Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006

P. J. Bacon, S. C. F. Palmer, J. C. MacLean, G. W. Smith, B. D. M. Whyte, W. S. C. Gurney, and A. F. Youngson

Sea age, size, and condition of adult Atlantic salmon (*Salmo salar*) are prime determinants of individual, and hence population, productivity. To elucidate potential mechanisms, 151 000 records of salmon returning to six Scottish coastal sites over 44 years were analysed for length, weight, and condition, by site, sex, sea age, and river age. After correcting for capture effort biases, all sites showed seasonal increases in length and weight for both 1 sea winter (1SW) and 2SW fish. However, whereas condition increased slightly with season for 2SW, it decreased notably for 1SW. Sites showed common decadal trends in length, weight, and condition. Within years, length and weight residuals from trends were coherent across sites, but residuals from condition trends were not. Rates of seasonal condition change also showed decadal trends, dramatically different between sea ages, but common across sites within sea-age groups. Longer salmon were disproportionately heavy in all seasons. 1SW condition was markedly lower in 2006. Detrended correlations with oceanic environmental variables were generally not significant, and always weak. A published correlation between the condition of 1SW salmon caught at a single site and sea surface temperatures in the Northeast Atlantic could not be substantiated for any of the six fisheries over the wider time-scales examined.

Keywords: climate change, condition, marine environment, NAO, *Salmo salar*, sea surface temperature.

P. J. Bacon, W. S. C. Gurney, and A. F. Youngson: FRS Freshwater Laboratory, Faskally, Pitlochry PH16 5LB, UK. S. C. F. Palmer: Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK. J. C. MacLean, G. W. Smith, and B. D. M. Whyte: FRS Freshwater Laboratory, Inchbraoch House, South Quay, Ferryden, Montrose, Angus DD10 9SL, UK. W. S. C. Gurney: Department of Statistics and Modelling Science, Livingstone Tower, University of Strathclyde, Glasgow G1 1XH, UK. Correspondence to P. J. Bacon: tel: +44 61224 294442; fax: +44 1796 473523; e-mail: baconpj@marlab.ac.uk.

Introduction

There is widespread concern about the current poor state of wild Atlantic salmon populations. The species' marine phase is poorly understood, and the marine environment subject to a complex of short , medium , and long term fluctuations (Crozier *et al.*, 2003; Friedland *et al.*, 2005). Factors affecting abundances of salmon from Norway and Scotland during the last century have been discussed recently (Vøllestad *et al.*, 2009). Scottish salmon catches, their sea age at maturity, and the seasonal return time have shown considerable fluctuations over the past 200 years (Summers, 1995). Oceanic conditions also influence growth (Friedland *et al.*, 2009) and the survival of post smolts (Peyronnet *et al.*, 2008).

Recent reports from fishers suggest that grilse (1SW salmon, returning after one winter at sea) returning to the Scottish coast have been unusually thin, especially in 2006 (Smith *et al.*, 2007). Thin grilse have also been reported from elsewhere in Europe (ICES, 2007), and, subsequently, from Norway in 2007 (Fiske *et al.*, 2008). Climate change has been suggested as a possible factor underlying the appearance of leaner fish (Todd *et al.*, 2008).

When marine fluctuations take place on multiple time scales, long term datasets are vital to the reliable identification of potential causes. Shorter terms (decadal periods) run a much more serious risk of identifying two (or more) factors that are only coincidentally inter correlated as potential cause and effect. We here analyse a large (150 000 records), 44 year dataset for Scottish Atlantic salmon, of both one and two sea winter (1SW and 2SW) ages, from six different fisheries, by length, weight, and condition. When combined with abundance estimates (Youngson *et al.*, 2002), these biometric data facilitate better understanding and modelling of the quantitative population dynamics (Gurney *et al.*, 2008a).

The aim of our study was to provide a rigorous empirical analysis as a focus for future dynamic modelling. The emphasis was on (i) detecting and quantifying trends in the length, weight, and condition of salmon returning to coastal waters, and (ii) contrasting such trends for 1SW with those for 2SW fish.

In addition to the general interest concerning sex, sea age, and annual differences in the average condition of salmon returning to the coast, an important question is why do some salmon return earlier in the season (early run) than others? The later returning fish have grown over a longer period and might, on average, be expected to have accumulated more energy reserves for breeding. However, they may also have suffered greater mortality. Nevertheless, a longer period at constant marine mortality risk could be outweighed if the later returning fish had disproportionately greater breeding reserves (than expected by purely volumetric increase in proportion to their size). Understanding the selective outcome of this survival and reserves trade off requires knowledge of the size dependent of mortality and breeding reserves. In particular, we investigated the hypothesis that for individual fish arriving in very short coincident periods, larger fish might have higher condition indices, and hence more reserves for gonad formation, within all such return periods. Such a finding would confirm the widespread view for other species that larger fish do indeed have disproportionately greater breeding reserves.

Methods
Fishery data
The data come from five east coast net and coble fisheries, on the estuaries of the Dee, North Esk, Spey, Tay, and Tweed, and from the Strathy fixed engine fishery on the north coast (Figure 1). Shearer (1992) gives descriptions of the fishery techniques involved. The Strathy site captures fish from mixed stocks. Although a small proportion of the fish captured in the estuaries probably originated from other rivers, the great majority is of local provenance. Previous spawners comprised fewer than 2% of the captures and were ignored. We note that roughly half the records came from the North Esk and that this was the only fishery which was represented throughout the entire sampling period (1963 2006).

Fish sampling
Typical annual open seasons varied slightly among the fisheries sampled (Dee, 11 February 26 August; North Esk, 16 February 31 August; Spey, 11 February 26 August; Tay, 5 February 20 August; Tweed, 15 February 14 September; Strathy, 11 February 26 August). In addition, the actual periods fished within each season varied, and differently among the fisheries, throughout the study period, as a result of voluntary and statutory restrictions. Fishery catches were subsampled throughout the entire season (the frequency of visits varied among sites and among years within sites). Sea and river ages of individual fish were determined from scale samples. The final records consisted of the site, date of return, sex, sea age, river age, fork length, and whole weight of fish recorded from a representative subsample. Fishing intensity differed by site, and throughout each season. All sites used fine mesh (barrier) nets that contained fish without entangling them (Shearer, 1992) that are not believed to select for particular fish sizes. Compliance with the commercial operators precluded sampling according to strict, formal statistical randomization, but the subsamples obtained are considered to be fully representative of the fish available.

Quality control
Multiple sea winter (MSW) fish of three or more sea winters and repeat spawners were excluded from the analysis, because they were too few for their findings to be representative. Serious potential outliers in the remaining data for 1SW and 2SW fish were removed in two stages: first, as outliers from a regression model that fitted length data to sea age, fishery, and year, and second, by regressing log weight against log length. Records with a Studentized residual of >4 in either model were discarded ($n = 725$ records). Certain combinations of fishery/year/sea age were also discarded from the dataset where there were too few records, or too short a sampling period, to which reliable seasonal trends could be fitted (see below). At some sites, early records (1960s) had the weight recorded at too low a precision for calculating individual condition: such weights were set to missing, although the records were retained for length analyses. In all, 151 002 records (of which 136 346 included an adequate weight measurement) were retained for analysis (Table 1).

Fish condition
The concept of describing the condition or well being of a fish as the ratio of its weight to the cube of its length dates back to the early 1900s and is often attributed to Fulton ($K = W/L^3$; see Nash et al., 2006, for a history of the concept's development). The underlying rationale is based on an assumed (approximate) constant shape of a fish during growth. Although constant shape seems inappropriate, in detail, for Atlantic salmon growing from immature smolts to mature adults, which accumulate reserves for breeding, it proved to be an adequate description of the field data available. The data preclude description of allometric growth trajectories, because there was only a single pair of (length, weight) measurements for each fish, at coastal return; these described the final states of the fish, but said nothing about the growth trajectories they took to reach those states. When poor feeding forces fish to stop growing, their lengths stay constant, but their weight, and hence condition, is likely to decrease to fuel metabolic demand. Several authors have recently discussed the statistical merits of different condition formulae (e.g. Bolger and Connolly, 1989; Blackwell et al., 2000; Marshall et al., 2004). We have reported the use of a simple index [$\log_{10}(W/L^3)$] elsewhere (Bacon and Palmer, 2007), along with of a set of more complex relationships, whereby the length exponent was not forced to be 3.00, but was separately estimated for different sex and sea age groups. As these more complex analyses gave virtually identical biological interpretations, we here report just the results using the simple index for brevity [$\log_{10}(W/L^3)$], where W is the wet (round) weight (kg) and L the length (m).

Statistical analysis
Preliminary inspection of the data indicated that: (i) fishing effort and/or capture rate varied hugely, both between and within fisheries and years, resulting in unbalanced sample numbers, as well as substantial data gaps for some fisheries; (ii) lengths and weights of both sea ages increased progressively during the course of a fishing season; and (iii) over the study period, variable durations of fishing season within fisheries resulted in seasonal distributions that were truncated, particularly for 2SW fish early in the year. It was therefore imperative that our analysis be robust to these complexities, to ensure that any estimated trends were not biased by such effects.

