine-mortality model variants would be unconstrained and uninformative in the absence of suitable data. If observed

changes in marine-mortality are either largely environmentally driven, or phenotypically plastic, then very detailed data on adult body-conditions and locations over time would be required to show this; such data are lacking and difficult to obtain. A better prospect lies in the discovery of suitable genetic markers for run-timing and sea-age. If found, and if those traits are reasonably heritable, such markers could allow heritability estimates of the phenotypic traits and, potentially the devising and parameterisation of better sub-stock models (by direct enumeration of smolt pheno-/genotypes). If the markers worked with DNA from fish-scales, such testing might well be possible from historical scale-collections which often include higher density situations than present populations.

In River (PEA to Spawner) Survival

The in-river PEA to spawner survivals were largely derived from direct adult-count data. Survivals of grilse and late2SW' from the North Esk's fisheries showed only small survival increases over the study period. In contrast, early2SW' salmon, the prime focus of management attention, showed strong in-river survival increases (40% to virtually 100%,). The ameliorative fishery constraints introduced to conserve earlyMSW salmon may indeed have partly induced those different trends. However, despite the detailed North Esk data, it was not possible to quantitatively partition the improvements between different management actions and other indirect process changes that were coincident (eg environmental or economic).

Reproduction

At high spawner densities and at a whole-river level, the total North Esk productivity was around 200,000 smolts (Fig.2.d), and equated to some 20, 35 and 18 smolts/spawner (for early2SW', late2SW' and grilse respectively). However, objective quantification of the smolt productivities per spawner at *low* population levels showed that the present over-simple reproductive model lead to unlikely sub-stock production estimates that varied too widely from one another. Proper incorporation of the true breeding structure (details of river-areas used by sub-stocks; sex-ratios; and assortative-mating patterns) and trait heritabilities (sea-age, run-timing and associated adult return-sizes), along with any consequent marine-mortality differences, would presumably do much to resolve these discrepancies (see Gurney *et al.* 2012). Lack of data currently prevents this.

Fecundities and Fecundity Anomalies

The maximum lifetime reproductive approach to productivity (Myers *et al.* 1999; Gibson *et al.* 2013) is powerful metric for comparing productivities across populations. Unfortunately lack of data precluded its use here.

The two most plausible candidate explanations for our observed productivity differences were either differing sex-ratios between sub-stocks (but sex-differences are far from able to bridge the gap - see Supplementary Material, part I, for an explanation of why) or else 'reproductive exchange' between the sub-stocks.

Reproductive exchange is most likely between grilse and lateMSW salmon, which are thought to be predominantly co-located in the lowlands (Bacon *et al.* 2012 and references therein). Grilse X grilse adult phenotype matings might produce not just grilse offspring but also a nett surplus of lateMSW offspring (*i.e.* they produce more MSW offspring phenotypes than lateMSW X lateMSW matings produce grilse offspring phenotypes); as also might grilse X lateMSW matings. Such explanation is entirely plausible. There is good evidence that the sea-age and within-year run-timing are heritable (Hansen and Jonsson 1991; Stewart *et al.* 2002; Vaha *et al.* 2010), as is development rate in both Atlantic salmon (Gjerde 1984) and other salmonids (Hankin *et al.* 1993). The likely degrees of heritability (eg Mousseau and Roff, 1987; Carlson and Seamons, 2008), combined with the sizes of the different North Esk sub-stocks (c. 6,000 grilse, 1,000 lateMSW), could readily make good our estimated fecundity discrepancy. Moreover, a sound numerical basis for the necessary mechanisms has already been provided (Gurney *et al.* 2012), which includes an evolutionary argument, the necessary population dynamics and has findings that are robust to a variety of inheritance mechanisms (trait-dominances, for the simplifying one locus, two allele case examined). Its complete genetic determination (as discussed by Gurney *et al.* 2012) would be an oversimplification, as environmental effects are also known to play a role in sea-age determination (Jonsson *et al.* 2013). But so too does genetics: reality is likely to be somewhere between the extremes (of completely genetic or environmental determination). Unfortunately, the genetic mechanisms and quantitative heritability values, necessary for an improved understanding of processes, are presently unknown (see Gurney *et al.* 2012).

The idea that these three *phenotypic* sub-stocks are neither genetically fully mixed nor fully independent is, of course, not new (Taggart *et al.* 2001; Webb *et al.* 2007),

although the corresponding genetic structuring has only recently been demonstrated (Vaha *et al.* 2010). The potentially important consequences for salmon management have often been ignored, given the general lack of appropriate information.

Managing a river like the North Esk as if the three phenotypic sub-stocks were *fully* independent will be slightly misleading (see next paragraph), at least until better data allow one to understand both the inter-breeding and the heritability consequences. However, it could also be argued that managing them as if they were a *single* stock would be much more misleading, given the very substantial differences in life history trends and parameters demonstrated here. Such single-stock approaches still occur: indeed a recent single-stock analysis (Massiot-Granier *et al.* 2014) uses much the same (but not all of) the North Esk data underlying the present analysis; but, as it has different assumptions, structure, data, data-corrections (no grilse-error adjustment) and emphases, and is based on so different a paradigm, it axiomatically reaches different conclusions.

Until the genetic interactions of the phenotypic sub-stocks are adequately understood, we note that treating a small lateMSW sub-stock as if it was fully independent (as here) is probably conservatively prudent (one would treat a small independent (isolated) sub-stock more cautiously than one that was insulated from deleterious influences by the contribution of offspring arising from the much larger grilse sub-stock (should this latter hypothesis be correct)).

Past Fisheries Management Actions and their Effects

There were appreciable challenges in assessing the effects of oceanic-fisheries' management actions (West Greenland, Faeroes) on the North Esk's salmon populations. Clear trends were not evident. The poorly-realistic marine-mortality models, allied with a high year-on-year variability in the estimated marine survivals, and exacerbated by one particularly extreme (high) survival estimate at the start of our data-series (see Supplementary Material, part J.1, for details of the strong effect of the 1980 cohort), obscured any clear underlying trends in marine survivals, despite the sub-stock decompositions attempted here.

More surprisingly, the effects of management actions which restricted the North Esk's within-river fisheries were also rather unclear, and could not be confidently ascribed to that cause alone. Unfortunately, as PEA abundances are not measured

at adjacent Scottish rivers, it is unknown whether similar in-river survival improvements also occurred elsewhere.

It should be noted that some biological mechanisms could potentially cause *delayed* responses to ameliorative management actions, thus blurring the expected synchrony of cause and effect. Assuming that run-times are heritable, Fishery Induced Evolution effects (FIE; for brief overviews see Heino and Dieckmann 2009 and Stenseth and Dunlop 2009; for summary reviews see Allendorf *et al.* 2008; Fenberg and Roy 2008; Jørgensen *et al.* 2007; Law 2007; Kuparinen and Merilä 2007) could result in salmon populations' responses to *previous* fishery-selection pressures becoming manifest as *delayed* changes. Any such prior-induced changes might then have carried over into our study period. However, such FIE effects on run-timing would be expected to also alter the seasonal distribution of run-times observed *during* our study (within the sub-stocks, to seasons that better matched months with reduced risk from fishing). Examination of the North Esk data (not reported here) failed to find such changes.

Implications for Future Salmon Population Management

The key to progress in our sub-stock study was to focus on the *fewest* sub-stock phenotypes (so as not to overwhelm the available data) that were biologically realistic and also of management interest.

In the absence of correction, the mis-reporting by rod-anglers (in Scotland) of some grilse as being the less-common lateMSW salmon (MacLean *et al.* 1996) can result in appreciable over-estimation of the uncommon, but important lateMSW sub-stock. Recording of the sizes and dates-of-capture of individual Atlantic salmon (Bacon *et al.* 2011) could greatly reduce grilse-error, which will vary over space and time depending on fishery practices and staff (Maclean *et al.* 1996).

Of some 2,000 rivers that support Atlantic salmon populations world-wide (Chaput, 2012) only 15, around 1%, have suitably detailed population data for SR parameter estimation (Crozier *et al.* 2003a). However, around 25%, have "*annual river-specific stock assessments*" (Chaput 2012), comprising monitoring that may be assessed against a stock-recruitment relationship transferred from another, donor, river. So it becomes important to try and generalise the understanding gained from the few data-rich (parameter donor) rivers like the North Esk, in order to allow transfer of *appropriate* information to other (recipient) rivers (eg Chaput 2012; Crozier *et al.*,

2003a; ICES, 2011; MacLean 2007). However, as the composition of salmon populations (sea age, run timing) often varies between rivers it would seem inherently more useful and appropriate to transfer information for sub-stock components (assuming they behave differently). Such allocation could be done in proportion to sub-stock abundances if utilised spawning areas were unknown. Otherwise, transferring 'single-stock' estimates (which are amalgamated over all sub-stocks) from a 'donor' river which may well have a different sub-stock composition to the recipient river, risks inaccuracy.

Scottish salmon managers took early pre-emptive action to reduce exploitation of earlyMSW stocks, which, based on an assessment of trends in rod catches (assumed to be strongly related to adult returns), were then in decline. Many practical ameliorative actions are already underway for Scottish earlyMSW phenotypes (e.g. catch-and-release, delayed starts to fishing seasons; see <http://www.gov.scot/Topics/marine/Salmon-Trout-Coarse/game/conservationreg> [Feb-2015]). However, grilse and lateMSW phenotypes are still both widely confounded and poorly documented, making it hard to evaluate the sustainability of their (sub-)stocks, even in catchments where they probably predominate.

