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

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.

199 word abstract

Abstract

<B1 Aim now clarified>

Sea-age, size and condition of adult Atlantic salmon 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 forty four 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 1SW and 2SW fish. However, while 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 had disproportionately high weights at all seasons. 1SW condition was markedly lower in 2006. De-trended correlations with oceanic environmental variables were generally non-significant, and always weak. A published correlation between the condition of 1SW salmon caught at a single site and Sea-Surface Temperatures in the north east Atlantic could not be substantiated at any of the six fisheries over the wider timescales here examined.

KEYWORDS: climate change; condition; marine environment; NAO; *Salmo salar*; sea surface temperatures.

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1 Introduction <B2 Rephrase, focus and clarify 1st para>

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 (Friedland *et al.*, 2005, Crozier *et al.*, 2003). Factors affecting abundances of salmon from Norway and Scotland during the last century have been recently discussed (Vøllestad *et al.*, 2009). Scottish salmon catches, their sea-age at maturity and the seasonal return time show considerable fluctuations over the last 200 years (Summers 1995). Oceanic conditions affecting the survival ofpost-smolts (Peyronnet *et al.*, 2008) and growth (Friedland *et al.*, 2009) are also being reported.

Recent reports from fishermen 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 (Hansen *et al.*, 2008) Climate change has been suggested as a possible factor underlying the appearance of thinner fish (Todd *et al.*, 2008).

When marine fluctuations take place on multiple timescales, long-term data sets 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 record), 44-year dataset for Scottish Atlantic salmon, of both one and two sea-winter ages (1SW and 2SW) and 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, work in progress).

The aim of this study was to provide a rigorous empirical analysis as a focus for future dynamic modelling endeavours. 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.

<B3 clarified the following paragraphs>

In addition to the general interest concerning sex, sea-age and annual differences in the average condition of salmon returning to the coast, there is an important question about why 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 higher mortality. But a longer period at constant marine mortality risk could be out-weighted if the later-returning fish had *disproportionately* higher breeding reserves (than expected by purely volumetric increase in their size). Understanding the selective outcome of this survival and reserves trade-off requires knowing the size-dependence of both mortality and breeding reserves. In particular, we investigated the hypothesis that, for individual fish arriving in very short co-incident periods, larger fish might have higher condition indices, and hence more reserves for gonad formation, within all such return periods. Such a finding **<B4: clarified & stated 2.6 results do answer this question>** would conform with the widespread view for other species that larger fish do indeed have disproportionately more breeding reserves.

2 Methods

2.1 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. <A1Origin stocks of fish> The Strathy site captures fish from mixed stocks. Although a few percent of the fish captured in the estuaries probably originated from other rivers the great majority are of local provenance **<A2. Previous spawners>** Previous spawners comprised less than 2% of captures, and were ignored. We note that roughly half of the records came from the North Esk, and this was the only fishery which was represented throughout the entire sampling period (1963 - 2006).

2.2 Fish sampling

Typical annual open-seasons <B5 we now give OPEN seasons below> varied slightly among the fisheries sampled[1]. In addition, the actual periods fished within each season have varied, and differently among the different fisheries, throughout the study period, as a result of voluntary and statutory restrictions. Fishery catches were sub-sampled 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 comprised the site, date of return, sex, sea age, river age, fork-length and whole weight of fish, recorded from a representative sub-sample of individuals. Fishing intensity differed at different sites, and throughout the season. <B6 were net meshes selective>. All sites used fine-mesh (barrier) nets that contained fish without entangling them (see Sheerer 1992) and are not believed to select for particular fish sizes. Compliance with the commercial operators precluded sampling according to strict, formal statistical randomisation, but the sub-samples obtained are considered to be fully representative of the fish available.

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[1] (e.g. Dee –11th February to 26th August ; North Esk –16th February to 31st August; Spey - 11th February to 26th August; Tay – 5th February to 20th August; Tweed – 15th February to 14th September; Strathy - 11th February to 26th August).

2.3 Quality control

Multiple sea-winter (MSW) fish of three or more sea-winters and repeat spawners were excluded from the analysis, as there were too few for any representative findings. Serious potential outliers in the remaining data for 1SW and 2SW fish were removed in two stages. Firstly, as outliers from a regression model that fitted length data to sea age, fishery and year. Secondly, by regressing log-weight against log-length. Records having a Studentised residual greater than 4, in either model, were discarded (n = 725 records). Certain combinations of [fishery / year / sea age] were also discarded from the data set 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 weight recorded at too low a precision for calculating individual condition: these weights were set to missing, although the records were retained for length analyses. A total of 151,002 records (of which 136,346 included an adequate weight measurement) were retained for analysis (Table 1).

2.4 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 fish-shape during growth. Although constant shape seems inappropriate, in detail, for the case of 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 a description of allometric growth trajectories, as there was only a single pair of (length, weight) measurements for each fish, at coastal return; these described the fishes' final states, 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 weights, and hence conditions, are likely to decrease, to fuel their metabolic demands. A number of 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 elsewhere (Bacon and Palmer, 2007) the use of both a simple index ($\log_{10}(W/L^3)$) and 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 wet (round) weight (kg) and L is length (m).

2.5 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 highly 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 the fishing season; and (iii) over the study period, variable durations of the fishing season within fisheries, resulted in seasonal distributions which were truncated, particularly in the case of 2SW fish early in the year. It was therefore imperative that our analysis should be very robust to these complexities, in order to be sure 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, as the relationships were curvilinear) on the length and weight of captured salmon were examined by fitting the data to general linear models (GLM). The inclusion of the seasonal Julian day term was crucial, in order to correct 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 then 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. Prior to examining formal statistical correlations across years between fisheries, any common temporal trend inherent in the data was removed by fitting a spline curve with 4 degrees of freedom, common across all fisheries, using a general additive model (GAM). This technique ensured that any two fisheries would not appear to be inter-correlated 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 this case a linear Julian day term fitted the data better than a squared term.

It should be noted that the extremely large sample sizes available in this study could produce estimated differences (e.g. in body length) between groups of fish which, while statistically significant on account of the sample sizes, are so small that their biological importance may be unclear or questionable. Thus we generally restrict reporting relationships to those which were both significant at $p < 0.001$ and which also explained useful proportions of the variance.

2.6 Fish condition and fish size within short periods

The data also enabled us to look for consistent relationships between individually achieved sizes and conditions, irrespective of the sea-age, site and the broad seasonal period of return. Within short ten-day periods within years, for individual fish, the simple condition index was regressed against length for each combination of site and sea age. Ten-day periods were chosen to give adequately large samples sizes of fish within periods, fishery sites and sea ages. The Spey, Dee and Strathy fisheries had too few data to include. For the Tay, Tweed and North Esk, years prior to 1968, when only North Esk was represented, were omitted to give balanced comparisons across these sites. Year was included as a random effect.