The effects of sea age, sex, river age, and time of capture during the year (represented by Julian day, which was fitted as a squared term, because the relationships were curvilinear) on the length and weight of captured salmon were examined by fitting the data to
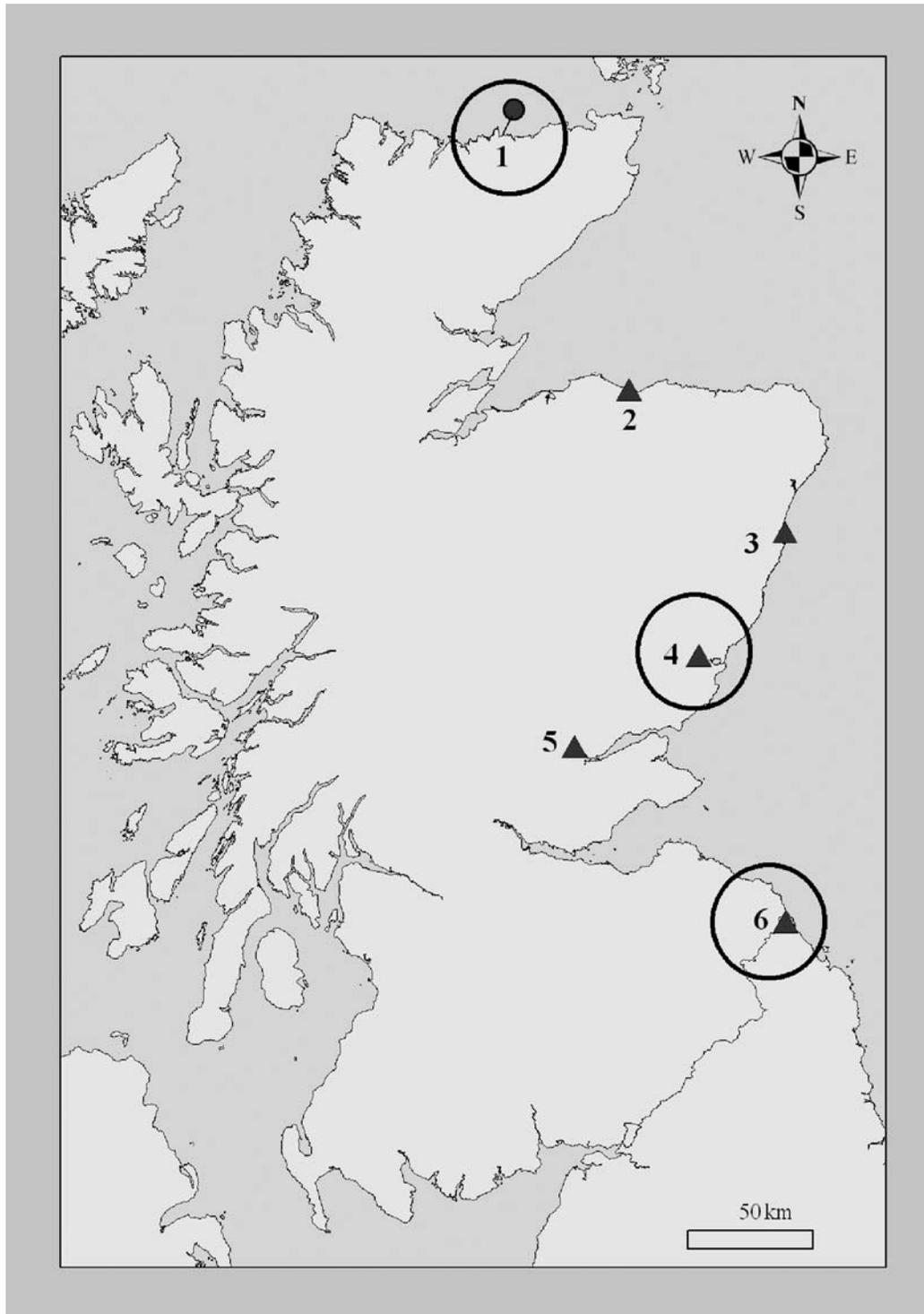
Figure 1. Sampling sites. Circles show those sampled in 2006. 1, Strathy; 2, Spey; 3, Dee; 4, North Esk; 5, Tay; 6, Tweed.

general linear models (GLMs). The inclusion of the seasonal Julian day term was crucial to correcting for variations in the dates of capture, especially those resulting from variable and unrecorded fishing efforts, between fisheries and years.

Differences between years and between fisheries were assessed by adding both year and fishery (site) terms to the models as factors, together with interaction terms where appropriate.

As the North Esk provided by far the largest sample, as well as the most continuous run of data, it was treated as the reference site against which the other fisheries were compared. "Year" was also alternatively fitted as a linear covariate to determine whether there were significant long term trends in mean length and weight of each age class. Before examining formal statistical correlations across years between fisheries, any common

Table 1. Summary by fishery and sea age of records available for analysis, including earliest and latest dates of capture (as Julian day) aggregated over all years.

Fishery	Type	Sea age	Number of years	First year	Last year	Number of records	Earliest day	Latest day
Dee	Net and coble	1	6	1974	1986	2 168	119	219
		2	6	1974	1986	2 127	43	219
		Total				4 295		
North Esk	Net and coble	1	44	1963	2006	38 255	107	244
		2	44	1963	2006	33 991	47	244
		Total				72 246		
Spey	Net and coble	1	16	1970	1986	9 584	128	242
		2	15	1970	1986	7 017	42	242
		Total				16 601		
Tay	Net and coble	1	25	1969	1996	10 976	106	233
		2	27	1968	1996	12 317	37	233
		Total				23 293		
Tweed	Net and coble	1	31	1969	2006	16 379	93	258
		2	29	1968	2006	13 086	46	258
		Total				29 465		
Strathy	Fixed engine	1	14	1993	2006	5 102	165	234

temporal trend inherent in the data was removed by fitting a spline curve with four degrees of freedom (d.f.), common across all fisheries, using a general additive model (GAM). This technique ensured that any two fisheries would not appear to be intercorrelated simply because they both showed a similar, long term trend. The same GLM and GAM analyses were then performed for the simple condition index, although in that case, a linear Julian day term fitted the data better than a squared term.

The extremely large sample sizes available in this study could have produced estimated differences (e.g. in body length) between groups of fish which, although statistically significant on account of the sample sizes, were so small that their biological importance may have been unclear or questionable. Hence, we generally restricted reporting relationships to those which were significant at $p < 0.001$ and that also explained useful proportions of the variance.

Fish condition and fish size within short periods

The data also allowed us to look for consistent relationships between individually achieved sizes and conditions, irrespective of sea age, site, and the broad seasonal period of return. Within short periods of 10 d within years for individual fish, the simple condition index was regressed against length for each combination of site and sea age. Periods of 10 d were chosen to give adequate sample sizes of fish within periods, sites, and sea ages. The Spey, Dee, and Strathy fisheries had too few data to include. For the Tay, Tweed, and North Esk, years before 1968, when only the North Esk was represented, were omitted to give balanced comparisons across those sites. Year was included as a random effect.