Our present analysis further emphasised the need for a sub-stock approach to Atlantic salmon rivers having diverse salmon phenotypes and spatially partially-segregated sub-stocks. It suggests that current information is inadequate to permit detailed modelling of such situations and draws attention to the considerations and types of new information [detailed population monitoring, genetic sub-stock-identification and spawning-zone delineation] which are most likely to lead to further progress and better management.

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Supplements

Supplement A

Definition of the Grilse Error Correction Procedure used in this paper.

The mis-reporting of 1SW (or grilse) salmon as multi-sea-winter fish was first documented by Shearer (1992), who noted that angler's distinctions were often carried out on the basis of fish weight without reference to scale samples. Bacon *et al.* (2010) give a statistically sound methodology for such distinction on a probabilistic basis, but that methodology was not available at the time the historical data used in this study was compiled. Moreover, the individual size and date of capture information which would facilitate retrospective application of the technique were not required parts of the reporting, and are thus not present in the data available to us.

MacLean, Smith and Laughton (1996) carried out a case-study of two Speyside estates, where scale samples were obtained from partial sub-samples of rod-catches, along with estimates of the overall ratio of grilse/MSW fish from both scale-reading and angler's reports. Both (Shearer 1992) and MacLean (FFL Pitlochry - pers.com.) state that anglers discriminations are made on the basis of simple, date-dependent, weight-thresholds, which are believed to vary between rivers, estates and even individual ghillies. Reporting done on this basis will grossly over-estimate rod-catches of MSW fish in every month in which grilse might be caught in significant numbers, especially from June onwards (Figure A.1). Table A.1 shows the weight thresholds used by the two estates in the Spey study (MacLean *et al.* 1996), together with the SALWRD size boundary, published by Bacon *et al.* (2010), for 50% of the fish being MSW.

Figure A.1 The weight-split-thresholds of the two Speyside Estates' and SALWRD discrimination boundary (see Table A.1) plotted against month of the year.

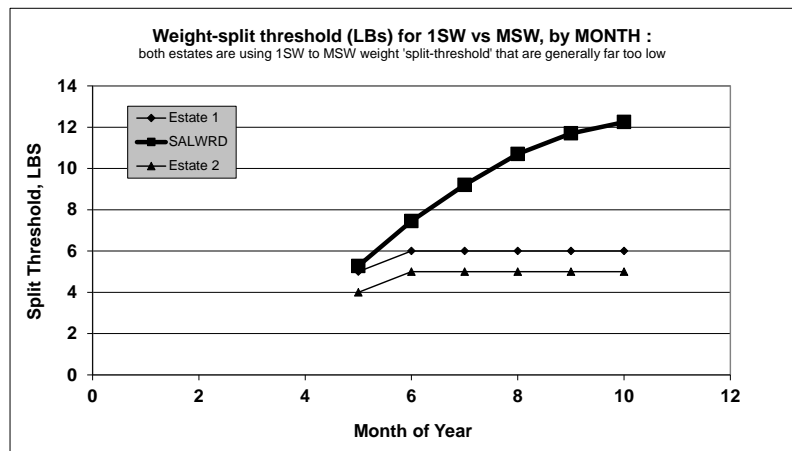


Table A.1 For each Speyside estate (Maclean *et al.* 1996) in each reported month the weight-threshold (in LBs) that the estate used to designate 1SW (below) or MSW (above) salmon is given, followed by the SALWRD probabilities (Bacon *et al.* 2010) that such a fish would actually be 1SW, 2SW or 3SW. After May, the probabilities that fish 'at the threshold' could be 2SW or older are extremely small.

Estate	Month	Estates' weight-split threshold		SALWRD Sea Age probability		
		LBs	p1SW	p2SW	p3SW	
1	May	5	0.64	0.36	0.00	
1	Jun	6	0.91	0.09	0.00	
1	Jul	6	0.99	0.01	0.00	
1	Aug	6	1.00	0.00	0.00	
1	Sep	6	1.00	0.00	0.00	
1	Oct	6	1.00	0.00	0.00	
2	May	4	0.95	0.05	0.00	
2	Jun	5	0.99	0.01	0.00	
2	Jul	5	1.00	0.00	0.00	
2	Aug	5	1.00	0.00	0.00	
2	Sep	5	1.00	0.00	0.00	
2	Oct	5	1.00	0.00	0.00	

The top two rows of Table A2 show the fraction of the Spey rod-catch designated as MSW fish by the rods, that were accurately determined by ageing the scale samples

to be either LateMSW or Grilse. The bottom two rows show the very similar correction proportions used for the raw data on rod-designated-MSW fish in this paper; these have minor adjustments from the Spey results, following comparison with other data sources, as discussed below.

Table A.2 Suggested correction proportions, by months of year, for rod-angler-designated MSW salmon into true-LateMSW salmon and ‘really Grilse’. Top two rows, Spey data of MacLean *et al* 1996; bottom to the rationalised proportions used in this paper (see text).

Months	Dec & Jan- to May	Jun	Jul	Aug	Sept	Oct	Nov	Average, Jun-Nov
SPEY : LateMSW	1.000	0.829	0.351	0.345	0.286	0.267	0.267	0.391
SPEY : ReallyGrilse	0.000	0.171	0.649	0.655	0.714	0.733	0.733	0.609
rodMSW --> Late-MSW	1.00	0.85	0.35	0.35	0.30	0.25	0.25	0.40
rodMSW --> ReallyGrilse	0.00	0.15	0.65	0.65	0.70	0.75	0.75	0.60

A number of other datasets relevant to the question of ‘grilse error’ are available, although all are either of lower quality than the main Spey dataset described here, or subject to confounding factors such as changes in catch-and-release policy. These datasets are: North Esk, Morphy Dyke (MacLean, FFL Pitlochry, pers.com); North Esk national statistics (MacLean, FFL, Pitlochry, pers. comm.); a draft National Study (Thorley, FFL Pitlochry, pers. Comm.). All show magnitudes and seasonal patterns of potential grilse error corrections which are closely comparable with those shown in the ‘Spey’ rows of Table A2. The values given last two columns of Table A2, which were used to correct for grilse error in the rod-catch data used in this study, were slightly adjusted from those given in column 4 of the same table, within their $\pm 5\%$ uncertainty, to reflect these additional data.

Supplement B

Single-stock SR parameter values and curves based on: rod-catch data not corrected for grilse-error; default allometric marine-mortality model (DAM).

For convenience Table B.1 tabulates both the non-corrected and grilse-error corrected (also in main text as Table 1) spawner to smolt SR data.

Table B.1 Posterior parameter distribution for the North Esk 1980-2004 spawner to smolt data regarding the system as comprising a single stock, using data not corrected for Grilse-error, and using a Beverton Holt Estimated Stock-Recruitment (ESR) curve with a control prior. First two columns show the pair of parameters O_{max} , H , defining the BH SR curve-shape. The third column, θ , represents the negative binomial error distribution factor. The next two columns are biologically informative values derived from the former three columns. The fourth column shows the (approximate) modal coefficient of error variation implied by θ (see Gurney *et al.* (2010), equation 2). The fifth column shows maximum individual productivity, β , (equation 12). The top line of each pair shows the mode and the lower line shows the upper and lower 95% credibility limits. The top pair of lines show results using grilse error corrected rod-catch data, and lower pair shows results using rod-catch data stratified using angler-reported sea-ages.

Parameters defining the BH SR curve		Estimated error		Derived biological param.s					
O_{max}		H		θ		CV(%) $\approx 1/\theta$		β $\approx O_{max}/H$	
mode		mode		mode		mode		mode	
2.5%	97.5%	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%
Data Corrected for grilse error									
24.80 × 10⁴		2.232 × 10³		8.08		35%		111	
20.00 × 10 ⁴	36.71 × 10 ⁴	0.978 × 10 ³	7.154 × 10 ³	3.85	17.09	51%	24%	51	204
Data not corrected for grilse error									
24.28 × 10⁴		2.018 × 10³		8.13		35%		120	
19.99 × 10 ⁴	35.99 × 10 ⁴	0.964 × 10 ³	6.840 × 10 ³	3.84	16.96	51%	24%	53	207

Supplement C

Multiple sub-stock SR parameter values and curves based on: rod-catch data not corrected for grilse-error; the default allometric marine-mortality model (DAM).

For convenience of comparison, Table C.1 tabulates both the non-corrected and grilse-error corrected (the latter is also in the main text as Table 2) spawner to smolt SR data, while Fig.C.1 illustrated the same set of SR curves for the un-corrected data.

Table C.1. Posterior parameter distribution for the North Esk 1980-2004 spawner to smolt data regarding the system as comprising three sub-stockswith the default allometric marine- marine mortality model (DAM) and using Beverton Holt ESRs with control priors. First two columns show the pair of parameters O_{max} , H , defining the BH SR curve-shape. The third column, θ , represents the negative binomial error distribution factor. The next two columns are biologically informative values derived from the former three columns. The fourth column shows the (approx) modal coefficient of error variation implied by θ (see Gurney *et al.* (2010) equation 2). The fifth column shows maximum individual productivity, β , (equation 8). The top line of each pair shows the mode and lower line shows the upper and lower 95% credibility limits. The upper section of the table shows results for the default (grilse-error corrected) data, while the lower section shows results without grilse-error correction.

