Fisheries Management and Ecology, 2007, **14**, 191–198

Seasonal variation in rod recapture rates indicates differential exploitation of Atlantic salmon, *Salmo salar*, stock components

J. L. THORLEY & A. F. YOUNGSON

Freshwater Laboratory, Fisheries Research Services, Pitlochry, Perthshire, UK

R. LAUGHTON

Spey Fishery Board Research Office, Knockando, Morayshire, UK

Abstract Differential exploitation of the various components of a fish stock can adversely affect the diversity, abundance and long-term survival of the entire stock. Many anadromous salmonid stocks exhibit a seasonal structuring of their run-timing that allows fisheries managers to map monthly rod catches onto stock components. To estimate the rod exploitation levels of the various run-timing groups, fishing guides on the River Spey, Scotland, floy-tagged 786 rod-caught and released Atlantic salmon, *Salmo salar* L., between 2000 and 2002 and recorded recaptures. Whereas 25% of the fish tagged early in March were recaptured, only 2% of those tagged early in June were caught a second time. Exploitation is biased towards the early-running stock components which current assessments show to be least abundant. Management of Atlantic salmon based on an average exploitation rate is inappropriate.

KEYWORDS: Atlantic salmon, River Spey, rod catch.

Introduction

Fishery managers must estimate exploitation rates to regulate fishing activity at appropriate levels. Failure to manage for the differential exploitation of the various components of a fish stock can lead to genetic and phenotypic changes (Consuegra, García de Leániz, Serdio & Verspoor 2005), the loss of genetic and phenotypic diversity (Youngson, Jordan, Verspoor, McGinnity, Cross & Ferguson 2003), the extinction of individual populations and a reduction in overall abundance (Smedbol & Stephenson 2001). Longer-term, the loss of components can leave a stock vulnerable to collapse in the face of environmental change (Hilborn, Quinn, Schindler & Rogers 2003).

Many anadromous salmonid stocks exhibit a temporal pattern in their run-timing that corresponds to the spatial pattern of spawning (Robards & Quinn 2002). This spatio-temporal relationship allows managers to map rod catches onto stock components (Youngson, MacLean & Fryer 2002; Youngson *et al.* 2003). The rod exploitation rate of each stock component can then be quantified by comparing the reported rod catch to an estimate of the abundance of the corresponding run-timing group based on data from a fish counter (Beaumont, Welton & Ladle 1991) or trap (Crozier & Kennedy 2001). A second approach, which does not require abundance estimates, is to net or trap fish as they enter the river and determine their subsequent fates by radio-tracking (Laughton 1991) or anglers' tag returns (Davidson, Cove, Milner & Purvis 1996). A third approach is to radio-track (Webb 1998) or tag (Whoriskey, Prusov & Crabbe 2000) rod-caught fish and determine their subsequent rod recapture rates. Given certain assumptions, the rod recapture rates of the various run-timing groups can be used to estimate the rod exploitation rates of the stock components (Pollock, Hoenig, Hearn & Calingaert 2001).

Atlantic salmon, *Salmo salar* L., enter the larger rivers of the Scottish East coast throughout the year, supporting rod fisheries that typically extend from

Correspondence: Dr Joseph L. Thorley, Poisson Consulting Ltd, 106 Richards St., Nelson, British Columbia, Canada, V1L 5J5
(e-mail: joethorley@poissonconsulting.ca)

February to October. This wide range of run-timings reflects a diversity of populations with fish that return early in the year tending to belong to populations that spawn further up the catchments (Laughton 1991; Webb 1998; Stewart, Smith & Youngson 2002; Youngson *et al*. 2003). However, due to increased marine mortality, the abundance of early-running Atlantic salmon has fallen dramatically in recent years (Youngson *et al*. 2002) raising concerns that in the upper parts of some catchments spawning may be insufficient to repopulate the streams and rivers with fry.

Previous studies have suggested that early-running Atlantic salmon in UK rivers experience higher rod exploitation rates than later-running fish (Table 1). However, with the exception of Davidson *et al*. (1996), all of these studies have been based on small numbers of fish (Laughton 1991; Webb 1998), have not considered intra-annual variation in exploitation (Crozier & Kennedy 2001) and/or have introduced uncertainty due to reliance on abundance estimates (Beaumont *et al*. 1991; Crozier & Kennedy 2001).