Environmental correlates

Brief investigation into whether environmental variables, such as the North Atlantic Oscillation (NAO), were intercorrelated with
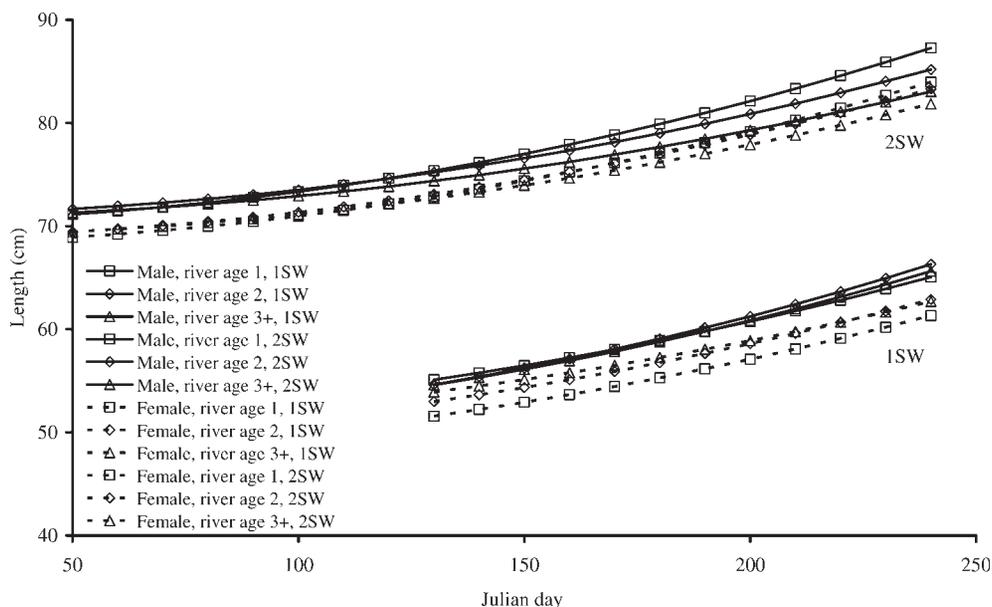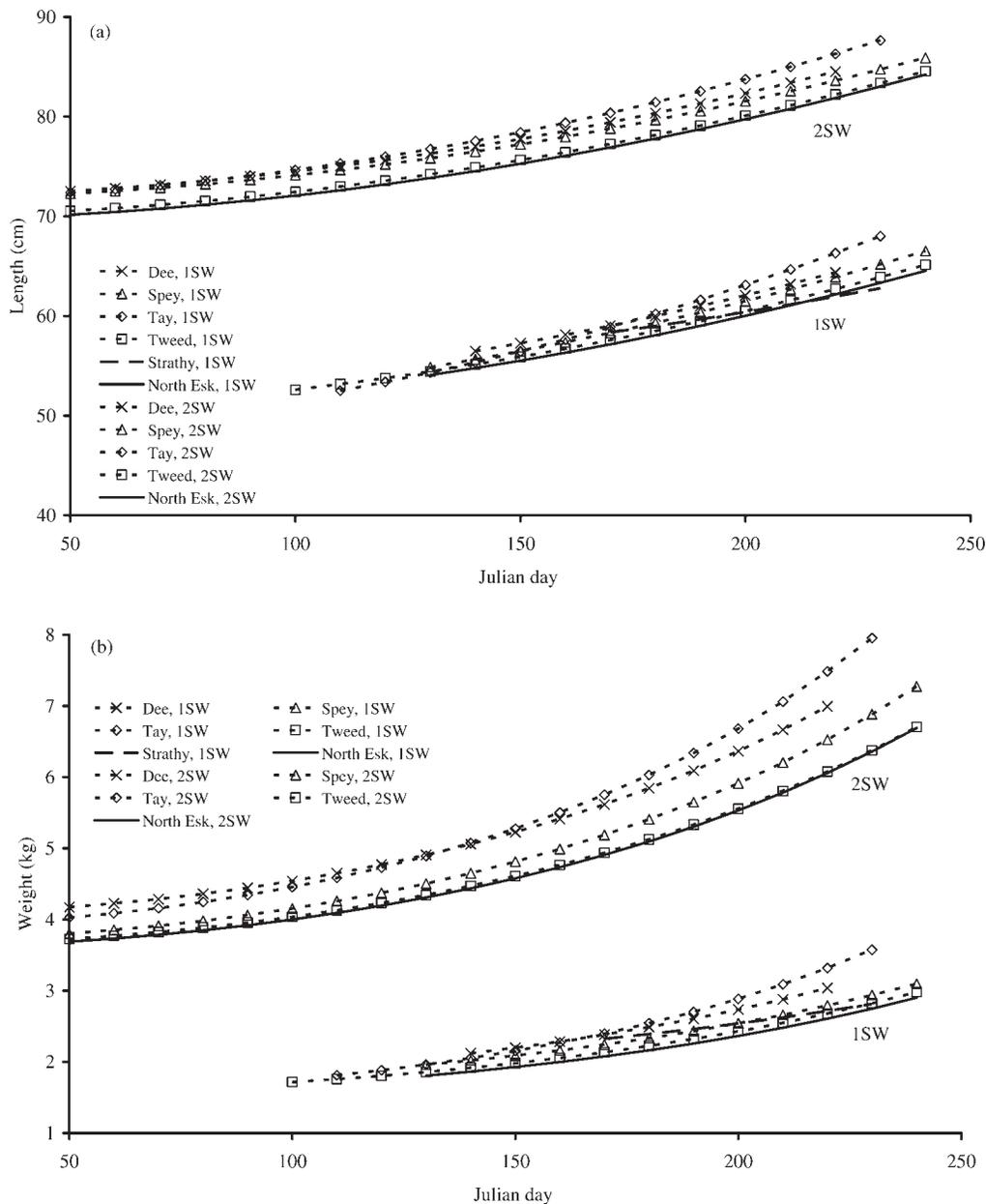

Figure 2. Seasonal changes in the mean length of Atlantic salmon returning to the North Esk, 1963 2006, by sea age, sex, and river age by Julian day (from 1 January).

changes in salmon length, weight, or condition was undertaken. A major difficulty in this endeavour was that many of the more per tinent environmental surrogates are available for a much shorter period than our salmon data, and often for too short a period to investigate reliably the cause effect possibilities when background levels are known to fluctuate. The indicative environmental vari ables considered were: (i) NAO winter index (December March mean); (ii) winter and spring mean sea surface temperature (SST) in the North Sea; (iii) potential 0 and 1+ age group sandeel availability in the North Sea; (iv) herring spawning stock biomass (SSB) in the North Sea; (v) capelin SSB in the North Atlantic; (vi) the West Greenland salmon catch ascribed to the European stock; (vii) all environmental variables (i) (vi) combined.

Northeast Atlantic SST

As the NOAA dataset used by Todd *et al.* (2008) does not extend back far enough, the Hadley Centre HadSST2 dataset (Rayner *et al.*, 2006) was used to examine trends over the longer period. HadSST2 data from 1960 were available on a grid of 5° latitude by 5° longitude, rather than the grid of 1° by 1° of the NOAA data. This coarser spatial resolution somewhat smooths the HadSST2 data over time, compared with the NOAA data (S. L. Hughes, pers. comm.). The methods of Todd *et al.* (2008) were followed for the HadSST2 data. After spatial averaging (centred on 67.5°N 2.5°E and using a Gaussian kernel with $\sigma = 500$ km) and temporal detrending, the residual monthly average temperature anomalies obtained were indeed similar to those reported by Todd *et al.* (2008; their Figure 6).

Figure 3. Seasonal changes in (a) mean length and (b) geometric mean weight of Atlantic salmon returning to six Scottish fisheries, 1963 2006.

Following Todd *et al.* (2008), correlations were investigated between our detrended annual average salmon condition indices with the previous 13 months of monthly average HasSST2 SST, when grilse were at sea. In addition, to smooth out the high inter monthly temperature variations, a sequence of seasonally averaged temperatures was constructed as follows: smolting (May July of the year before return as 1SW); autumn (September November before 1SW return); winter (December February); spring (February April); summer (May and June of the year of return to coastal waters).

Estimating ova fecundity

The likely effects of the reported average female length differences were interpreted in terms of their potential effects on ova pro duction. We used parameters from a log(length) to log(ova

numbers) equation given by Pope *et al.* (1961) as typical for several east coast Scottish rivers. As fish condition changes in unknown ways between coastal return and spawning, we were unable to make similar reliable deductions.

Results

Changes in length and weight within a season

The effects of sea age and Julian day far outweighed those of river age and sex, as illustrated for seasonal trends in length for the North Esk (Figure 2). Although the marginal effects of sex (males were ~1.8 cm longer than females) and river age (for the North Esk, fish that had spent only 1 year in the river before smolt ing were, as adults, 0.6 cm shorter than those spending 2 or more years) were statistically significant (partly because of the very large sample sizes), their biological importance was less clear. Therefore,
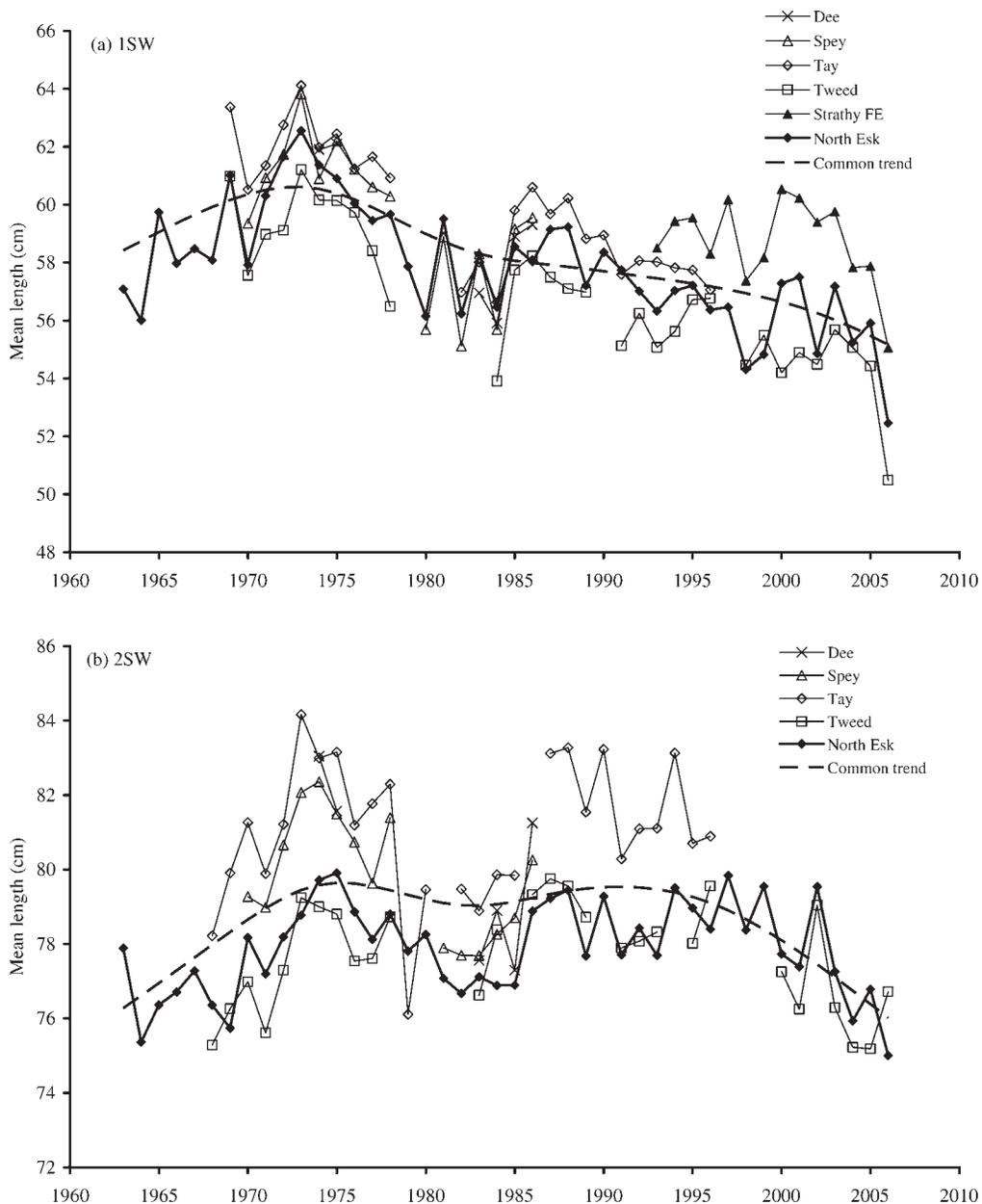
Figure 4. Annual mean lengths of (a) 1SW and (b) 2SW Atlantic salmon captured in six Scottish fisheries, 1963 2006.