Sub-stock	O_{max}		H		θ		CV(%)		β	
	mode	mode	mode	mode	mode	mode	$\approx 1/\theta$	mode	$= O_{max}/H$	mode
	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%				
Data Corrected for grilse error										
MSW early	7.52×10 ⁴		785		7.64		36%		95.8	
	5.95×10 ⁴	11.8×10 ⁴	330	2242	3.78	16.8	51%	24%	53	180
MSW late	4.11×10 ⁴		261		3.26		55%		157	
	3.13×10 ⁴	6.87×10 ⁴	125	874	1.65	6.78	77%	38%	78	250
Grilse	13.72×10 ⁴		1313		7.96		35%		104	
	11.1×10 ⁴	19.4×10 ⁴	585	3961	3.92	17.1	51%	24%	49	190
Data not corrected for grilse error										
MSW early	7.64×10 ⁴		773		7.38		37%		98.8	
	5.97×10 ⁴	11.8×10 ⁴	328	2235	3.79	16.7	51%	24%	53	182
MSW late	4.70×10 ⁴		150		3.30		55%		313	
	3.46×10 ⁴	7.58×10 ⁴	79.9	436	2.16	7.07	68%	38%	174	433
Grilse	13.9×10 ⁴		1410		7.64		36%		98.6	
	11.1×10 ⁴	19.7×10 ⁴	626	4410	3.89	17.3	51%	24%	45	177

Note that, for both the grilse and the early-run 2SW' fish, the stock-recruitment parameters for grilse-error corrected and un-corrected data-sets (Table C.1) yield posterior parameter distributions which differ by amounts very small compared to their uncertainty. However, for the late-run 2SW' fish, O_{max} increases a little relative to the corrected data, while, in particular, the half-saturation stock (H) is approximately halved, leading to an implied individual productivity, β , twice that implied by the grilse-error corrected data.

For completeness Supplement Fig.C.1 shows the equivalent results for Fig. 4 when calculated from data *not* corrected for grilse error, along with some explanatory text. Comparing these two figures reconfirms that grilse-error correction has few serious implications for the analyses of early running MSW fish and the grilse. In the case of late-running 2SW' fish the major change occurs in the calculated number of spawners, and consequently in the stock -recruitment relation. However, neither the PEA nor the numbers of smolts assigned to the late 2SW' sub-stock were much altered. The reason for this is that the large majority of the rod-fishery kills occur above the Logie counter, and grilse-error correction thus affects only the calculated number of spawners.

Fig.C.1 Decadal trends in the density independent parts of the life-cycle of three North Esk sub-stocks, derived using data not corrected for rod-capture grilse-error and the default allometric marine- mortality model (DAM). Frames a), d) and g) show the component processes of the pre-estuary to spawner survival shown in frames b), e), and h). Frames c), f) and i) show the smolt to pre-estuary survival. All frames show yearly values (points) and a smoothed trend (line) obtained by loess smoothing using R routine *loess* with default parameters. Frames a), d) and g, show the percentage of the pre-estuary numbers surviving the estuarine (net) fishery (circles with dashed line) and the percentage of those survivors who also survive the rod fishery (squares with solid line). Vertical dashed lines show dates of management interventions: 1991: Morphy Dyke nets moved to rods, 2000: net season delayed until April 1st , 2001: MSW rod-caught fish released, 2005: net season delayed until May 1st . For further details see text and legend to Fig.4. ...

Fig.C.1 Multiple sub-stock description for data not corrected for Grilse-Error fitted with the default allometric marine mortality model (DAM). Compare to main text, Fig.4.

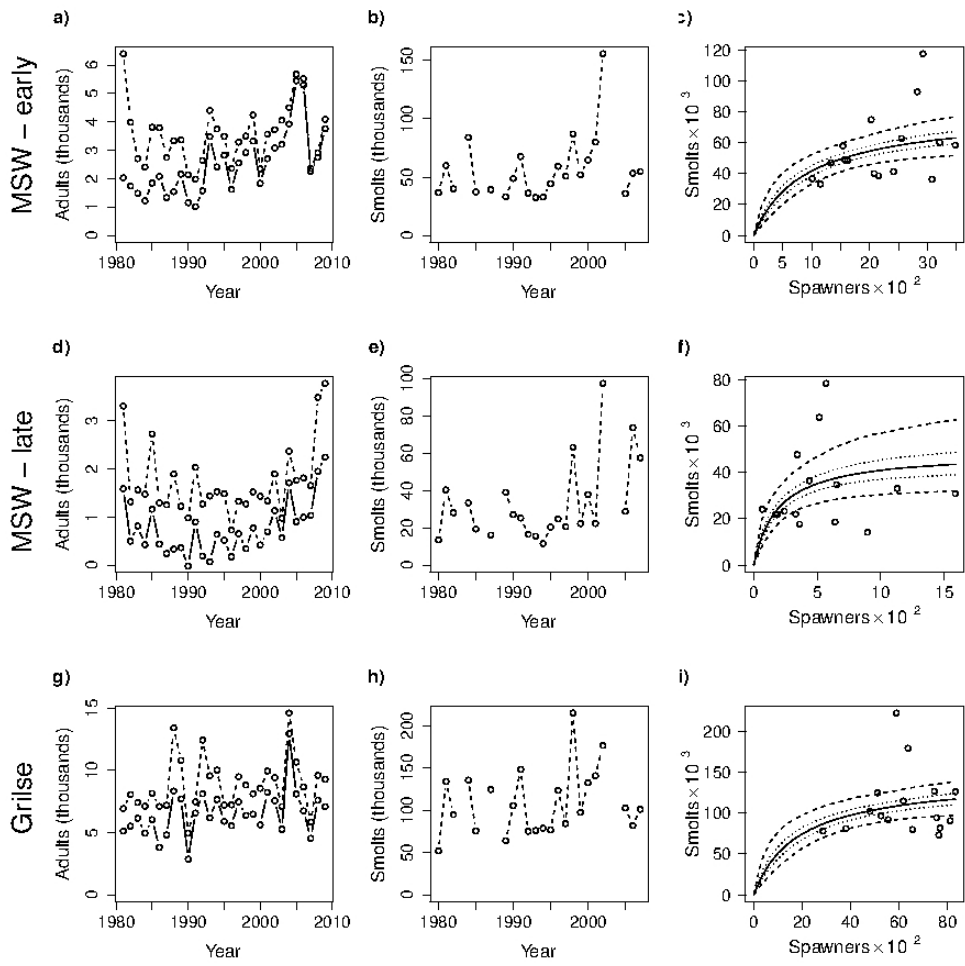
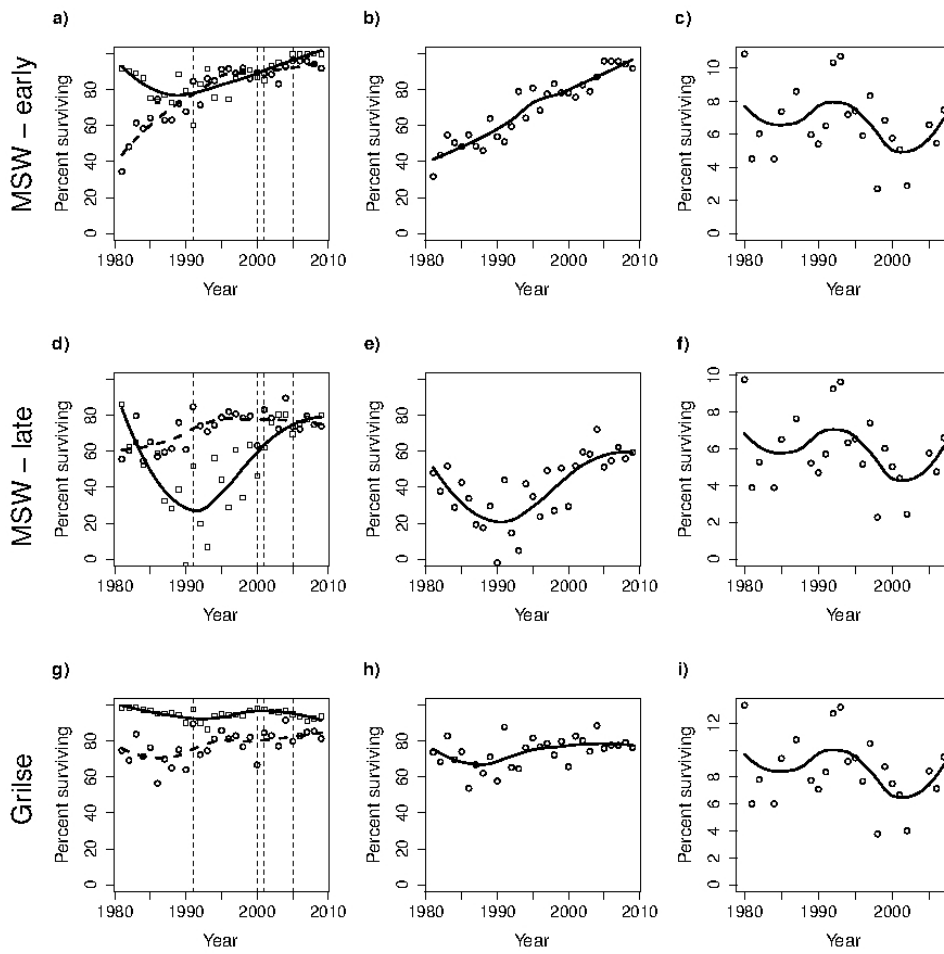


Fig.C.2. Multiple sub-stock survival description for the data not corrected for Grilse-Error fitted with the default allometric marine-marine mortality (DAM). Compare to main text, Fig.5



Supplement D

Derivation of the equation for obtaining unbiased fish-counter grilse/MSW ratios despite biased rod-fishery sea-aging returns.

We define E to represent the total escapement from the estuarine net and coble fishery, and note that, since this fishery is unbiased, the ratio of grilse to MSW fish in this escapement is the same as that measured in the samples of fish taken from the net and coble fishery, which we denote by F_N .

Between the net and coble fishery and the resistivity counter in the Logie Burn there is a rod fishery, which extracts a (known) total catch T_{RB} (where RB denotes “rods below the counter”) in which the (known) grilse to MSW ratio is F_{RB} . The resistivity counter records a “catch” T_c , and we wish to know what value we should assign to its (unknown) grilse to MSW ratio F_c .