2.7 Environmental correlates

Brief investigation into whether environmental variables, such as the North Atlantic Oscillation (NAO), were inter-correlated with changes in salmon length, weight or condition were undertaken. A major difficulty in this endeavour was that many of the more pertinent environmental surrogates are available for a much shorter period than our salmon data, and often for too short a period to investigate reliably cause-effect possibilities when background levels are known to fluctuate. The indicative environmental variables considered, were: (1) NAO winter index (December to March mean); (2) winter and spring mean sea surface temperature (**SST**) in the North Sea; (3) potential 0 and 1+ age-group sandeel availability in the North Sea; (4) herring spawning stock biomass in the North Sea; (5) capelin spawning stock biomass in the

North Atlantic; (6) the West Greenland salmon catch ascribed to European stock; (7) all environmental variables (1) to (6) combined.

2.8 North-Eastern Atlantic sea surface temperature (SST)

As the NOAA data set (used by Todd *et al*., 2008) does not extend back far enough, the Hadley Centre HadSST2 data set (Rayner *et al.*, 2006) was used instead to examine trends over the longer period. HadSST2 data, from 1960 onwards, were available on a 5° latitude by 5° longitude grid, rather than the 1° by 1° grid of the NOAA data. This coarser spatial resolution will somewhat smooth the HadSST2 data over time, in comparison to the NOAA data (S. Hughes, *pers. comm.*). The methods of Todd *et al.* (2008) were followed using 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 closely similar to those reported by Todd *et al.* (2008, their Figure 6). Following Todd *et al.* (2008), correlations were therefore investigated between our detrended annual average salmon condition indices with the previous 13 months' monthly average HasSST2 SST temperatures, when grilse were at sea. In addition, in order to smooth out the high inter-monthly temperature variations, a sequence of seasonally-averaged temperatures was constructed as follows: **smolting** (May, June, July of the year prior to return as 1SW); **autumn** (September, October & November prior to 1SW return); **winter** (December, January & February); **spring** (February, March & April); **summer** (May and June of the year of return to coastal waters).

2.9 Estimating ova fecundity

The likely effects of the reported average female length differences are interpreted with regard to their potential effects on ova production. We use parameters from a log(Length) to log(Ova numbers) equation given by Pope *et al.* (1961) as being typical for several east-coast Scottish rivers. As fish condition will change in unknown ways between coastal return and spawning, we are unable to make similar reliable deductions.

3 Results

3.1 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 at the North Esk (Figure 2). Although the marginal effects of sex (males were about 1.8 cm longer than females) and river age (for the North Esk, fish which had spent only one year in the river prior to smolting were, as adults, 0.6 cm shorter than those spending two or more years) were statistically significant (partly on account of the very large sample sizes), their biological importance was less clear. Therefore, in order to simplify interpretation of the similarities and differences between sea ages, years and fisheries, the data were pooled across river age and sex; this reduced the explained variance in both length and weight by less than 2%. All subsequent analyses were conducted on pooled data.

The average lengths and weights of both 1SW and 2SW salmon increased markedly with the day of the year on which they were captured at all fisheries (Figure 3). Generally, the seasonal trends were similar at all fisheries, although there were some small but significant differences in the rates of length increase. Of particular note was the appreciably higher 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 about 0.5 kg heavier than at the North Esk (when corrected to a common, comparable date).

3.2 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, $P < 0.001$ in all cases; Figure 4a) and all except the Spey showed similar decreases in weight (t > 4.2, $P < 0.001$ in all cases; Figure 5a). In contrast, tests for broad long-term (linear) trends of 2SW fish were either not significant or of much lower magnitude and hence of little biological importance (Figures 4b and 5b). The mean lengths and weights of 2SW fish in the Tay were substantially higher 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 error (RMS) of 4.5 cm for the lengths of individual fish (95% confidence range ~18 cm). The weight model accounted for about 65% of the variation 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. We note that individual weights varied much 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 potentially introduce bias for the shorter, and interrupted runs of data that characterised some sites. Accordingly, spline curves were considered more suitable than linear relationships for the purpose of de-trending the data prior to 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 of them 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 annual mean length deviations of 1SW fish were highly inter-correlated between fisheries whenever there was temporal coincidence of at least 10 common years, as were the annual mean weight deviations (Pearson $r > 0.64$, $P < 0.001$ in all cases, with the exception of Strathy v Tweed). Similar inter-correlations occurred for 2SW fish (Pearson $r > 0.60$, $P < 0.001$ in all cases except Strathy v Tweed lengths and Spey v Tweed weights). Thus, for both sea age classes, years in which fish were generally longer / heavier (for a given stage in the season) in the North Esk also tended to have longer / heavier than average fish in the other fisheries for which there were sufficient contemporaneous years sampled.

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

3.3 Fish condition

Whilst the simple condition index of 2SW fish increased slightly during the season in all estuary^2 fisheries (t > 5.5, $P < 0.001$ in all cases; Fig 6b), the seasonal index for 1SW fish declined significantly in all fisheries as the season progressed (t > 3.6, $P < 0.001$ in all cases, except the Dee n.s.; Figure 6a).

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 showed a sharp decrease from around 1997 onwards ($t = 8.5$, $P < 0.001$ and $t = 8.5$, $P < 0.001$ respectively) and there was no difference in the rate of decrease between these two rivers. A similar, but slightly less pronounced, recent trend occurred at Strathy ($t = 7.0$, $P < 0.001$).

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 onwards ($t = 2.6$, $P < 0.05$ and $t = 5.3$, $P < 0.01$ respectively).

Whereas 1SW fish formerly showed, on average, slightly higher condition than 2SW fish (particularly up to about 1990, Figure 7), this situation has recently changed; since 2002, 1SW fish have consistently shown 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 amongst 2SW fish (Figure 8b). After de-trending 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 closer (Figure1), were significantly correlated (Pearson r = 0.69, n = 23, $P < 0.001$). This finding was in contrast to mean lengths and weights, which showed high degrees of inter-correlation 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 North Esk (Pearson 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 all 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). Thus, for most of the study period, the

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[2] There were too few 2SW fish caught at the Strathy Point fixed-engine for analysis. All other 2SW fish were caught by net and coble fishing gear in river estuaries.

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[3]. Following de-trending, the annual seasonal rates of change in condition of 1SW fish on the Tay and North Esk were correlated (Pearson 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 non-significant up to about the year 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 seasonal decreases in both 2005 and 2006. The corresponding period on the Tweed is unclear, as, not only were the sampling periods short, but the sample sizes within each year were rather too small to estimate rates of change with a high degree of confidence. Following de-trending, 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.