to simplify interpretation of the similarities and differences between sea ages, years, and fisheries, the data were pooled across river age and sex, which reduced the explained variance in both length and weight by <2%. All subsequent analyses were conducted on pooled data.

The average lengths and weights of 1SW and 2SW salmon increased markedly with the day of the year on which they were cap tured in all fisheries (Figure 3). Generally, the seasonal trends were similar for all fisheries, but with some small but significant differ ences in the rates of increase in length. Of particular note was the appreciably faster rate of seasonal change for 1SW fish in the Tay compared with the North Esk ($F_{1,\infty} = 384$, $p < 0.001$), resulting in the average 1SW Tay fish towards the end of the season being almost 4 cm longer and ~0.5 kg heavier than North Esk fish (when corrected to a common, comparable date).

Changes in fish length and weight across years and fisheries

The broad trend for 1SW fish was that all fisheries except Strathy showed significant long term (linear) decreases in lengths ($t > 7.0$, $p < 0.001$ always; Figure 4a), and all except the Spey showed similar decreases in weight ($t > 4.2$, $p < 0.001$ always; Figure 5a). In contrast, tests for broad long term (linear) trends of 2SW fish were either not significant or of much lower magni tude and hence of little biological importance (Figures 4b and 5b). The mean lengths and weights of 2SW fish in the Tay were substantially greater than the corresponding means in the North Esk. The length model accounted for almost 75% of the individual variation and resulted in a root mean squared (RMS) error of 4.5 cm for the lengths of individual fish (95% confidence range ~18 cm). The weight model accounted for ~65% of the variation
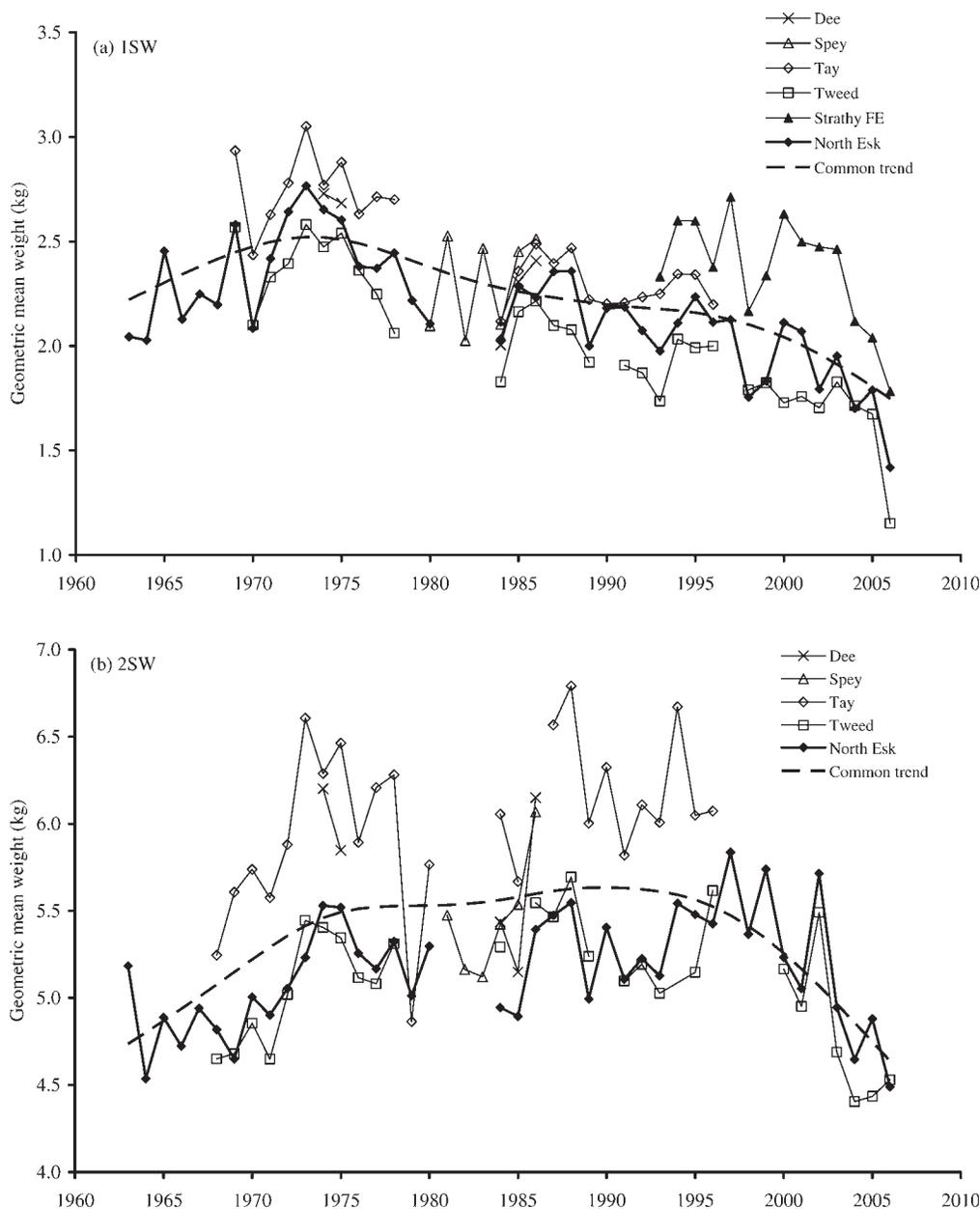

Figure 5. Annual mean weights of (a) 1SW and (b) 2SW Atlantic salmon captured in six Scottish fisheries, 1963 2006.

in log(weight), RMS ~0.24 log(weight), equivalent to an asymmetric 95% confidence range about the overall mean of the order of 4.5 kg. Individual weights varied more than lengths.

However, careful inspection showed that the long term trends were more complex than straight lines, as can be seen from Figures 4 and 5. Indeed, fitting fishery specific trends simplified to straight lines to these data could introduce bias for the shorter, interrupted runs of data that characterized some sites. Therefore, spline curves were considered more suitable than linear relationships to detrend data before examining correlations between the annual mean length and weight residuals from the different fisheries. The more detailed relationships, for both sea age classes, estimated as a common trend across the fisheries, revealed wide convex curves, all interrupted by two shallow humps, but generally following the broader linear trends described above, as depicted in Figures 4 and 5.

Having removed the common long term trends within each sea age class, the deviations in annual mean length of 1SW fish were highly intercorrelated between fisheries whenever there was temporal coincidence of at least 10 common years, as were the annual mean weight deviations (Pearson's $r > 0.64$, $p < 0.001$ always, except Strathy vs. Tweed). The intercorrelations were similar for 2SW fish (Pearson's $r > 0.60$, $p < 0.001$ always except Strathy vs. Tweed lengths and Spey vs. Tweed weights). Therefore, for both sea age classes, years in which fish were generally longer/heavier (at a given stage in the season) in the North Esk also tended to be longer/heavier than average fish in the other fisheries for which sufficient contemporaneous years were sampled.