To solve this problem we assume that all fish not caught by the rod fishery below the counter are registered by the counter. This amounts to assuming that natural mortality during passage through the rod fishery is negligible and that the counter “sees” all fish passing through it.

Under this assumption the number of grilse seen by the counter is given by

$$T_c F_c = E F_N - T_{RB} F_{RB}$$

and the number of MSW fish seen by the counter is

$$T_c (1 - F_c) = E (1 - F_N) - T_{RB} (1 - F_{RB})$$

These equations contain two unknowns (E and F_c) so we first eliminate E between the two equations, showing that

$$\frac{1}{F_N} [T_c F_c + T_{RB} F_{RB}] = \frac{1}{1 - F_N} [T_c (1 - F_c) + T_{RB} (1 - F_{RB})]$$

which can easily be rearranged to yield a closed form expression for the quantity of interest, namely

$$F_c = F_N + \frac{T_{RB}}{T_c} [F_N - F_{RB}]$$

Supplement E

Relative fecundity (productivity) ratio calculations between the sub-stocks, across the three marine mortality models and for three ova-productivity metrics.

Supplement E illustrates how the fecundity predictions based on the SR analyses of the main paper are robustly compared between the three sub-stocks. It starts by creating 'expectation ratios' for those values, based on information taken from Bacon *et al.* (2012), as shown in Table E.1. It next (Table E.2) illustrates like calculations based on the SR analyses in the main paper. Tables E.1 and E.2 thus contain ratio estimates of the same qualitative comparisons. Accordingly, if those comparisons, although derived by different approaches, actually estimated the same quantitative values, their joint ratios would always be close to 1.00. Table E.3 (also Table 3 of the main text) presents that final comparison, and shows that most of the resulting 27 ratios (three sub-stock comparisons * three mortality models * three fecundity metrics) differ from 1.00 very considerably.

Table E.1 Illustrates the calculation of fecundity-expectation ratios between sub-stocks, based on findings in Bacon *et al.* (2012). The header-column denotes each phenotype or sub-stock-comparison, with the first three rows the phenotypes and the next four their comparison ratios. Thenext, and first numeric, column shows the fork-lengths of typical females. Then, consequent on those fork-lengths and calculated using the equations in Bacon *et al* (2012), the subsequent columns show: the total volume (mass) of ova produced by such typical females (which is independent of the river-zone they breed in); the numbers of ova expected from such typical females *when breeding in the uplands* (also the classic expectation from earlier, standard publications, such as Pope (1961); the numbers of expected ova from such typical females *when breeding in the lowlands*; the final column (river-zone adjusted) is only completed for comparisons between phenotypes.

The final four rows of Table E.1 are the comparison ratios. Their values are obtained by taking the relevant pair of phenotypic sub-stock values in the same column and, depending on the row-header, dividing each numerator by each denominator to obtain the tabulated ratio-value. In the final 'zone-adjusted' column however, the relevant numerators/ denominators are taken from whichever column represents the river-zone in which the phenotype sub-stock would normally breed (thus giving different values to those in the previous two columns).

Observations: North Esk ova-fecundities parameters (based on Bacon <i>et al.</i> 2012)					
	Female size	Total Ova volume, Litres	Ova numbers / female		
	Typical fork- length, mm		Upland	Lowland	zone-adjust
				Fewer, larger	More, smaller
early MSW	725	0.680	5,715	8,274	
late MSW	800	0.923	7,206	10,432	
Grilse	600	0.378	3,660	5,299	
Calculated Ova-Fecundity ratios					
early MSW / early MSW	1	1	1	1	1
late MSW / early MSW	1.10	1.36	1.26	1.26	1.83
Grilse / early MSW	0.83	0.56	0.64	0.64	0.51
late MSW / Grilse	1.33	2.44	1.97	1.97	1.97

The first ratio-row of **Table E1**, earlyMSW/earlyMSW is included simply to emphasise that the procedure results in values of 1.00 when the quantities are identical. Only two of the three sub-stock comparison rows are fully statistically independent. However, the third, lateMSW/Grilse, is also included as it represents a comparison where the two phenotypes typically breed within the same lowland river-zone, and the comparison thus represents a different biological hypothesis from the other two (in which earlyMSW which typically breed in the upland river-zone) is the denominator.

Table E.2 Has a similar purpose and overall format (three phenotype rows, four sub-stock comparison rows) to **Table E.1**. However, its numeric columns represent the values, or ratios, of fecundity estimates obtained from the SR β coefficients estimated from the SR analysis of the main paper. One set of values is tabulated for each of the three marine-mortality sub-models.

Smolts per female from SR β parameter, this paper			
Mortality Model	Smolt production per female		
	Constant monthly, UR	Default allometric, DAM	Uniform survival, US
Sub-stock	<u>Beta, absolute</u>		
Early MSW	124	95.8	92.1
Late MSW	292	157	128
Grilse	70.8	104	212
	<u>Beta, ratios</u>		
Early MSW / early MSW	1	1	1
Late MSW / early MSW	2.35	1.64	1.39
Grilse / early MSW	0.57	1.09	2.30
Late MSW / Grilse	4.12	1.51	0.60

Accordingly, both **Tables E.1** and **E.2** contain fecundity ratios representing the same sub-stock comparisons of relative fecundity obtained from two different numeric estimates of the same qualitative comparison. Thus, if both methods (E.1, from body sizes; E.2 from SR analyses) genuinely reflected the same quantitative values, then the ratio of the estimates (E1/E2) would always closely approximate 1.00. In **Table E.3** below it can be seen that this is rarely the case. **Table E.3** is identical to Table 3 in the main text, and is reproduced below for convenience, along with some further explanatory remarks.

Table E.3. The table gives a comparative productivity index, calculated between different pairs of sub-stocks, identical productivity estimates via both estimation routes, would always produce an index value of 1.00. The rows show the different pairs of sub-stocks compared. Blocks of three columns show results calculated for three different marine mortality models. Within these triplet-blocks, individual columns show the index as calculated for different productivity metrics (calculated from Bacon *et al.* 2012 for typically-sized females per sub-stock). Shading and font-style differences (see key) emphasise that none of the marine mortality models produce productivity estimates that are reasonably close to those expected (from female salmon of typical sizes and productivities for the same sub-stocks) across all sub-stock comparisons. Productivity metrics for typically-sized females per sub-stock are: Ova Vol.=total volume of all ova produced per female; Upl.Ova#s=total numbers of ova produced per female in ‘upland’ river zones (as normally used); Adj.Ova#s= numbers of ova produced per female adjusting for the up-/low-land spawning situations).

Note that ratios differing by only 10 or 20% would imply very large selective advantages. See the main text, and the notes below, for further explanation.

Standardised production ratios for three mortality models and three female production metrics

Sub-stock comparisons	Blocks are different models of Marine Mortality								
	Constant monthly Rate			Allometric, B>0			Allometric, B=0		
	Ova Vol.	Upl. Ola#s	Adj. Ola#s	Ova Vol.	Upl. Ola#s	Adj. Ola#s	Ova Vol.	Upl. Ola#s	Adj. Ola#s
Sub-stocks ratios	1	1	1	1	1	1	1	1	1
Early MSW / early MSW	1.74	1.87	1.29	1.21	1.30	0.90	1.02	1.10	0.76
Late MSW / early MSW	1.03	0.89	1.12	1.95	1.70	2.14	4.14	3.59	4.53
Grilse / early MSW	1.69	2.09	2.09	0.62	0.77	0.77	0.25	0.31	0.31
Late MSW / Grilse									

Shadings denote ratios not within the given ranges

Shading key

Range	Magnitude description
0.5~1.5	±50%
0.5~2	Factor of 2
0.25~4	Factor of 4

Notes on Table E.3

- Whatever marine-mortality model is used to provide the fecundity estimate ($SR-\beta$), several ratios of $SR-\beta$ /female_size_expectation are highly disparate from 1.00.
- Although only two comparisons are statistically independent the third, lateMSW / grilse, illustrates a different biological assumption regarding the ova-numbers comparison (as both sub-stocks are lowland with the same individual egg volumes).
- The large discrepancies frequently involve the comparison lateMSW/grilse where different egg sizes and numbers between river-zones are irrelevant.
- Of the three marine-mortality models here investigated, that for $B>0$ has fewer and smaller discrepancies, but still has a set of discrepancies that are unbelievably large [1.95, 1.7, 2.14].
- The trio of columns representing the 'adjusted-river-zone' ('upland/lowland') comparison of fecundity also has fewer (but still several unbelievable) high values. However, invoking this as an explanation not only still has problems of several high values but also inherently implies a sub-stock difference anyway (due to their segregation between river-zones).
- No marine-mortality model block has a single column (production metric) without at least one highly unacceptable index value.
- The Allometric $B>0$ marine-mortality model does best overall, but its earlyMSW/grilse ratios are consistently very poor, and especially so for the OvaVol and Adj.Ova#s, which one might expect would be the more similar index values.
- The Constant Monthly marine mortality model does next well overall (but still badly). Its Grilse/earlyMSW comparisons are consistently good, but its other comparisons are very bad to extremely bad.
- theAllometric $B=0$ marine mortality model does extremely badly for most comparisons, with is lateMSW /earlyMSW being least awful.

Supplement F

Multiple sub-stock description for data not corrected for Grilse-Error fitted with the uniform survival marine-mortality model (US, $\beta_m=0$,). Compare to main text, Fig.4.