3.4 Fish condition and fish size within short periods

Table 2 presents the slope coefficients between fish length and condition, estimated for 107 combinations of fishery site, sea-age and 10-day period, together with their significance values, both direct and adjusted for multiple comparisons[4]. The biological hypothesis is that the slopes of the length to condition relationships should

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[3] Note, however, (i) as a rule-of-thumb, rates less than about ±0.01 tended to be not significant, i.e. there was no discernable 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, and are therefore less reliable.

[4] By Cumulative Binomial probability calculations

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 of the 107 estimates had positive coefficients with $p<0.01$ (overall $p \ll 0.0001$) and thirty-six percent of them had positive coefficients individually significant at $p<0.0001$. It is curious that, whilst the 1SW fish from all sites analysed (Tay, Tweed and North Esk) consistently showed a high 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, $p\approx1.0$), whereas 2SW salmon from both the Tay and North Esk showed high preponderances of significant positive correlations (both with overall $p \ll 0.0001$).

3.5 Environmental correlates **<B8 some details moved to methods and Appendix B removed>**

Correlations between the seasonally-corrected estimates of fish size (length, weight) and condition with both (i) 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 de-trending over time, became either non-significant, or else explained so little of the response variance that the relationships were uninformative.

3.6 North Eastern Atlantic sea surface temperature

Having detrended our annual mean condition indices for 1SW fish, using a spline curve common to all fisheries (Figure7.a), 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 to 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 combinations of months. Nor did we find any significant correlation between SST and mean fish condition indices at the North Esk, or 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 (see Table 1, Figure 4).

However, we were able to produce very similar correlations to those obtained by Todd *et al.* (2008) for the Strathy by detrending just 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, when 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).

3.7 Estimated ova fecundity effects. <B8 moved some to METHODS >

Table 3 shows the expected ova numbers for a range of instructive female lengths for both 1SW and 2SW salmon. Rather than just show the expected ova productions for early-, mid- and late- running fish of each sea-age (the rows in bold type) we also provide comparisons (italic type) between typical mid-season-running fish and three variant groups representing: (1) mid-running plus the minimum length difference these large sample sizes can show as statistically significant between sub-groups; (2) the magnitudes of size differences between different freshwater-age groups; (3) either (i) the magnitude of fishery (site, river) differences or (ii) the amounts by which the common trend lines (Figure 4) have varied over decades. We further 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 enables us to show statistically significant effects of factors which, by such correlations to ova numbers, would have really tiny implications for average female fecundities (1mm length change, about 0.5% increase in ova numbers). The small average differences in river-ages detected might represent 2% differences in ova numbers, while the larger effects of sites, or the magnitudes of size-trends over time, represent 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, contrasting the ova differences between sea-ages for the various types of 2SW fish, compared to their similar 1SW counterparts, shows large and consistent differences of some +80% (75%~82%).

4 Discussion <A0 would like more discussion and new hypotheses>

4.1 General aspects <B9>

These results represent the first detailed analysis of a very large long-term data set 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 thereby making due allowances for differences in sampling periods and intensities, when comparing between years, sites and run-time groups.

The many common trends over years which we documented between sites, and the coherent annual differences from several of these, hint at broad, common causes rather than random or chaotic variation. 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 need be marine, and could include the direct effects of human fisheries and their delayed, and, potentially, even evolutionary, consequences (Hard *et al.*, 2008). Resolution of these questions will probably require the simultaneous modelling of salmon numbers, return ages, growth and fecundity, and the quantitative contrast between well defined hypotheses. Such topics are beyond the scope of this paper.

4.2 Environmental aspects

Although the growth and survival of salmon at sea must clearly depend on marine conditions, our attempts to correlate salmon performance with a variety of marine environmental variables were conspicuously 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 relevant 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. Equally plausible, but as yet untestable, 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 extent. We have no way of knowing if these downward trends will continue.

We found no convincing correlations between the growth of salmon and either 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 sea-surface temperatures off the Irish coast[5]. 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 strongly influence the return sizes of those that survive.

However, our longer-term data shows it is extremely unlikely that such changes in salmon condition have been continually strongly driven by SSTs, in the sense that January SSTs impaired ocean conditions next spring which lead to thin grilse in the summer (Todd *et al.*, 2008). In comparison to that previous work, our data are more powerful over time, and more general due to the extra sites, while the commonality of trends between sites makes our inferences robust.

4.3 Population and Genetic aspects

Broad population processes, including genetic aspects, could also be involved. Over the period of our study, numbers of returning 3SW fish declined to near zero (by 1970s), and 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 the season. Without objective data on the detailed run-time propensities of individual fish arriving in particular periods, we are unable 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, while annual variation in their achieved times of arrival would alter seasonal changes in size within years. Our results (Figures 7, 9) show that such annual

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[5] Although it is not clear whether their method accounted for possible spurious temporal co-linearity between survival and their predictor variables, by first de-trending all variables

and seasonal changes do indeed occur. While we do not claim that (genetic) run-time groups necessarily dominates these responses, either within or between sites, we do emphasise that, until objective data allow us to de-confound such competing explanations, progress will be hampered.

4.4 Structured populations within rivers

As run-timing 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 possibly have different genetic compositions, body conformations, 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 fortnightly periods, seasonal size increases were still evident within the groups, and these merged rather naturally into each other to produce a single relationship of the form here described.

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 maintained. Conversely, they could arise rather naturally if the salmon stocks from different rivers were either 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 as 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 environmental constraints, or more indirect mechanisms such as Fisheries Induced Evolution (see Hard *et al.*, 2008, Jorgensen *et al.*, 2007, Dieckmann and Heino, 2007)

4.5 Physiology, growth and maturity

The ratio of wet-weight to length can be a poor index of the body or energetic reserves of fish, which often replace metabolised lipid or protein with water (Gardiner and Geddes, 1980). Todd *et al.* (2008) demonstrate that the lipid levels of Scottish salmon caught on the coast are not linearly related to their condition index, but that lower indices are disproportionately associated with much poorer lipid levels. Thus, 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 the actual fecundity decreases will be more severe than those implied by the length and condition changes we report (Figure 7, Table 3).

<B11 shortened Check-Mark para > North Esk salmon that return with ‘growth check-marks’ on their scales do not have shorter lengths on return to the coast (MacLean *et al.*, 2000). However, as the check marks usually occurred 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 Vietch, 2007; Gurney *et al.*, 2007, 2008 B; 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 (e.g. Brooker *et al.*, 2008) and implicitly assumes that any smolt from any particular river could become either a 1SW or a MSW fish (e.g. 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, while slower growers would be obliged to stay out 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 notably unsuccessful (Gurney *et al.*, 2008 A).