Three fisheries provided data for 2006, when lean 1SW fish were widely reported throughout Scotland. All showed a common pattern. On the Tweed, 1SW fish in 2006 were shorter (53 vs. 60 cm, $t = 3.4$, $p < 0.001$) and lighter (1.4 vs. 2.5 kg, $t = 4.8$, $p < 0.001$) than expected from the long term average before 2006. This was also the case for the North Esk (length 54 vs. 61 cm, $t = 3.8$, $p < 0.01$; weight 1.6 vs. 2.6 kg, $t = 4.6$, $p < 0.001$). Differences were similar at the Strathy fixed engine fishery (length 56 vs. 63 cm, $t = 3.6$, $p < 0.01$; and 2.0 vs. 3.0 kg, $t = 4.0$, $p < 0.001$), despite a substantially shorter run of years before 2006.

Fish condition

Although the simple condition index of 2SW fish increased slightly during the season in all estuary fisheries ($t > 5.5$, $p < 0.001$ always; Figure 6b), the seasonal index for 1SW fish declined significantly for all fisheries as the season progressed [$t > 3.6$, $p < 0.001$ always, except the Dee, not significant (n.s.); Figure 6a]. Too few 2SW fish were caught at the Strathy Point fixed engine site for analysis; all other 2SW fish were caught by net and coble fishing gear in river estuaries.

The annual mean condition indices of 1SW fish in the Dee, Tay, Tweed, and North Esk were similar up to about 1990 (Figure 7a) and showed little long term variation. From the mid 1990s, the means from the Tweed and North Esk were less closely related, and both decreased sharply from around 1997 ($t = 8.5$, $p < 0.001$, and $t = 8.5$, $p < 0.001$, respectively). Moreover, there was no difference in the rate of decrease between these two rivers. At Strathy, there was a similar, but slightly less pronounced, recent trend ($t = 7.0$, $p < 0.001$).

In contrast to 1SW fish, the annual mean condition indices of 2SW salmon showed a greater degree of variation between fisheries, and a somewhat more pronounced upward trend, again until about the mid 1990s (Figure 7b). This trend was significant on the Tay and the North Esk up to 1997 ($t = 6.7$, $p < 0.001$, and $t = 2.6$, $p < 0.05$, respectively). Thereafter, as was also observed for 1SW fish, the annual condition indices for the North Esk and, in particular, the Tweed showed a sharp decrease from around 1997 ($t = 2.6$, $p < 0.05$, and $t = 5.3$, $p < 0.01$, respectively).

Whereas 1SW fish initially showed, on average, slightly higher condition than 2SW fish (particularly up to about 1990; Figure 7), this situation changed recently; since 2002, 1SW fish have consistently been of lower condition than 2SW fish. This change was due to a downward shift in the condition of all 1SW fish within the annual populations (rather than a largely unaltered maximum but an increase in the variance), as illustrated by the frequency distributions of condition indices for individual North Esk fish (Figure 8a). In contrast, there was no similar shift among 2SW fish (Figure 8b). After detrending the 1SW means, deviations in the annual mean condition indices of 1SW fish were mostly uncorrelated between fisheries where there was temporal coincidence of at least 10 common years; only the Tay and North Esk, whose estuaries are geographically close (Figure 1), were significantly correlated (Pearson's $r = 0.69$, $n = 23$, $p < 0.001$). This finding was in contrast to the results for mean length and weight, which showed high degrees of intercorrelation between fisheries (see above). Likewise, having removed the long term trends, deviations in the annual mean condition indices of 2SW fish showed the same lack of correlation between fisheries, other than, again, between the Tay and the North Esk (Pearson's $r = 0.64$, $n = 25$, $p < 0.001$).

In the thin grilse year of 2006, grilse on the Tweed had, on average, a much lower condition index (by 8%) than expected from the long term average between 1968 and 2005 ($t = 5.8$, $p < 0.001$), although the sample size from which the Tweed's 2006 mean was calculated was limited, and sampling was restricted to late in the season. Similar, but less marked, disparities between 2006 and previous years were observed for the North Esk ($t = 4.1$, $p < 0.001$), and at the Strathy fixed engine fishery ($t = 2.8$, $p = 0.060$, n.s.).

Over the decades, there was a general tendency for seasonal rates of change in the condition of 1SW fish to become, annually, more negative up to the early 1980s, and thereafter to become more positive (Figure 9a). Therefore, for most of the study period, the condition index of 1SW fish declined during the course of the season, but from the late 1990s, in the North Esk and the Tweed, the rate of change tended to be positive, indicating an increase during the season. Note, however, (i) as a rule of thumb, rates less than about ± 0.01 tended to be not significant, i.e. there was no discernible trend throughout the season, and (ii) rates on the Tweed since the late 1990s and for the Strathy throughout were estimated from relatively short runs of data, so are less reliable. Following detrending, the annual seasonal rates of change in condition of 1SW fish on the Tay and the North Esk were correlated (Pearson's $r = 0.51$, $n = 23$, $p < 0.05$), but otherwise the net and coble fisheries were uncorrelated. In contrast, the seasonal rates of change in condition of 2SW fish were either positive (i.e. condition improved as the season progressed) or not significant up to about 2000 (Figure 9b). From around 2000, there was a sharp decline in the seasonal rate of condition change on the North Esk, sufficient to turn it into significant
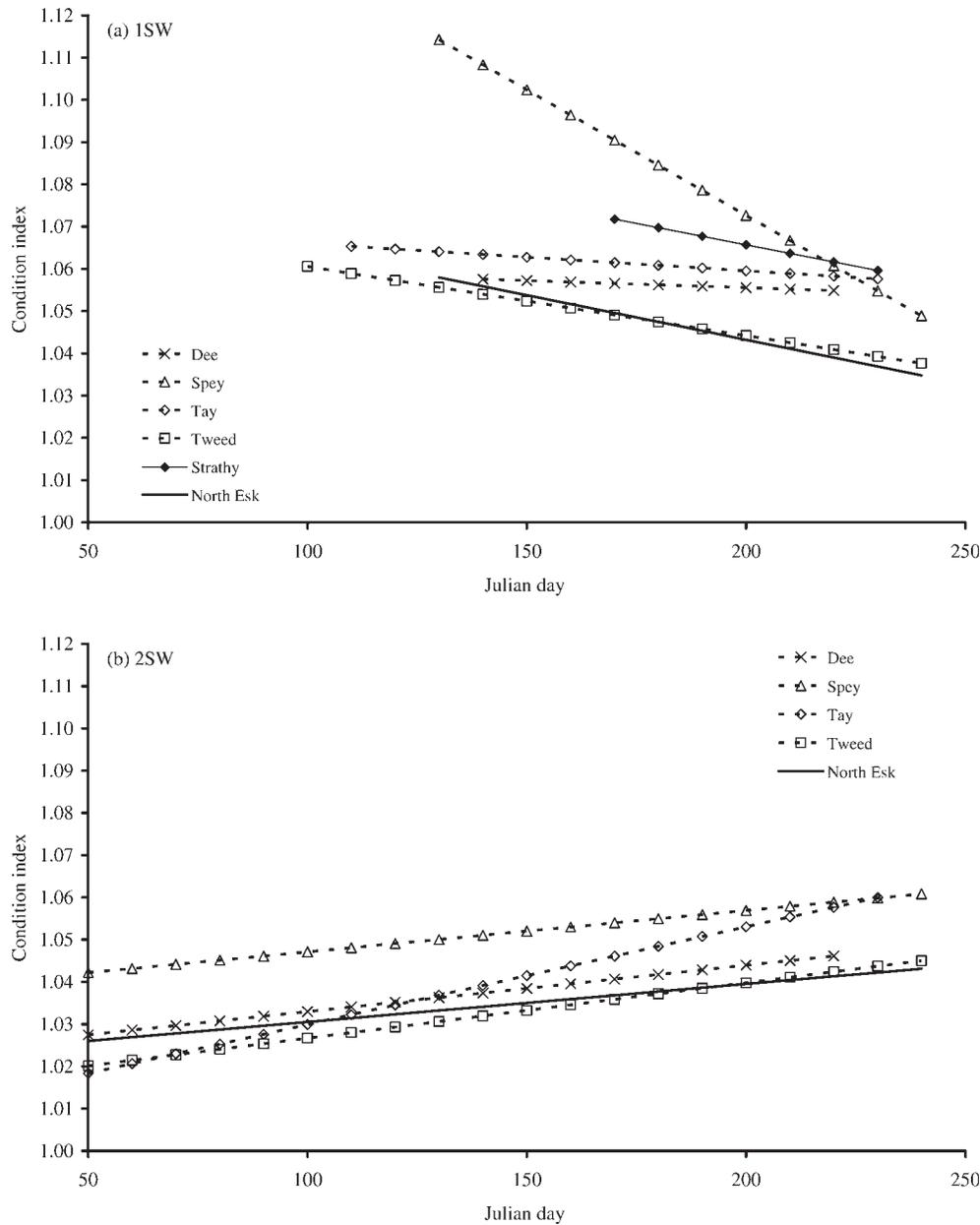
Figure 6. Seasonal changes in mean condition index of (a) 1SW and (b) 2SW Atlantic salmon returning to Scottish fisheries, 1963 – 2006.

seasonal decreases in both 2005 and 2006. The results for the corresponding period on the Tweed are unclear, because not only were the sampling periods short, but the sample sizes within each year were too small to estimate the rates of change with confidence. Following detrending, the seasonal rates of change in condition of 2SW fish on the Tay were correlated with those on the Tweed and the North Esk ($r = 0.54$, $n = 20$, $p < 0.05$; $r = 0.44$, $n = 25$, $p < 0.05$, respectively), but otherwise the different estuary fisheries were uncorrelated.