Figure F.1 (compare to main text Figure 4). Trends in sub-stock numbers and SR relationships for each of the three sub-stocks, as predicted by the *uniform survival marine-mortality model* (US, $\beta_m=0$). For full legend see Annex Fig.C.1 or main text, Figure 4

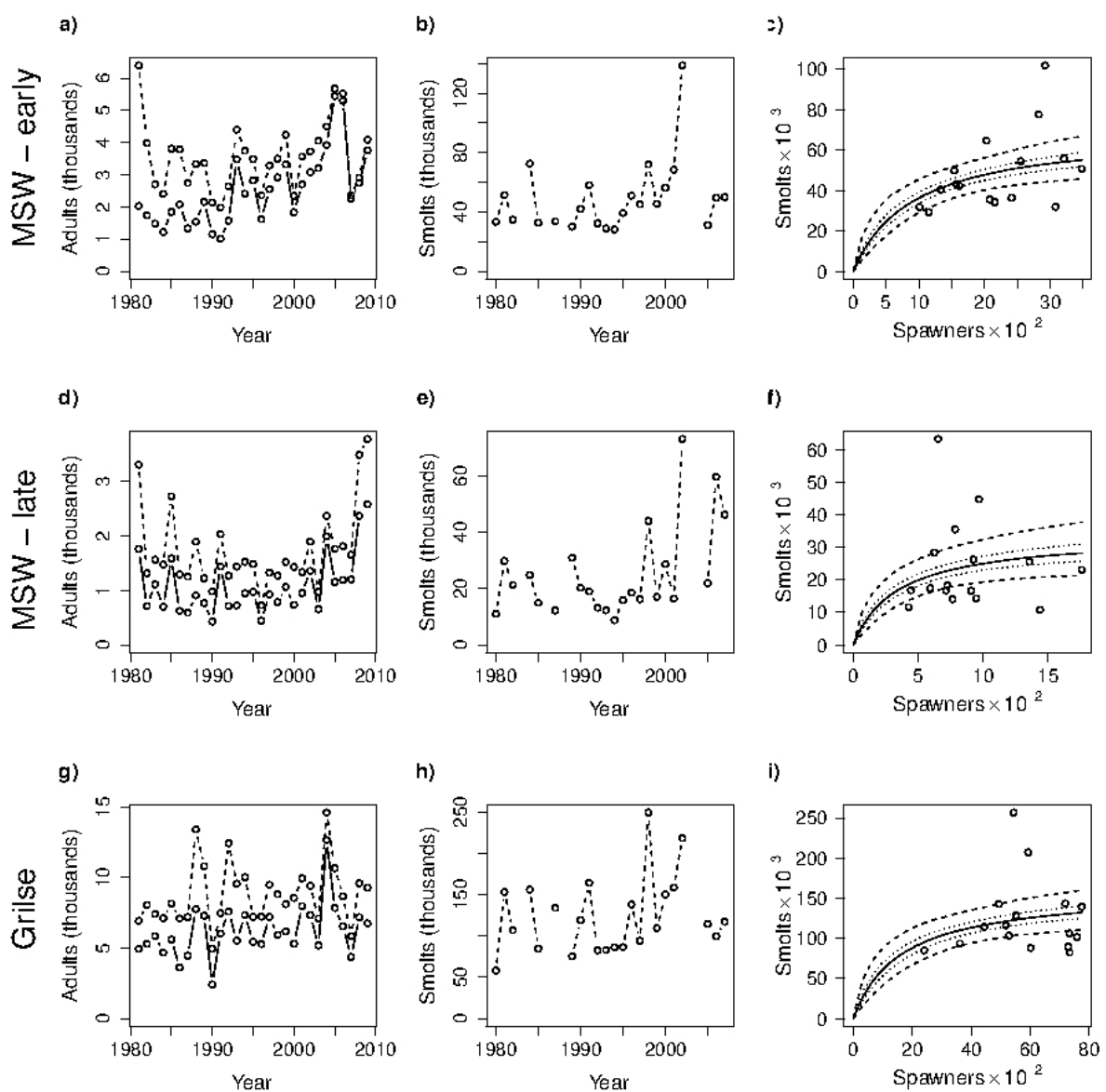


Figure F.2 (compare to main text, Figure 5). Trends in sub-stock survivals for each of the three sub-stocks, as predicted by the *uniform survival marine-mortality model* ($US, \beta_m=0$). For legend see Annex Fig.c.2 or main text, Figure 5.

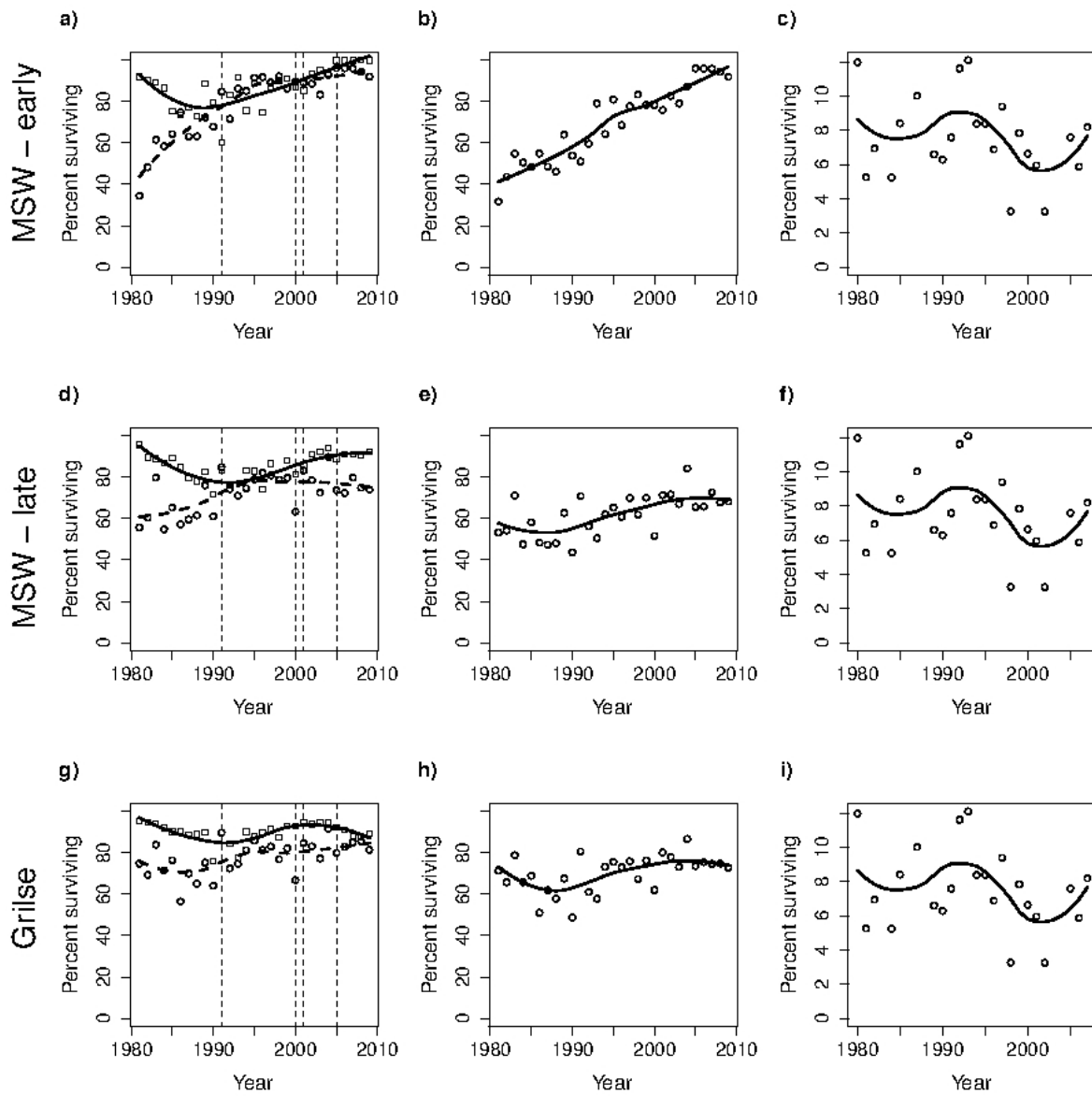


Table F.1 (compare to main text, Table 2). **Posterior parameter distribution for the North Esk 1980-2004 spawner to smolt data regarding the system as comprising three sub-stocks, using Beverton Holt ESRs with control priors, as predicted by the uniform survival marine-mortality model $model (US, \beta_m=0)$.** First two columns show the pair of parameters O_{max} , H , defining the BH SRcurve-shape. The third column, θ , represents the negative binomial error distribution factor. The next two columns are biologically informative values derived from the former three columns. The fourth column shows the (approx) modal coefficient of error variation implied by θ (see Gurney *et al.* (2010) equation 2). The fifth column shows maximum individual productivity, β , (equation 8). The top line of each pair shows the mode and lower line shows the upper and lower 95% credibility limits. The upper section of the table shows results for the default (grilse-error corrected) data, while the lower section shows results without grilse-error correction.