<B12 rephrased> In contrast, genetic data suggest (Jónasson *et al.*, 1997; Hankin *et al.*, 1993) 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 much better and have subtle consequences for the population dynamics (Gurney *et al.*, 2008 A).

4.6 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 historic data on fresh-run fish, at least in Scotland, come from samples obtained from net catches. However, since 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 degree that it becomes tiny, unrepresentative sub-samples. < B13 net fisheries>

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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	No. of years	First year	Last year	No. of records	Earliest day	Latest day
Dee	Net & coble	1	6	1974	1986	2 168	119	219
		2	6	1974	1986	2 127	43	219
		total				**4 295**		
North Esk	Net & coble	1	44	1963	2006	38 255	107	244
		2	44	1963	2006	33 991	47	244
		total				**72 246**		
Spey	Net & coble	1	16	1970	1986	9 584	128	242
		2	15	1970	1986	7 017	42	242
		total				**16 601**		
Tay	Net & coble	1	25	1969	1996	10 976	106	233
		2	27	1968	1996	12 317	37	233
		total				**23 293**		
Tweed	Net & 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

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

		Total	**SLOPE significantly POSITIVE**		
Site	**Sea age**	**comp-arisons**	**# with p < 0.01**	**Prob. obs n < 0.01**	**# 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 details

Comparison category	**Fish length (mm)**	**Estimated ova #s**	**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. Signif	*581*	3 608	*100.2*		*100.4*	
:+ RiverAge	*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. Signif	*751*	6 570	*100.1*	*129.3*	*100.3*	*182.1*
:+ RiverAge	*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**

Legends to Figures

Figure 1 Sampling sites. Circles show those sampled in 2006. 1, Strathy; 2 Spey; 3 Dee; 4 North Esk; 5 Tay; 6 Tweed.

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 against Julian day of the year (from 01-Jan).

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

Figure 4 Annual mean lengths of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon captured in six Scottish fisheries, 1963-2006.

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

Figure 6 Seasonal changes in mean condition index of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon returning to Scottish fisheries, 1963-2006.

Figure 7 Annual mean condition index trends of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon captured in six Scottish fisheries, 1963-2006.

Figure 8 Proportionate distribution (PDF) of fish in each of eight condition-index classes for (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon returning to the North Esk in two periods, 1985-2002 and 2003-2006.

Figure 9 Seasonal rates of change in mean condition index of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon returning to Scottish fisheries, 1963-2006.

Figure 1

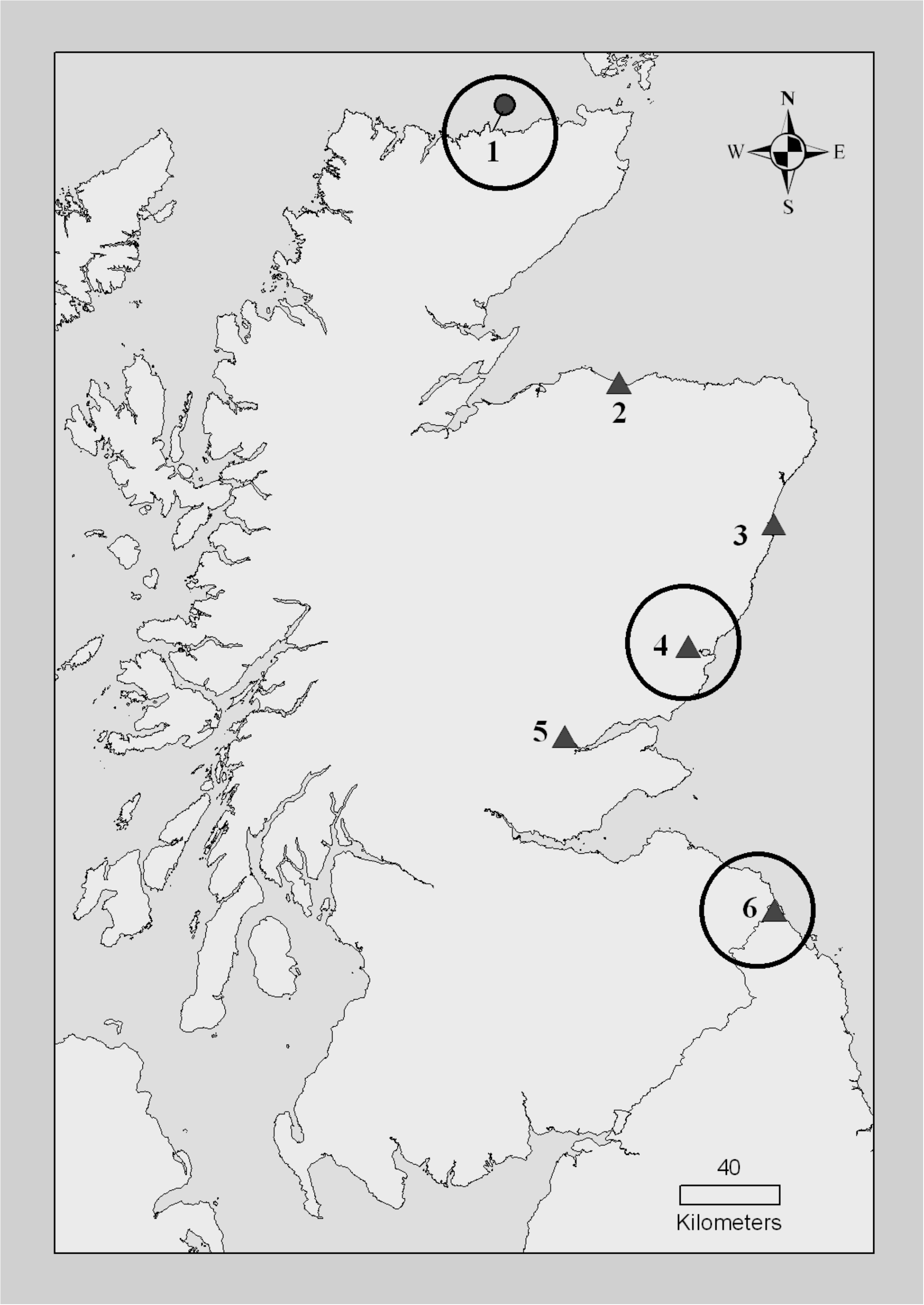
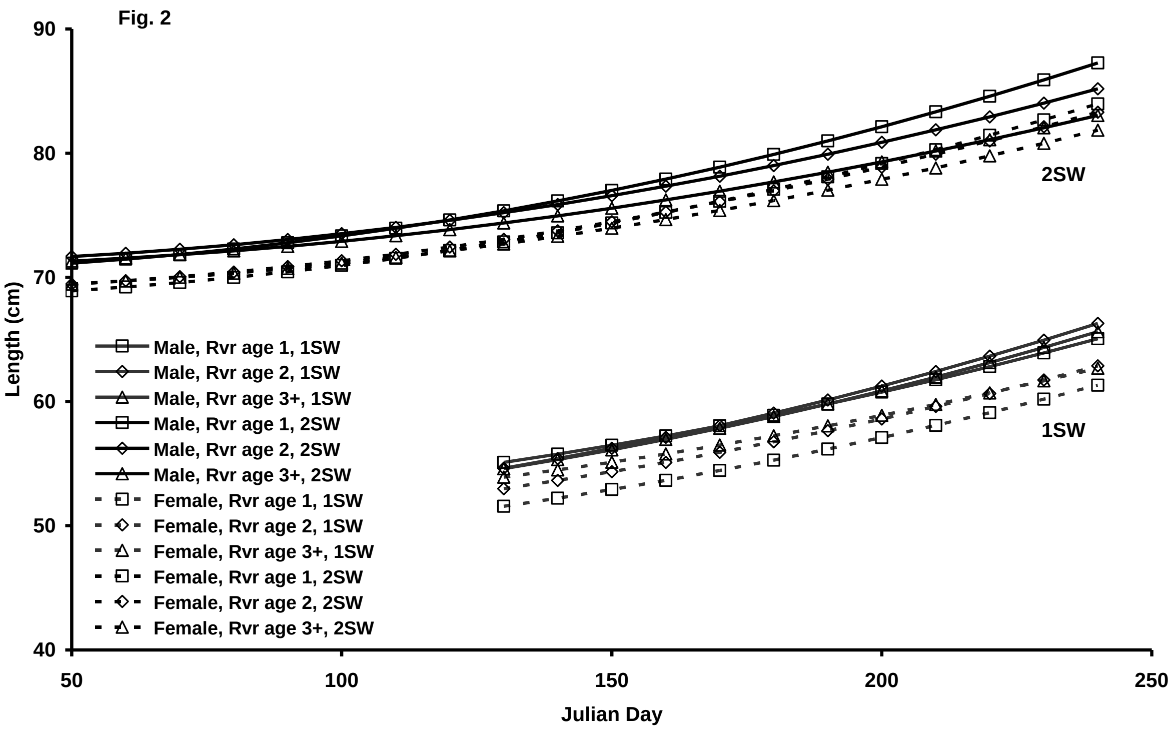