Fish condition and fish size within short periods

Table 2 lists the slope coefficients between fish length and condition, estimated for 107 combinations of fishery site, sea age, and 10 d period, together with their significance values, both direct and adjusted for multiple comparisons (by cumulative

binomial probability calculations). The biological hypothesis is that the slopes of the length to condition relationships should be positive. Only 2 of 107 regression coefficients had negative coefficients with $p < 0.01$, and the overall probability of this is not significant ($p = 0.26$). However, half the 107 estimates had positive coefficients, with $p < 0.01$ (overall $p \ll 0.0001$), and 36% had positive coefficients individually significant at $p < 0.0001$. It is curious that, whereas the 1SW fish from all sites analysed (Tay, Tweed, and North Esk) consistently showed a predominance of significant positive correlations, this was not consistently so for 2SW fish. There was no firm evidence whatever for positive correlations for 2SW Tweed fish ($0/22$, $p \approx 1.0$), whereas 2SW salmon from both the Tay and the North Esk showed preponderances of significant positive correlations (both with overall $p \ll 0.0001$).
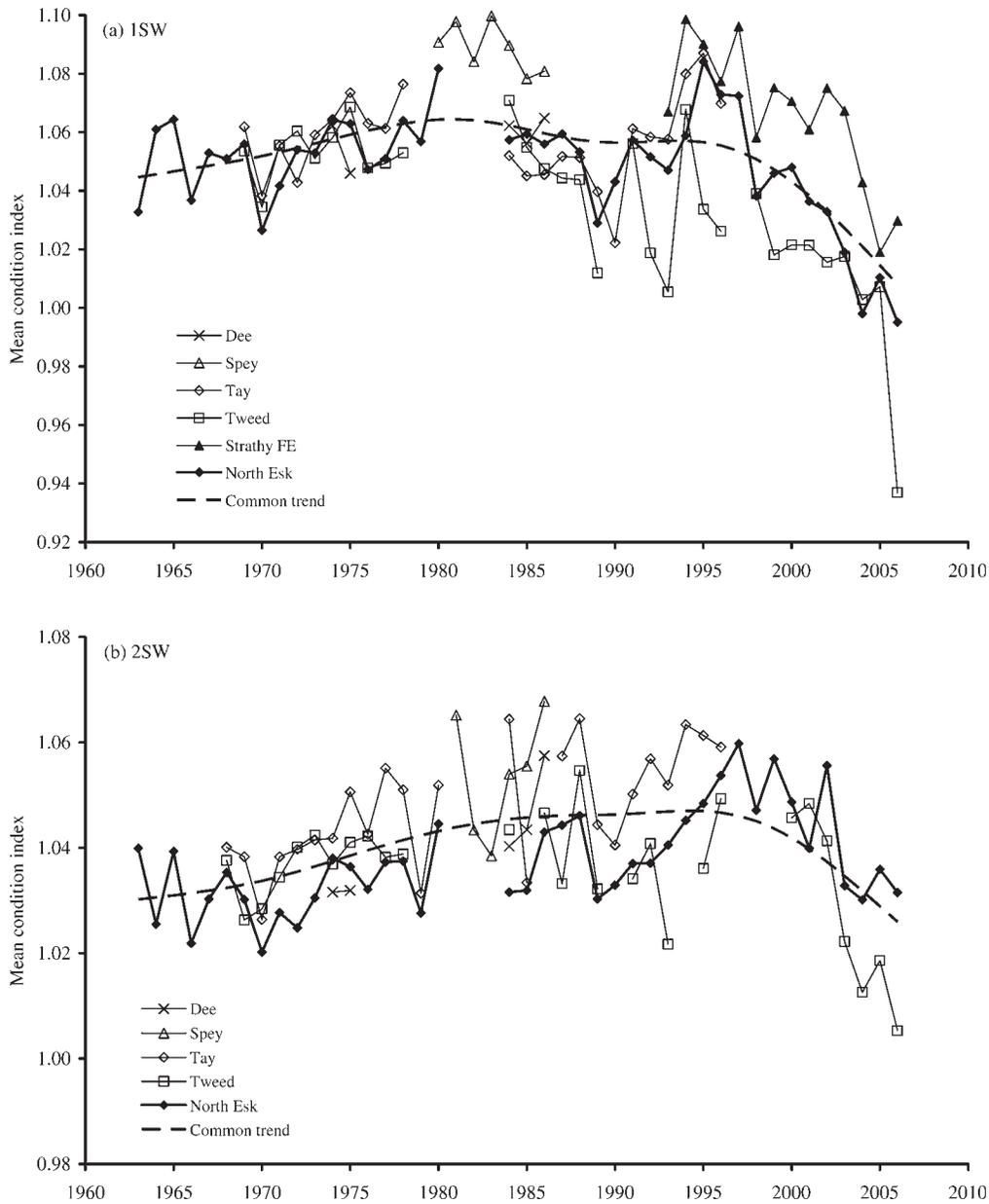
Figure 7. Annual mean condition index trends of (a) 1SW and (b) 2SW Atlantic salmon captured in six Scottish fisheries, 1963 2006.

Environmental correlates

Correlations between the seasonally corrected estimates of fish size (length, weight) and condition (i) with a suite of environmental variables, and (ii) between the 1SW and 2SW cohorts were briefly investigated for the North Esk. The direct correlations were weak, and, following detrending over time, became either not significant or else explained so little of the response variance that the relationships were uninformative.

Northeast Atlantic SST

Having detrended our annual mean condition indices for 1SW fish, using a spline curve common to all fisheries (Figure 7a), we were unable to reproduce the high correlation between average annual 1SW fish condition at the Strathy fixed engine fishery and SST in the NE Atlantic during the previous January, as

reported by Todd *et al.* (2008; viz. their results: Pearson's $r = 0.719$, unadjusted $p = 0.0038$). Our 1SW fish condition indices were correlated with January HadSST2 SST data, but to a markedly lesser degree ($r = 0.584$, unadjusted $p = 0.028$). Moreover, we found no significant correlation (unadjusted $p > 0.05$) with HadSST2 SST for mean Strathy 1SW fish conditions in any other single month or with any of our seasonal combi nations of months. Nor did we find significant correlations between SST and mean fish condition indices for the North Esk, the Tay, or the Tweed in any month or season, either during the period 1993 2006 (corresponding to the period analysed by Todd *et al.*, 2008) or for the whole run of data available at each fishery since 1963 (Table 1, Figure 4).

However, we were able to produce similar correlations to those obtained by Todd *et al.* (2008) for the Strathy by detrending just
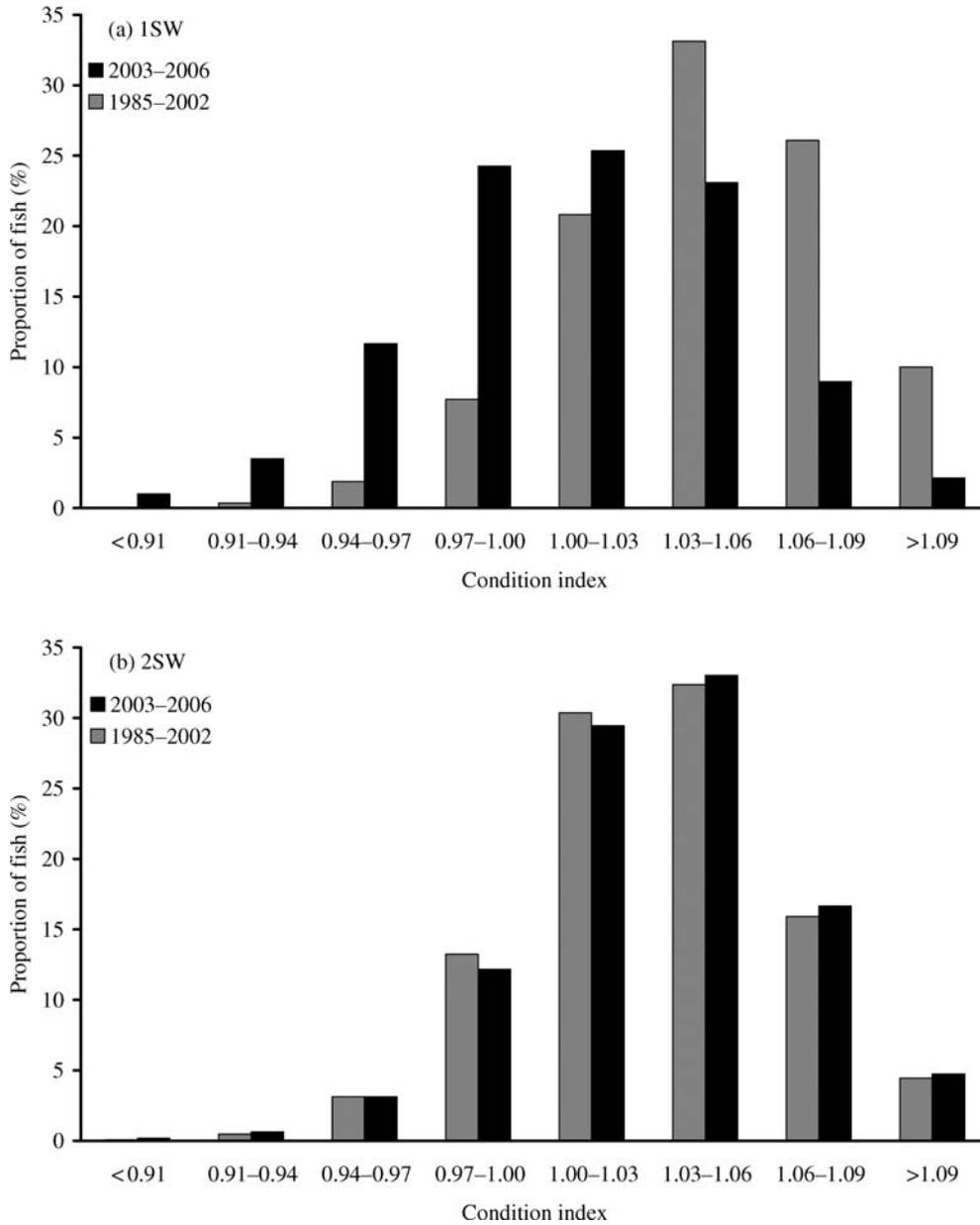
Figure 8. Proportionate distribution of fish (PDF) in each of eight condition-index classes for (a) 1SW and (b) 2SW Atlantic salmon returning to the North Esk in two periods, 1985–2002 and 2003–2006.