Sub-stock	O_{max}		H		θ		CV(%)		β	
	mode	mode	mode	mode	mode	mode	$\approx 1/\theta$	$= O_{max}/H$	mode	mode
	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%	mode			
Data Corrected for grilse error										
MSW early	6.64×10 ⁴		721		8.76		34%		92.1	
	5.20×10 ⁴	10.4×10 ⁴	331	2315	4.02	18.3	50%	23%	45	157
MSW late	3.27×10 ⁴		255		3.22		56%		128	
	2.40×10 ⁴	5.24×10 ⁴	129	876	1.65	6.82	78%	38%	60	186
Grilse	15.3×10 ⁴		1264		7.96		35%		121	
	12.5×10 ⁴	22.2×10 ⁴	589	4012	3.64	16.0	52%	25%	55	212
Data not corrected for grilse error										
MSW early	6.67×10 ⁴		758		8.78		34%		88.0	
	5.23×10 ⁴	10.3×10 ⁴	334	2266	4.02	18.6	50%	23%	45	157
MSW late	3.43×10 ⁴		159		3.24		56%		216	
	2.66×10 ⁴	5.90×10 ⁴	80.2	445	1.58	7.20	80%	37%	133	332
Grilse	15.9×10 ⁴		1330		7.77		36%		120	
	12.6×10 ⁴	22.5×10 ⁴	639	4487	3.67	16.2	52%	25%	50	197

Supplement G

Multiple sub-stock uniform risk-rate (UR) marine mortality model ; Graphs and Table.

Figure G.1 (compare to main text Figure 4). Trends in sub-stock numbers and SR relationships for each of the three sub-stocks, as predicted by the uniform risk-rate (UR) marine-mortality model. For full legend see Annex Fig.C.1 or main text, Figure 4.

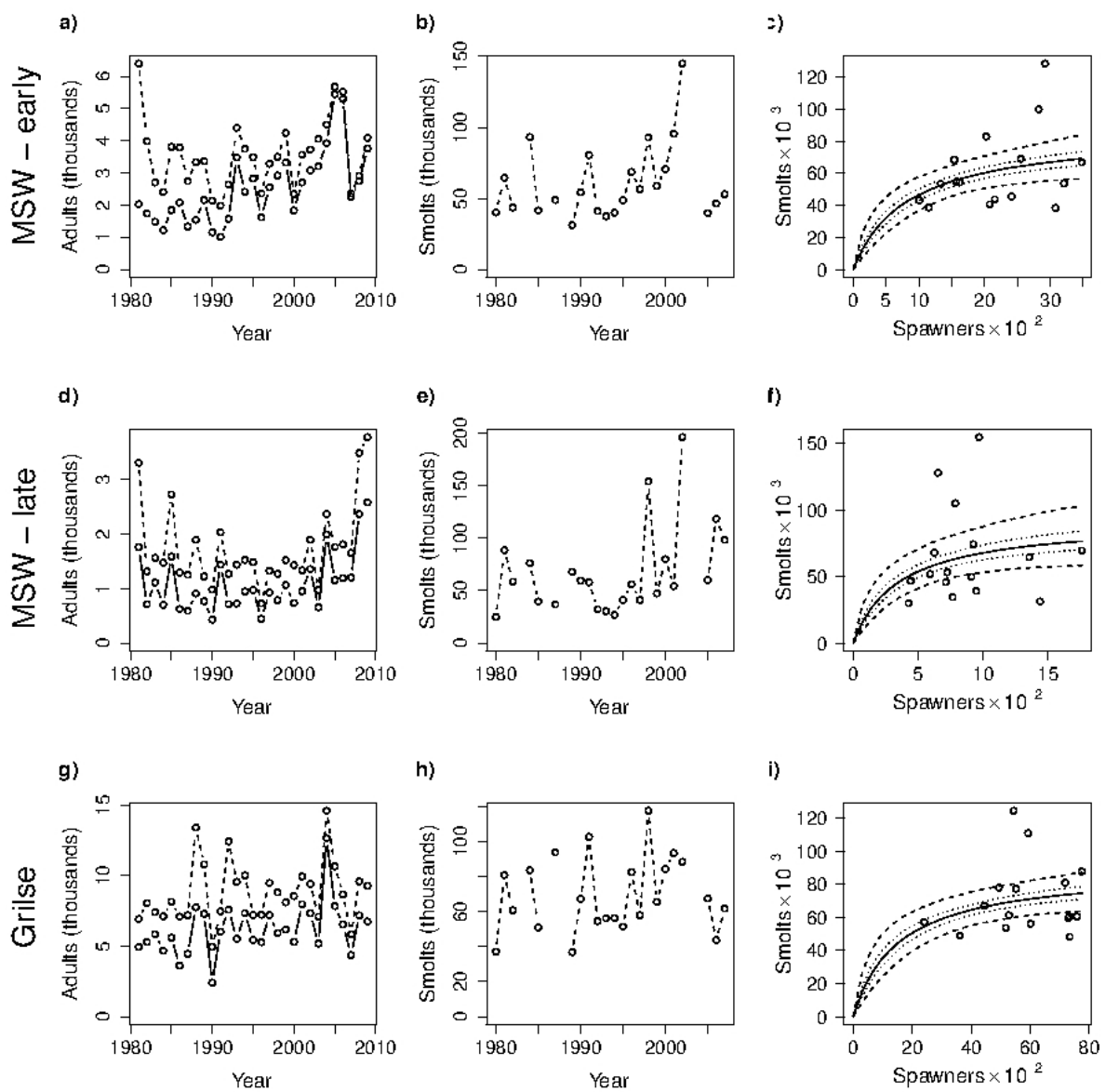


Figure G.2 (compare to main text Figure 5). Trends in sub-stock survivals for each of the three sub-stocks, as predicted by the uniform risk-rate (UR) marine-mortality model. For full legend see Annex Fig.C.2 or main text, Figure 5.