Figure 2 Seasonal changes in the mean length of Atlantic salmon returning to the North Esk, 1963-2006, by sea age, sex and river age against Julian day of the year (from 01-Jan).

Fig. 2



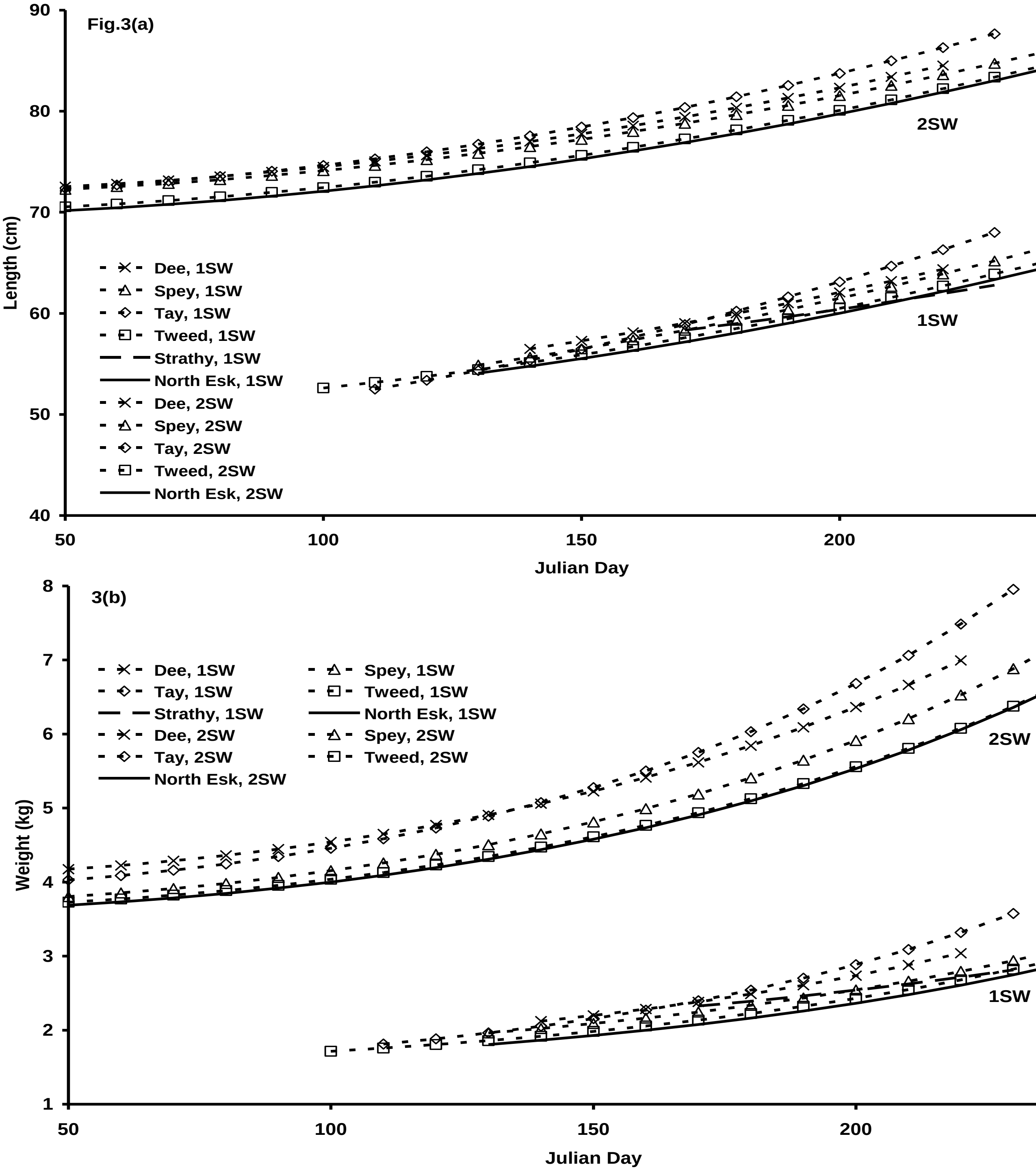


Figure 3 Seasonal changes in (a) the mean length and (b) the geometric mean weight of Atlantic salmon returning to six Scottish fisheries, 1963-2006.