the 1993–2006 Strathy 1SW fish data using a Strathy-specific spline curve having 6 d.f. (January SST: $r = -0.732$, unadjusted $p = 0.0029$; winter SST: $r = -0.618$, unadjusted $p = 0.018$). We note that, using this locally specific analysis, the correlation between our detrended annual mean 1SW conditions and the predicted 1SW annual mean weights (PWt) reported by Todd *et al.* (2008) was rather closer ($r^2 = 0.86$) than when we detrended using a common relationship for all fisheries ($r^2 = 0.73$).

Estimated ova fecundity effects

Table 3 lists the expected ova numbers for a range of instructive female lengths for 1SW and 2SW salmon. Rather than just showing the expected ova productions for early-, mid-, and late-running fish of each sea age (the emboldened rows), we also provide comparisons (the italicized typeface) between typical

mid-season running fish and three variant groups representing: (i) mid-running plus the minimum length difference these large sample sizes can show as statistically significant between subgroups; (ii) the magnitudes of size differences between different freshwater age groups; (iii) either (a) the magnitude of fishery (site, river) differences or (b) the amounts by which the common trend lines (Figure 4) have varied over decades. We also provide ova differences as percentages, relative to both the means of the same sea age group (penultimate column) and the advantage of 2SW fish over 1SW of the same type (final column).

The analytical power of our large sample sizes allows us to show statistically significant effects of factors which, by such correlations to ova numbers, would have very small implications for average female fecundities (1 mm length change, ∼0.5% increase in ova numbers). The small average differences in river ages detected
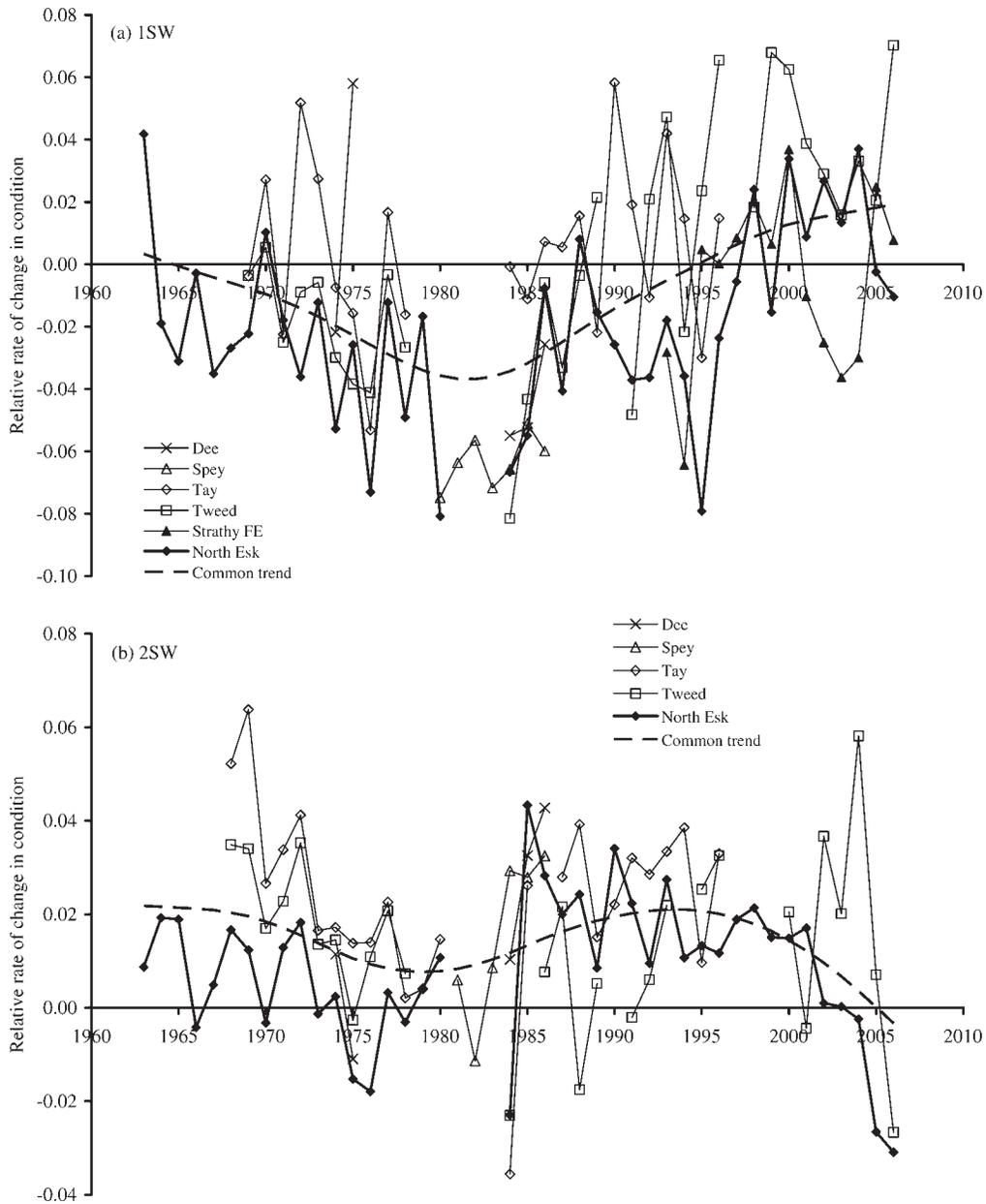
Figure 9. Seasonal rates of change in the mean condition index of (a) 1SW and (b) 2SW Atlantic salmon returning to Scottish fisheries, 1963 2006.

might represent 2% differences in ova numbers, whereas the larger effects of sites, or the magnitudes of size trends over time, rep resent around 4% potential fecundity differences for 1SW and 3% for 2SW. In contrast, the differences between early and late run fish, relative to mid run fish of the same sea age, are an appreciable 20% for early and +16 21% for late. Finally, con trasting the ova differences between sea ages for the various types of 2SW fish with their 1SW counterparts reveals large and consist ent differences of some +80% (75 82%).

Discussion

Our results represent the first detailed analysis of a very large, long term dataset on the biometrics of adult Atlantic salmon sampled from a wide geographic spread of Scottish fisheries. Their proper interpretation depends on suitably controlling for large seasonal changes and making allowances for differences in sampling periods and intensities, when comparing between years, sites, and run time groups.

The many common trends over years documented between sites, and the coherent annual differences from several of these, hint at broad, common causes rather than random or chaotic vari ation. Such mechanisms could have both environmental (Friedland et al., 2000, 2009) and genetic components (Garcia de Leaniz et al., 2007). The environmental aspects need not all be marine and could include the direct effects of human fisheries and their delayed, and, potentially, even evolutionary, conse quences (Hard et al., 2008). Resolution of these questions will probably require simultaneous modelling of salmon numbers,

Table 2. Correlation between individual salmon length and condition [$\log_{10}(W/L^3)$] within multiple 10-d periods of return to the coast, by sea age and fishery.

Site	Sea age	Total comparisons	Slope significantly positive		
			Number with $p < 0.01$	Probability observations $n < 0.01$	Number with $p < 0.0001$
Tay	1SW	12	4	<0.0001	4
Tweed	1SW	17	8	<0.0001	8
N Esk	1SW	14	8	<0.0001	8
Total	1SW	43	20	<0.0001	20
Proportion significant at p level			0.47		0.47
Tay	2SW	21	8	<0.0001	2
Tweed	2SW	22	0	1.0	0
N Esk	2SW	21	17	<0.0001	16
Total	2SW	64	25	≪0.0001	18
Proportion significant at p level			0.39		0.28
Grand total	1SW + 2SW	107	45	≪0.0001	38
Proportion significant at p level			0.42		0.36

Table 3. Implications of length differences for ova fecundity (see text for detail).