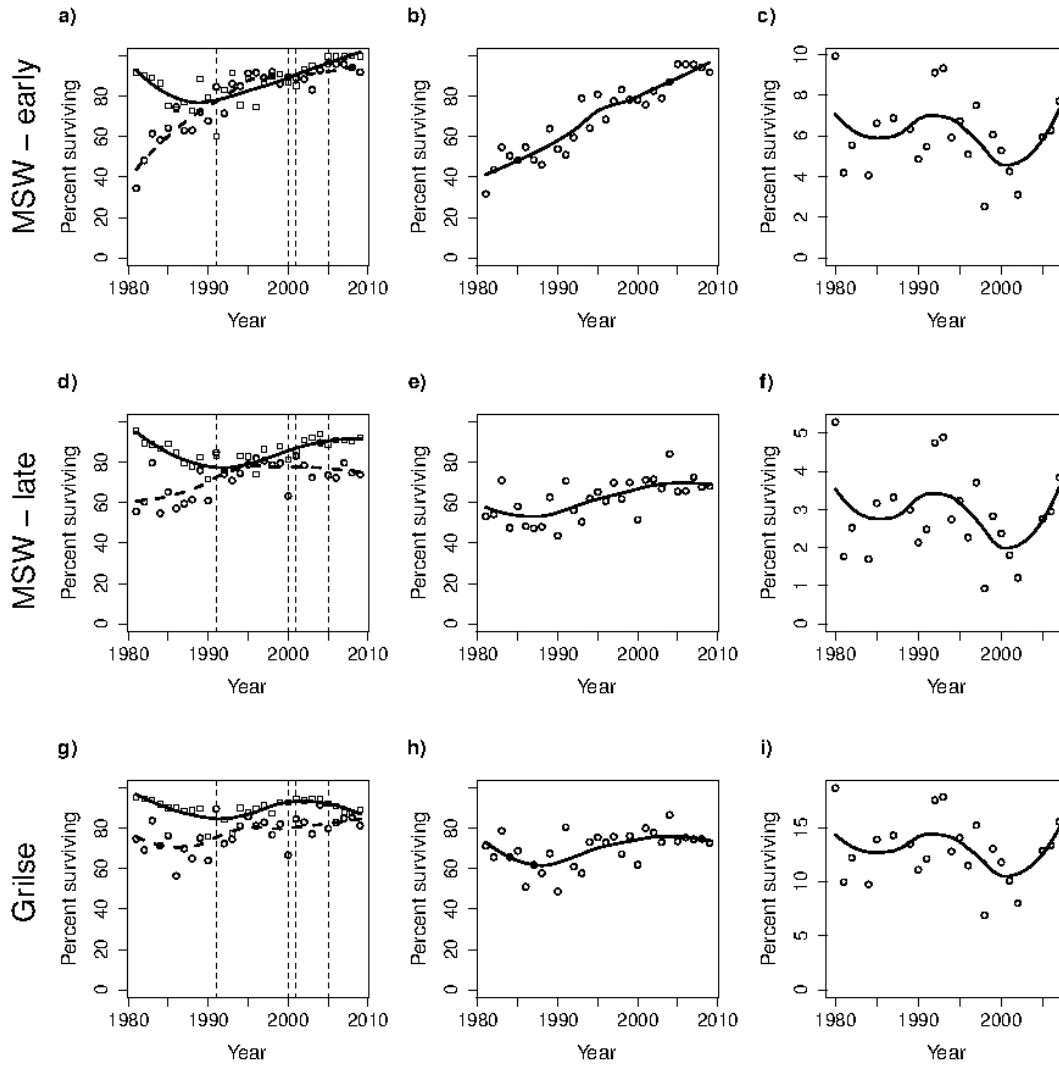


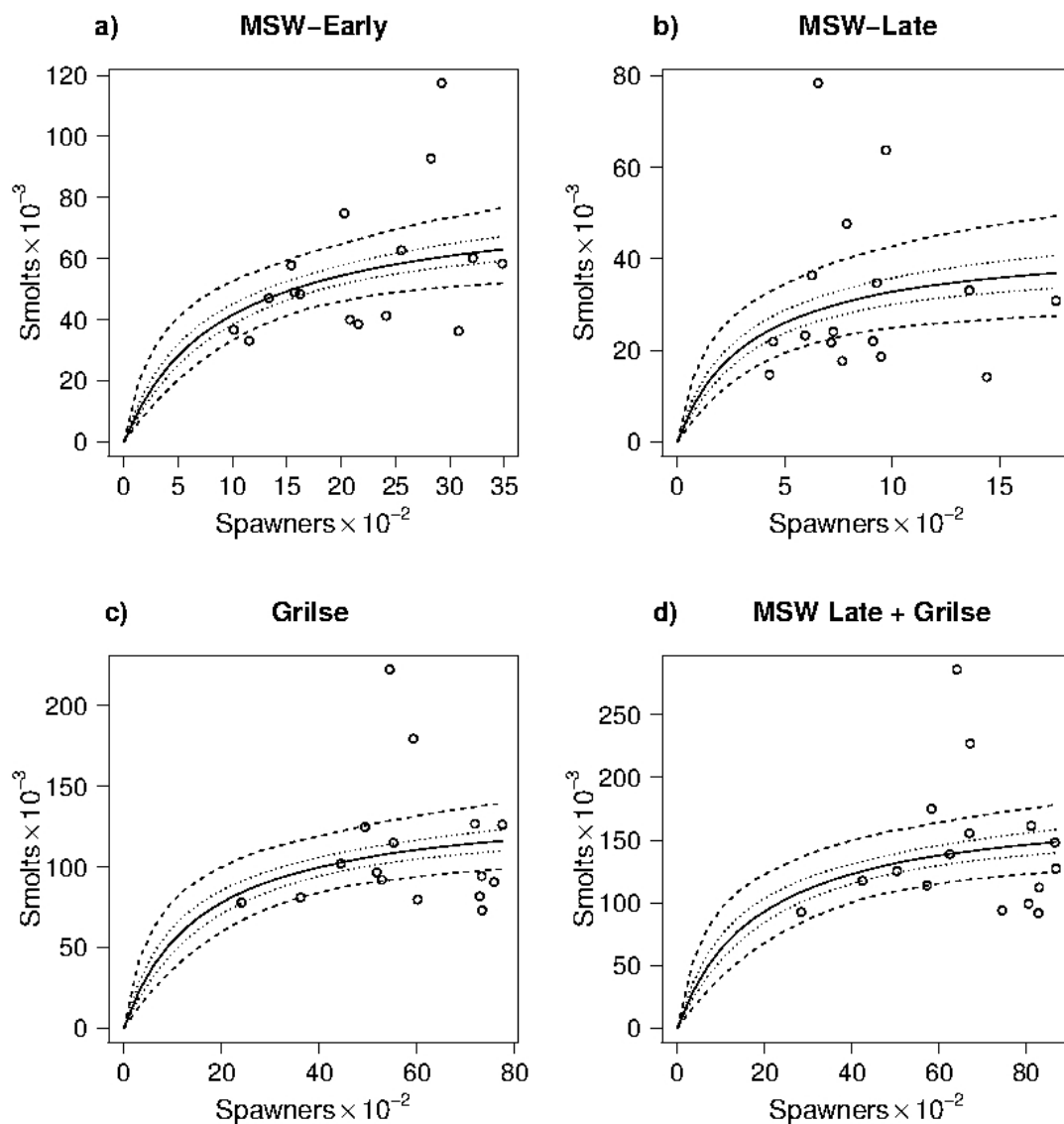
Table G.1 (compare to main text, Table 2). **Posterior parameter distribution for the North Esk 1980-2004 spawner to smolt data regarding the system as comprising three sub-stocks**, using Beverton Holt ESRs with control priors, as predicted by the uniform risk-rate (UR) **marine-mortality model**. First two columns show the pair of parameters O_{max} , H , defining the BH SRcurve-shape. The third column, θ , represents the negative binomial error distribution factor. The next two columns are biologically informative values derived from the former three columns. The fourth column shows the (approx) modal coefficient of error variation implied by θ (see Gurney *et al.* (2010) equation 2). The fifth column shows maximum individual productivity, β , (equation 8). The top line of each pair shows the mode and lower line shows the upper and lower 95% credibility limits. The upper section of the table shows results for the default (grilse-error corrected) data, while the lower section shows results without grilse-error correction.

Sub-stock	O_{max}		H		θ		CV(%)		β	
	mode		mode		mode		$\approx 1/\theta$		$= O_{max}/H$	
	2.5%	97.5%	2.5%	97.5%	2.5%	97.5%	mode		mode	
Data Corrected for grilse error										
MSW early	7.54×10 ⁴		607		10.92		30%		124	
	6.33×10 ⁴	11.1×10 ⁴	272	1628	4.96	21.9	45%	21%	64	253
MSW late	8.06×10 ⁴		276		4.93		45%		292	
	6.41×10 ⁴	12.6×10 ⁴	122	781	2.49	10.7	63%	31%	146	584
Grilse	8.67×10 ⁴		1225		15.5		25%		70.8	
	7.35×10 ⁴	11.8×10 ⁴	588	3582	6.89	30.9	38%	18%	32	133
Data not corrected for grilse error										
MSW early	7.67×10 ⁴		555		10.24		31%		138	
	6.34×10 ⁴	11.3×10 ⁴	274	1705	5.05	22.5	44%	21%	64	253
MSW late	8.93×10 ⁴		133		4.60		47		671	
	6.86×10 ⁴	13.2×10 ⁴	65.5	331	2.24	11.1	67%	30%	346	1,197
Grilse	8.84×10 ⁴		1446		15.4		25%		61.1	
	7.35×10 ⁴	11.9×10 ⁴	645	3981	7.05	32.6	38%	18%	28	120

Supplement H

SR curve estimates, including a combined [lateMSW and grilse] prediction, based on the default allometric (DAM) marine-mortality model.

Figure H.1 This figure shows the estimated Stock-Recruitment curves, with the data as points and the credibility limits as dotted lines various sub-stocks, based on the default allometric marine-mortality model (DAM). Panes a,b,c of this figure are, for ease of comparison, the same as Fig.4.c,f,i in the main text. Pane d of the present figure is a new prediction, produced by assuming that the lateMSW and grilse sub-stocks might comprise a single combined stock with the offspring having equal viabilities. For full legend see Annex Fig.c.1 or Fig.4, main text.



Supplement I

Discussion details of ‘Reproductive Implications’ of the models. N.B. This example is based on the Uniform Risk-Rate marine-mortality model.

We next consider potential causes of these productivity (fecundity) differences. Equation [12] decomposed β into the products of the proportion of the spawning stock which is female (F), the ova fecundity per female (B_0) and the ova to smolt survival (L_{os}). To understand these in a wider context one needs to further decompose the ova-fecundity into a female weight W and an ova fecundity per unit female weight B_w , because (certainly at the North Esk), although females of all sub-stocks produce the same *biomass* of ova per unit of female weight, lowland-breeding salmon (here the late 2SW’ and grilse sub-stocks) produce 45% more-but-smaller eggs from each unit of ova biomass (Bacon *et al.* 2012). Hence in this extended formulation

$$\beta = FWB_wL_{os} \quad [13]$$

Comparing the reproductive capacities of grilse and late 2SW’ pheontypes (whose offspring are generally considered to be co-located in the ‘lowlands’ (*sensu*Bacon *et al.*2012) one can reasonably assume that both L_{os} and B_w are the same for those two putative sub-stocks.

Hence, to explain the productivity anomaly by different sex ratios, F, given that the female weight ratio is $W_{LM}/W_G=2.5$ (see Fig.2) would require, by taking β_G and β_{LM} from Table 2, and substituting values into a re-arrangement of equation [13], that

$$\frac{F_G}{F_{LM}} = \frac{\beta_G}{\beta_{LM}} \frac{W_{LM}}{W_G} = \frac{64.2}{324} 2.5 = 0.495$$

This implies that if the late 2SW’ sub-population had a 1 to 1 sex ratio ($F_{LM}=0.5$) one would require the grilse population to have $F_G=0.25$, equivalent to a male to female ratio of 3 to 1. The North Esk data shows the grilse sub-stock to be some 55% male (a ratio of just 1.2 to 1): so differing sex ratios between the sub-stocks seem an unlikely explanation.

To similarly compare the productivities between grilse and *early 2SW'*, one takes the appropriate seasonal fish sizes (Fig.2) and allows the numerical ova-fecundity per unit weight, B_w , to be 45% higher for 'lowland' grilse. Hence, in this case, self-consistency of productivity estimates would require that $L_{EM}/L_G = 1.23*(F_G/F_{EM})$. If grilse and *early 2SW'* salmon have broadly the same sex ratio (which North Esk data suggest they do) then this suggests that self-consistency would require the ova to smolt survival of *early 2SW'* to be some **23%** higher than that of (lowland) grilse. Larger ova-volumes (per individual egg) are a very plausible mechanism to achieve such improved survival in such circumstances (see Einum *et al.*, 2002, Heath *et al.* (2003), Einum, 2003, Rombough, 2007, van den Berghe and Gross, 1984; Crisp & Carling, 1989, Steen & Quinn, 1999; for details and see Bacon *et al.* 2012 for an overall, structuring, argument).