Figure 4 Annual mean lengths of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon captured in six Scottish fisheries, 1963-2006.

Editorial note : Figs 4 & 5 on facing pages please.

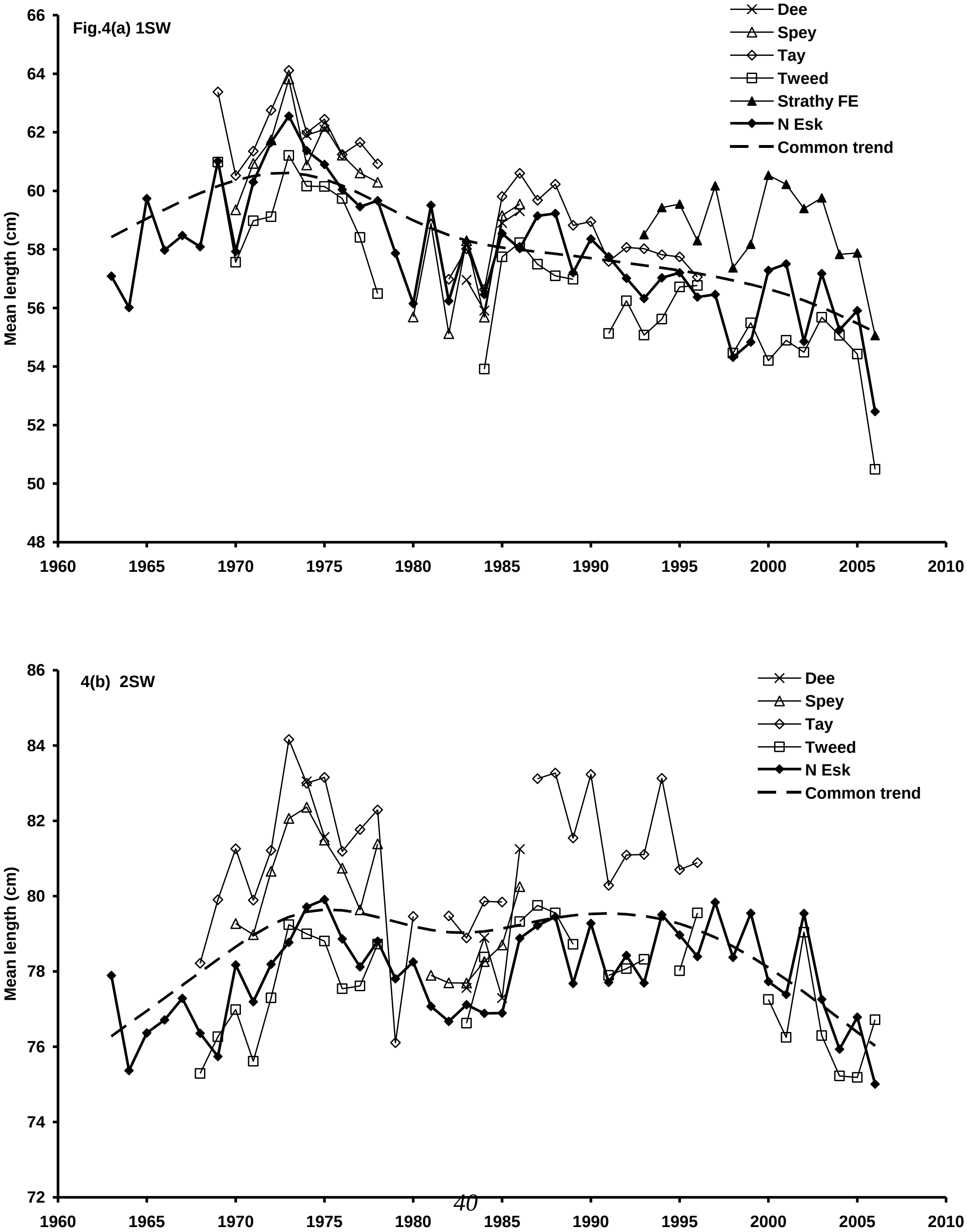


Figure 5 Annual mean weights of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon captured in six Scottish fisheries, 1963-2006.

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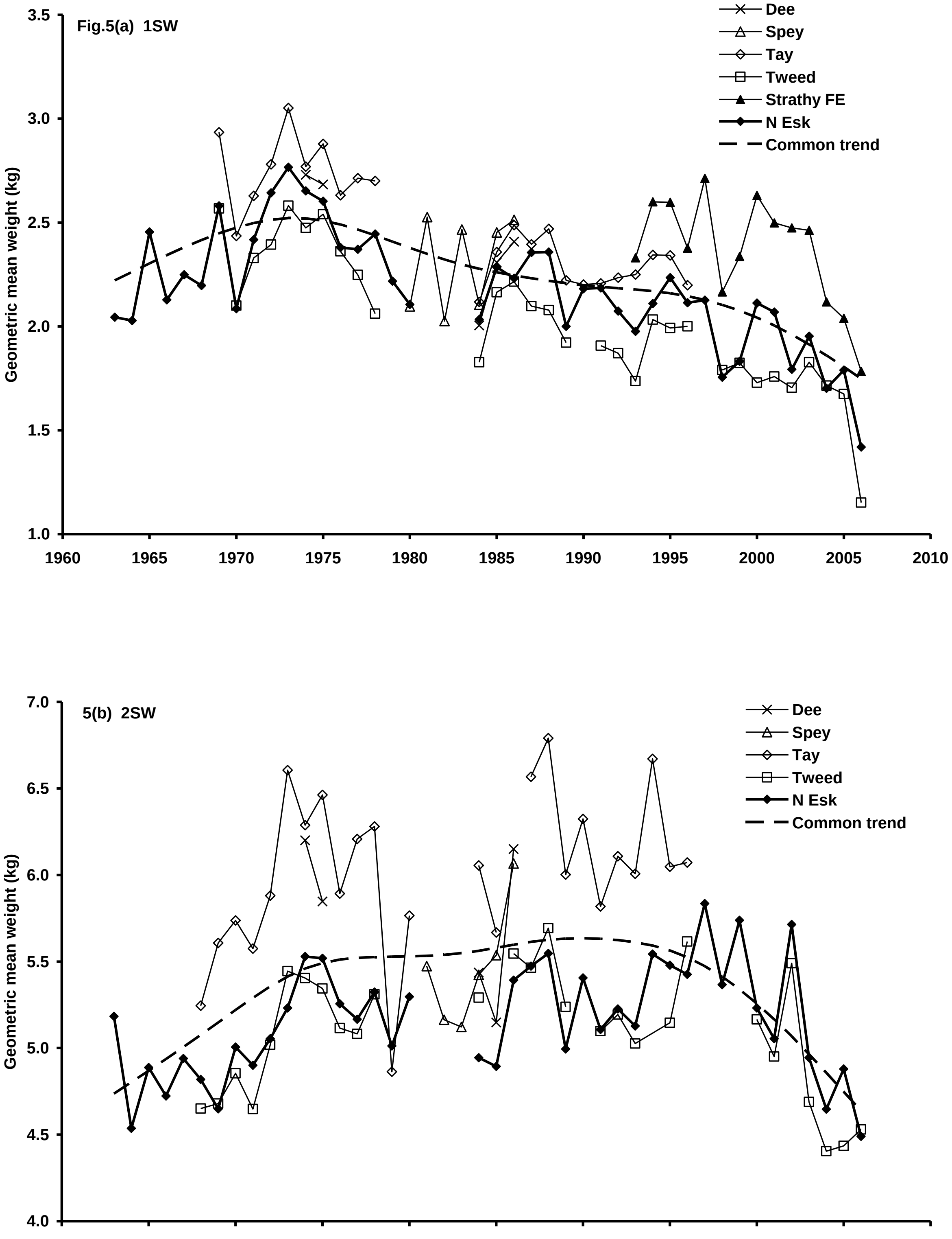