Comparison category	Fish length (mm)	Estimated ova numbers	Length comparisons		Ova comparisons	
1SW			1SW/1SW%		1SW/1SW%	
Early	530	2 912	91.4		81.0	
Mid	580	3 594	100.0		100.0	
Min. Significant	581	3 608	100.2		100.4	
River age	585	3 666	100.9		102.0	
Site/Trend	590	3 740	101.7		104.1	
Late	630	4 359	108.6		121.3	
2SW			2SW/2SW%	2SW/1SW%	2SW/2SW%	2SW/1SW%
Early	680	5 210	90.7	128.3	79.6	178.9
Mid	750	6 549	100.0	129.3	100.0	182.2
Min. Significant	751	6 570	100.1	129.3	100.3	182.1
River age	755	6 652	100.7	129.1	101.6	181.4
Site/Trend	760	6 755	101.3	128.8	103.1	180.6
Late	800	7 614	106.7	127.0	116.3	174.7

return ages, growth, and fecundity, and the quantitative contrast between well defined hypotheses. Such topics are beyond the scope of this paper.

Environmental aspects

Although the growth and survival of salmon at sea must depend on marine conditions, our attempts to correlate salmon perform ance with a variety of marine environmental variables were con spicuously unrewarding. A plethora of alternative surrogate marine variables could easily be proposed, but the likely absence of long term data on them and ignorance of the areas of ocean rel evant to salmon in general let alone to salmon from different sub populations, currently militates against success.

The long term trends in salmon biometrics were less similar across sea ages, implying some degree of spatial separation. The unexplained variations were relatively larger for weights than for lengths, giving plenty of scope for the condition of individual fish to vary widely, which they did. Clearly, the environment experienced during those final weeks at sea may be expected to differ between different parts of the Scottish coast, and may account for some of the site differences. An equally plausible, but as yet untested, hypothesis is that salmon from the different

rivers might go to different parts of the ocean, or even to the same parts at slightly different times.

Despite these long term fluctuations, 2006 represented the worst year for the condition of 1SW fish since 1963, being, currently, the low point of a downward dip, which started around 2000. There were also suggestions that the condition of 2SW fish might be heading the same way, although to a lesser degree. We have no way of knowing if these downward trends will continue.

We found no convincing correlations between the growth of salmon and marine environmental factors (including NAO and temperature) or marine biotic variables. Peyronnet *et al.* (2008) reported strong relationships, since 1980, between the survival of wild and ranched Atlantic salmon from Ireland and marine factors, including the NAO and SST off the Irish coast (although it is not clear whether their method accounted for possible spur ious temporal co linearity between survival and their predictor variables, by first detrending all variables). In any event, the two results are not inconsistent; it would be quite possible for factors that affect the mortality of early post smolts not to influence the return sizes of those that survive. However, our longer term data show that it is very unlikely that such changes in salmon condition

have been continually strongly driven by SST, in the sense that January SST impaired ocean conditions the next spring, leading to thin grilse in summer (Todd *et al.*, 2008). Compared with that previous work, our data are more powerful over time, and more general because of the extra sites, and the commonality of trends between sites makes our inferences robust.

Population and genetic aspects

Broad population processes, including genetic aspects, could also be involved. Over the period of our study, the numbers of return ing 3SW fish declined to near zero (by 1970s), and the numbers of 2SW fish declined dramatically after 1980 (ICES, 2008). Both changes might well have affected the status and growth of the remaining population components. Such mechanisms could be involved at finer scales too. The average condition of 1SW fish decreased sharply during a season. Without objective data on the detailed run time propensities of individual fish arriving in particular periods, we are unable to investigate either the relative condition of different putative run time genotypes or the effects on annual means of them arriving prematurely in some years and late in others. We note that simple thought experiments show that if such disparate size or condition groups exist, either within or between rivers and irrespective of cause [environment (marine or freshwater) or genetic], then variations in just their numbers will cause fluctuations in annual averages and seasonal trends within years, whereas annual variation in their achieved times of arrival would alter seasonal changes in size within years. Our results (Figures 7 and 9) reveal such annual and seasonal changes. Although we do not claim that (genetic) run time groups necessarily dominate these responses, either within or between sites, we do emphasize that, until objective data allow us to de confound such competing explanations, progress will be hampered.

Structured populations within rivers

As run time differences are also heritable (Hansen and Jonsson, 1991; Stewart *et al.*, 2002), we also specifically investigated the possibility that the seasonal trends in size (evident in Figure 3) might potentially be artefacts of varying proportions of early , middle , and late running fish, both 1SW and 2SW, as the season progressed. Such run time groups might have different genetic compositions, body conformations, and migration routes, and hence different final sizes and condition indices on return to the coast. The results of these analyses were notably inferior to the simpler explanation presented above. Indeed, even within fort nightly periods, seasonal size increases were still evident within the groups, and they merged rather naturally into each other to produce a single relationship of the form described here.

If the oceanic stages of 1SW and 2SW salmon from different Scottish rivers followed similar marine migratory routes at similar times, it is difficult to see how our findings of common decadal trends of size and condition, but with consistent long term differences between fishery sites, as well as coherent annual residual deviations across sites, would arise or could be main tained. Conversely, they could arise naturally if the salmon stocks from different rivers were of different composition, or had different ocean migration schedules, or both.

As the basic feeding grounds and migration routes of (Scottish) 1SW and 2SW Atlantic salmon are poorly known, it is impossible to assess what differences might arise during the oceanic phase, although the current SalSea project (http://www.nasco.int/sas/)

may start to shed light on this in the coming decades. In the absence of directly measured environmental variables, such as the temperatures experienced at sea, it is similarly difficult to speculate usefully as to what extent the biometric changes of salmon sizes reported here are likely to result from direct environ mental constraints, or more indirect mechanisms such as fisheries induced evolution (Dieckmann and Heino, 2007; Jorgensen *et al.*, 2007; Hard *et al.*, 2008).

Physiology, growth, and maturity

The ratio of wet weight to length can be a poor index of the body or energy reserves of fish, which often replace metabolized lipid or protein with water (Gardiner and Geddes, 1980). Todd *et al.* (2008) demonstrated that the lipid levels of Scottish salmon caught on the coast were not linearly related to their condition index and that lower indices were disproportionately associated with much poorer lipid levels. Therefore, in contrast to length (Table 3), the implications of our condition findings cannot be sensibly extrapolated to likely reductions in fecundity. However, the findings of Todd *et al.* (2008) suggest that actual fecundity decreases will be more severe than those implied by the length and condition changes we report here (Figure 7, Table 3).

North Esk salmon that return with growth checkmarks on their scales do not have shorter lengths on return to the coast (MacLean *et al.*, 2000). However, as checkmarks are usually laid down before the first winter at sea (for both 1SW and 2SW fish), there would be many months when any growth deficiencies could be made good. Indeed, von Bertalanffy growth alone (*sensu* Gurney and Veitch, 2007; Gurney *et al.*, 2007, 2008b; but see also Lester *et al.*, 2004) means that subsequent compensation is likely. These principles probably also apply to the regaining of condition following short periods of starvation at sea.

A classic paradigm for Atlantic salmon at sea considers that they disperse with the aid of ocean currents (Booker *et al.*, 2008) and implicitly assumes that any smolt from any particular river could become either a 1SW or a MSW fish (Gardner, 1976). Indeed, mortality estimates for different sea ages were published on this basis (Crozier and Potter, 2000; Friedland *et al.*, 2000). Elaborations to this idea have suggested that faster growing fish might become 1SW fish, whereas slower growers would be obliged to stay at sea longer before reaching a breeding threshold, and thus returned as MSW fish. Our early attempts to reconcile such growth concepts with the quantitative details of the Scottish sea age, seasonal, and sex difference findings reported here were unsuccessful (Gurney *et al.*, 2008a).

In contrast, genetic data suggest (Hankin *et al.*, 1993; Jónasson *et al.*, 1997) that sea age is a strongly heritable trait, raising the possibility that these types might behave in appreciably different ways, as well as then being more likely to have fundamentally different migration routes. Our early attempts to match such genetic models to details of the biometric data reported here have fared better and have subtle consequences for the population dynamics (Gurney *et al.*, 2008a).

Informed management

Detailed analyses of biometric data on wild adult Atlantic salmon are a vital part of understanding and monitoring the well being of wild populations. Most historical data on fresh run fish, at least in Scotland, come from samples obtained from net catches. However, because such nets have increasingly ceased to operate in Scotland (Anon., 2007), these crucial data are

becoming increasingly rare and much less representative. Similar statistics are not, and to some degree cannot be, replaced by information from rod fisheries (for which the dates of river entry are unknown). Informed management would not be helped if the enlightening net caught information should disappear entirely, from all sites, or even to the extent that it becomes small, unrepresentative subsamples.

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