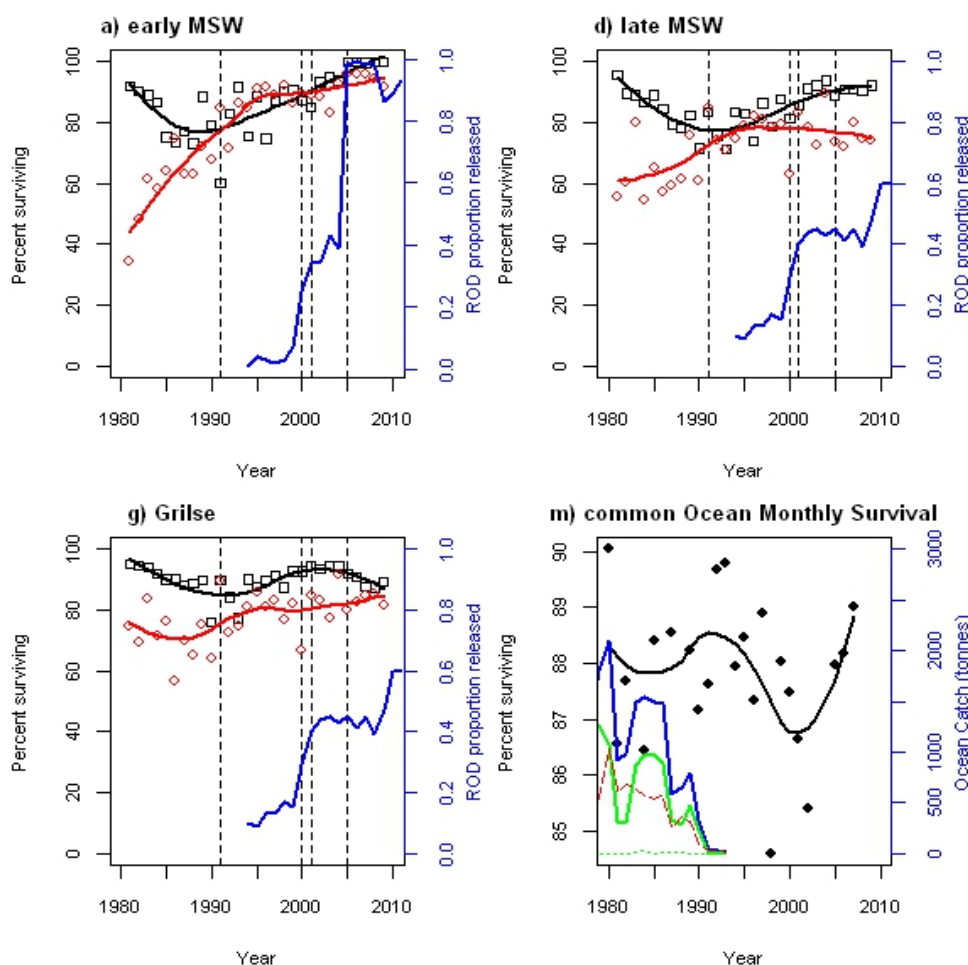
Consideration of the likely magnitudes other possible contributory causes to the productivity anomaly between *late 2SW'* and grilse (such as the truncated size-distribution of the North Esk grilse and *lateMSW* fish, due to the end of the netting season in autumn seem unlikely to bridge the gap, with the exception of inter-breeding between *lateMSW* and grilse as discussed in the main text.

More detailed discussion of such aspects (which might ultimately depend on habitat 'quality') should probably await more reliable calculations based on more appropriate and realistic models of both marine mortalities, inter-breeding and heritabilities.

Supplement J

Discussion details of 'Fisheries Management Implications'

Fig. J.1 The temporal coincidence between estimated North Esk salmon survivals and various fishery pressures. The first three frames show percentage survivals from the estuary nets and river rods; they are labelled (a,d,g) to cross-refer to the like frames of Fig.5, main text . In frames (a,d,g) 'Year' means year of adult return and escapement from/ death due to, the fisheries. Red points and red smoothed fit line show survivals from the estuary nets; black points and black smoothed fit line survival from rods; the blue line shows the recorded change in the proportion of rod-caught salmon that were also released alive. Note the different patterns of rod-release early and late in the season [(a) versus (d and g)]. Vertical dotted lines are the times of the main fishery management actions (see legend Fig.5). Frame (m) shows the estimate percentage monthly oceanic survival, common to all sub-stocks, as black points with a black smoothed fit line. Note the very different survival scale for frame (m) compared to (a,d,g). In frame (m) 'Year' is the year of smolting for each cohort. The coloured lines are oceanic fishery takes in tonnes, offset to reflect the appropriate years the cohorts were at sea. Blue is total oceanic take; solid green the take at West Greenland; dotted green the take at East Greenland; dashed red the take at Faroes.



Mangement Implications; Marine fisheries, Scottish Fisheries and Conservation Limits

J.1 Marine Fisheries

The constrained nature of the marine mortality model necessarily used here, combined with the influential marine survival estimate for the 1980 cohort (Fig.s 5, J.1) make it very hard to see any effect on survival of the declining oceanic fishery catches between 1980 and 1994. Despite high tonnages of ocean catches in that period (Fig.J.1.m) it seems likely that the expected beneficial effects are masked by the high year-on-year variability and the evident large underlying fluctuations of natural mortality processes. Note especially that fluctuations in estimated marine mortality subsequent to 1990 (Fig.J.1.m), when oceanic fisheries were very low to absent, show fluctuations from unknown causes that were of similar magnitude to those seen between 1980 to 1990 (when the oceanic fisheries declined); there is no reason to believe that these other unknown causes would not have been acting from 1980 to 1990, further complicating the ability to discriminate potential causes.

J.2. In-River Fishery Management

Local fisheries management actions at the North Esk were aimed mainly at the early MSW stock, so it was not unexpected to see no evident effect of those actions on the grilse or late MSW sub-stocks. Fig.5.b provides an encouraging message for the conservation of the North Esk's early-run MSW salmon, namely that in-river fishing mortality has decreased steadily from 60% to under 5% between 1980 and 2009.

However, the message is less clear concerning the relative merits of specific management actions to aid early MSW salmon. Early MSW survivals from both the nets and the rods (Fig.s 4.a,5.a) were well underway before either the formal delays to the netting season or the recorded introduction of rod catch-and-release around 2001 and 2005 (Fig.4.a) and marked increases in C&R do not show clear responses in survival (Fig.5.a). Nor does the pattern of late-season C&R closely match estimated survival changes (Fig.5.d,g). However, discerning the benefits from those formal management actions (net season delay, C&R) was inevitably constrained by the already high survivals (around 80%, Fig.s.4,5), and any sudden improvements could have been masked by annual variation in the estimated survivals. Moreover, that masking has probably been exacerbated by lack of detail on other potential causal factors, such as fishing effort (both net and rod) and other environmental

factors affecting fishes' catchabilities. Nevertheless there is now nearly complete escapement for early MSW salmon, a situation which could not have arisen with the former levels of takes from the fisheries.

J.3. Conservation Limit (CL) 'Parameter Transportation' Considerations

The key population parameters that are frequently outside the knowledge and control of the local fishery managers (who monitor and/or control the in-river takes by different fishery methods) are the spawner-to-smolt SR production and the marine mortality ³.

Overall understanding of marine mortality is severely constrained, but with scant evidence of any large or well understood local (river-to-river) effects (eg Chaput 2012). So there is little option but to transfer the widely-differing overall (smolt to PEA) survivals for the different sub-stocks⁴.

Transferring the information about the (deterministic) SR relationships is aided by reference to the productivity values, β (see Eqn.7, main text). The SR β reflects both the average fecundity of individual spawning fish of the sub-stock of interest (which could rather plausibly be assumed not to vary greatly between catchments within sub-stocks) and, secondly, the survival from spawner to smolt at low (fry) density. As a first approximation in the absence of appropriate 'habitat' information, then *at low densities*, that survival might plausibly be viewed as reasonably constant ⁵.

The maximum smolt productivity (O_{max}) for a given sub-stock in a given catchment almost axiomatically scales with the ratio of the amount of suitable habitat for the given sub-stock between the two catchments (eg Chaput 2012). However, as the habitat requirements for both redds and juvenile salmon (*let alone* the important finer details of their spatial distribution, such as whether there are many (small) adjacent patches of each, or not) are quite complex,

³ Usually spawner to spawner S-R data, with or without a year-trend to allow for changing marine survival

⁴ Or, if details of times spent at sea within sub-stocks were known to differ between the donor and recipient rivers, then one could instead transfer the overall *monthly* survival rate (as here defined and estimated) and then scale that to be appropriate to the alternative periods spent at sea by the *local* sub-stocks.

⁵ If densities were considered comparable between the catchments, but smolt ages were not, then the 'survival' aspect might plausibly be transferred by including a risk-rate adjustment for the mortality period, according to the appropriate smolt-ages (if known), thus allowing for differences in mean age at smolting between the parameter 'donor' and 'recipient' catchments.

the central problem would seem to be measuring the quality and quantity of available habitat in the donor and recipient rivers. Investigation of the use of simple river-catchment- or wetted-surface-area ratio metrics in Scotland have met with mixed success (MacLean 2007).

The considerations discussed above suggest that the present lack of knowledge about 'extent of suitable habitats' in different rivers may well be the biggest constraint on transferring (sub-stock or any other) population parameters from 'donor' to 'recipient' catchments. If so, this suggests that a modest amount of well-targeted additional research will be needed to determine a set of broad environmental parameters which, together, define an aggregated 'habitat measure' and thus allow the re-scaling of maximum smolt productivity (O_{max}) between rivers. While such work is likely to concentrate on environmental parameters readily determined by GIS methods, it seems probable that inter-catchment comparisons will play a vital role. Accordingly, if the presumed 'generality' of such smolt production estimates across rivers (and its relationship to habitat metrics) is to move from being an act of faith to one established by data, then suitable fish population data will also be needed from several rivers. Given the presently small number of catchments for which appropriate salmon population data exists to enable such comparisons (currently only three in Scotland), this reasoning reinforces the views of Chaput (2012) that a more carefully targeted approach to the collection of population data is a key future management requirement for Atlantic salmon. Once an effective aggregate 'habitat' measure has been defined (probably involving environmental metrics such as water quality and temperature as well as remotely-sensed river-water characteristics), and collated in a GIS framework, then inter-catchment transfer of relevant population parameters for phenotypically homogeneous sub-stocks of Atlantic salmon could become both more reliable and routine.

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