Figure 6 Seasonal changes in mean condition index of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon returning to Scottish fisheries, 1963-2006.

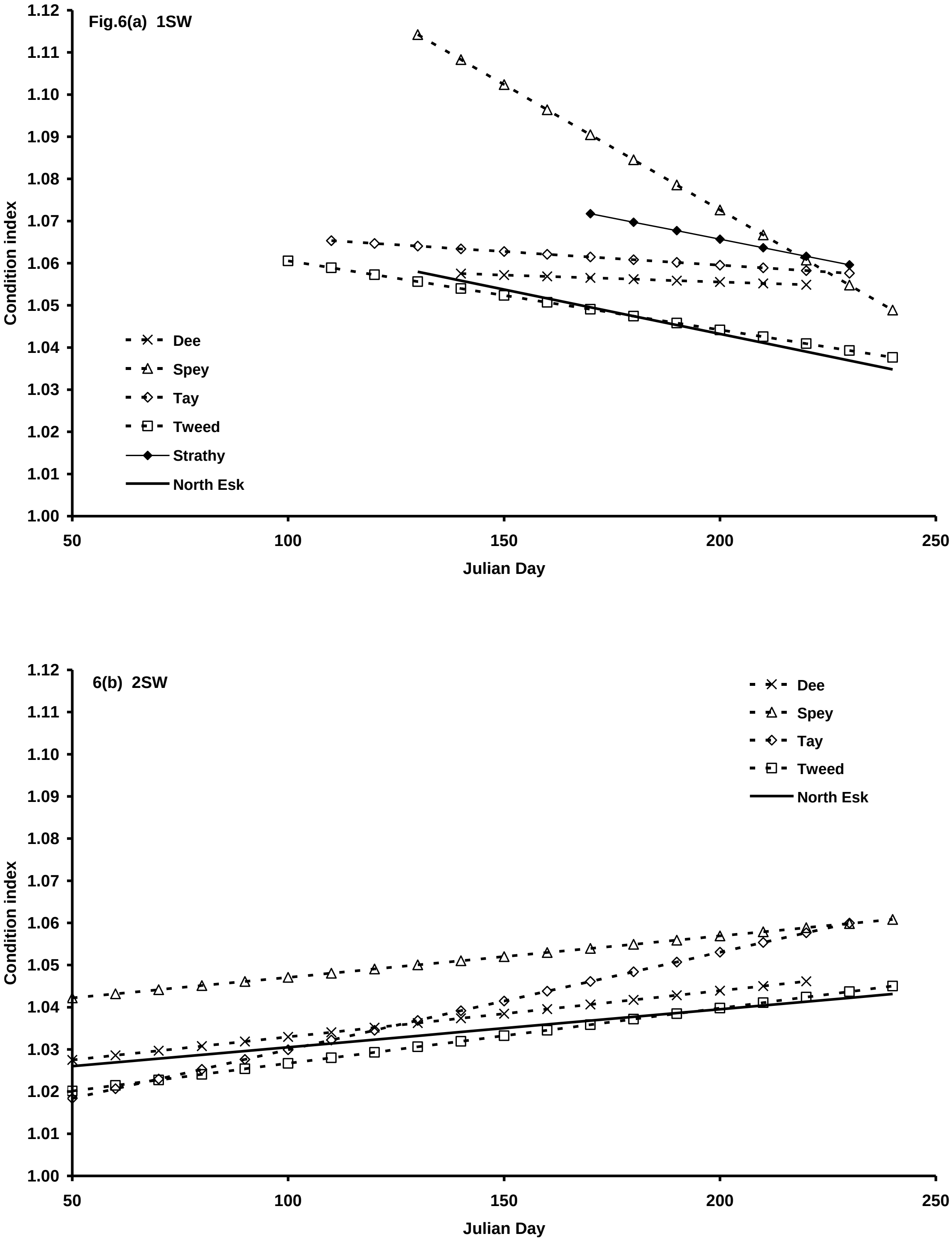

Figure 7 Annual mean condition indices of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon captured in six Scottish fisheries, 1963-2006.

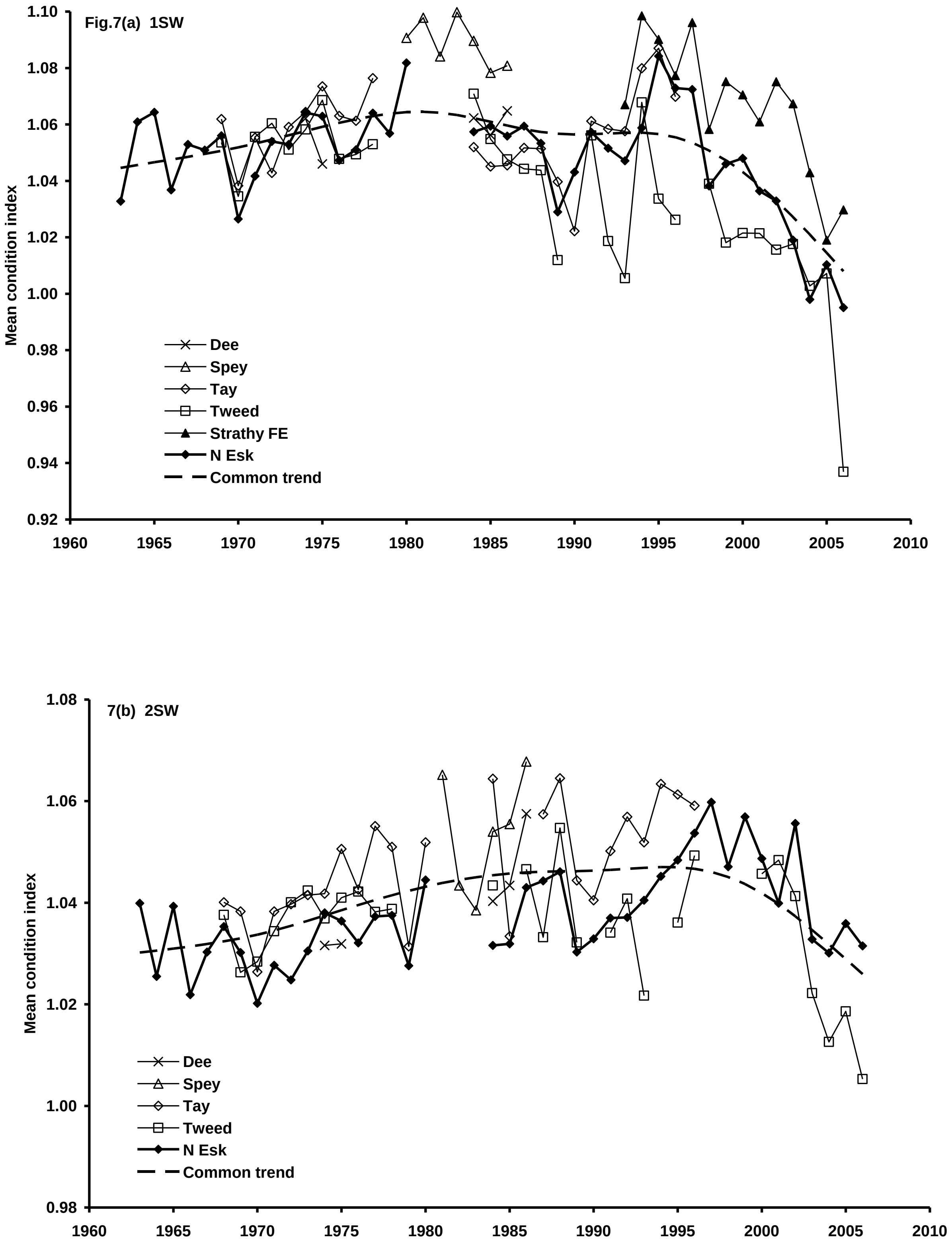

Figure 8 Corrected proportions of fish in each of eight condition index classes for (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon returning to the North Esk in two periods, 1985-2002 and 2003-2006.

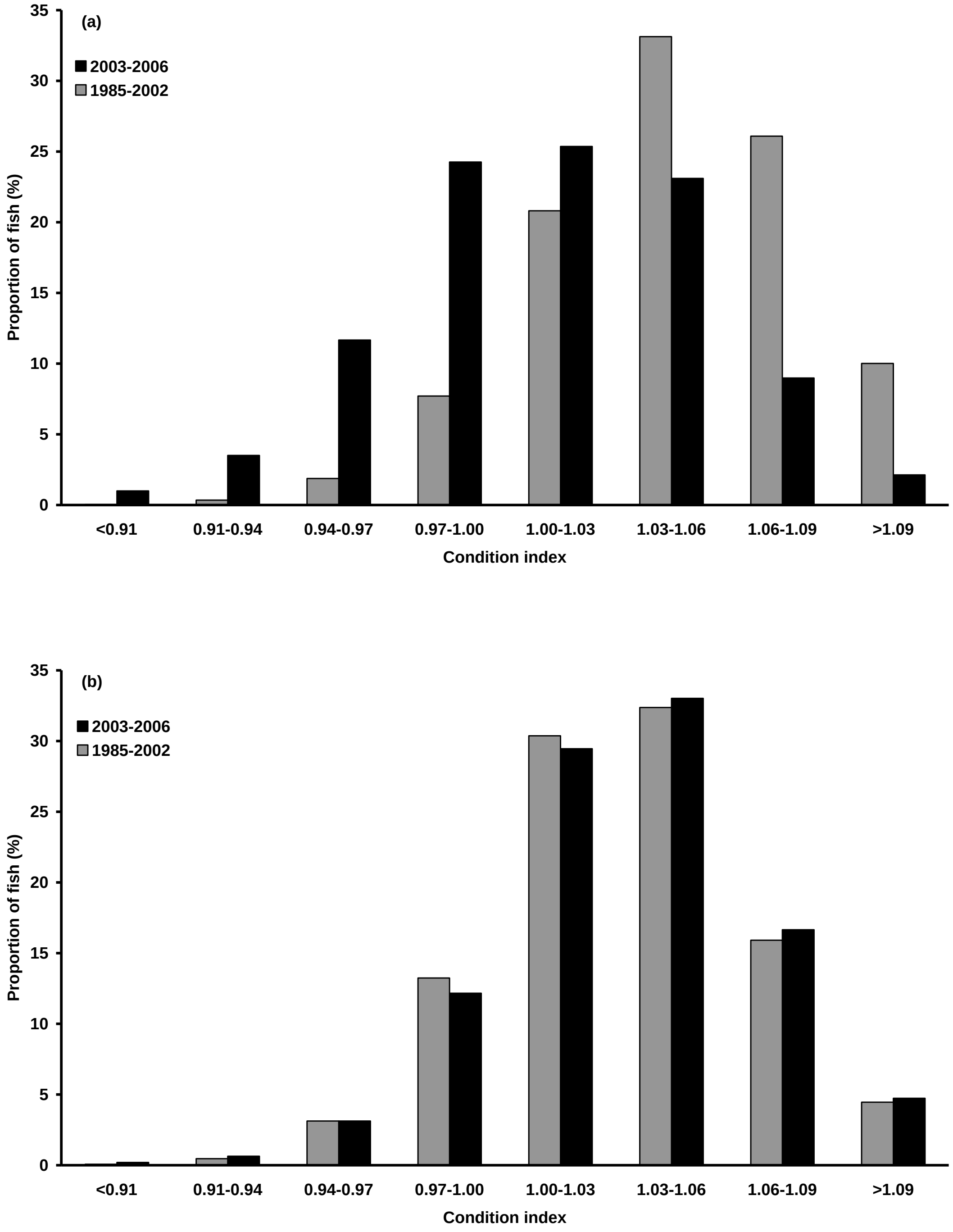

Figure 9 Seasonal rates of change in mean condition index of (a) 1 sea-winter and (b) 2 sea-winter Atlantic salmon returning to Scottish fisheries, 1963-2006.