To estimate the exploitation of Atlantic salmon by rod anglers, fishing guides (ghillies) on the River Spey, Scotland, were trained to floy-tag Atlantic salmon caught by their clients. The Atlantic salmon recapture data were analysed using logistic regression (Collet 2003) and event (survival) analysis (Hosmer & Lemeshow 1999). An information-theoretic approach was used to make inferences based on all the models within each analysis (Burnham & Anderson 2002). The implications of the findings for the management of Atlantic salmon on the Spey and other rivers are discussed.

Study area

The River Spey is one of the largest rivers in Scotland. From its source at Loch Spey in the Monadhliath Mountains, it flows approximately 157 km to Spey Bay in the Moray Firth. The River Spey has a total catchment of 2988 km^2 (Goody 1988) and an average daily flow of 64 $m^3 s^{-1}$ at Boat o'Brig, the lowest main stem gauging station (Inglis, McEwen & MacLean 1988).

The Spey is an alpine river with melting snow sustaining high flow rates into late spring (Goody 1988). The watercourse is relatively simple consisting of a single main stem with a handful of major tributaries. Most of the major tributaries enter the Spey in its higher reaches. The one exception, the Avon, enters the main stem at Ballindaloch some 50 km upstream from Speymouth. A multitude of smaller tributaries also enter the Spey, many of which support small spawning populations of Atlantic salmon.

Materials and methods

Fish capture and recapture

The Atlantic salmon rod angling season on the River Spey runs from 11 February to 30 September. During the 2000–2002 angling seasons, guides floy-tagged (Floy Tag Inc., Seattle, WA, USA) and released 786 rod-caught Atlantic salmon. The floy-tags were inserted in the basal musculature of the dorsal fin. As well as recording the site of capture (and release), the guides also estimated the fish's sea-age and mass to the nearest half pound (0.23 kg). To maximise the number of fish floy-tagged, as well as the reporting of recaptured fish, the Spey Fishery Board widely publicised the project and offered incentives for participation (Pollock *et al*. 2001).

The number of individuals tagged in each month is shown in Figure 1. Three of the fish were found in a diseased state the month after tagging and were

Table 1. The estimated rod exploitation rates of Atlantic salmon on UK rivers from published studies

Exploitation (%)	*n*	Run-timing	Sea-age	River	Study
30	36	February to March	MSW	Spey, Scotland	Laughton (1991)*
15	15	March to April	MSW	Aberdeenshire Dee, Scotland	Webb (1998)†
35–25	> 500	March to May	MSW	Welsh Dee, Wales	Davidson *et al*. (1996)‡
30–15	NA	March to June	MSW	Frome, England	Beaumont *et al*. (1991)§
10	> 50 000	March to September	1SW	Bush, Northern Ireland	Crozier & Kennedy (2001)¶
15–10	NA	June to August	1SW	Frome, England	Beaumont *et al*. (1991)§
5	23	June to August	1SW	Spey, Scotland	Laughton (1991)*
25–5	> 2000	June to September	1SW	Welsh Dee, Wales	Davidson *et al*. (1996)‡

The estimates are from comparison of rod catches with counter data (§) or trap catches (¶), salmon netted or trapped at the river mouth that were radio-tracked (*) or tagged (‡) and angled fish that were radio-tracked (†).
Estimates based on fewer than 15 individuals were excluded.

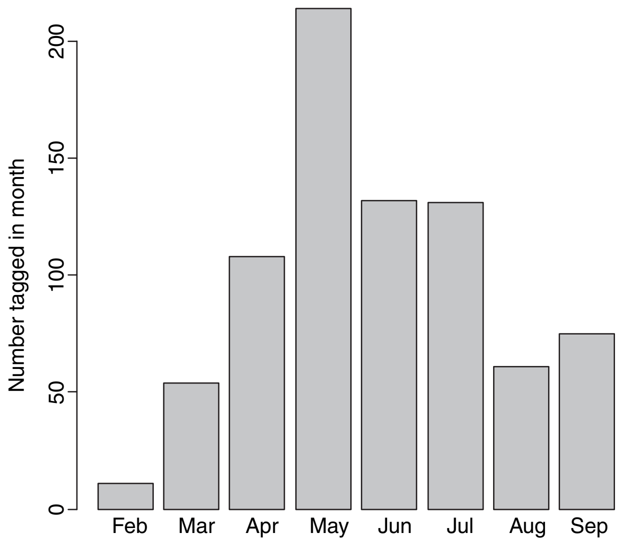

Figure 1. The number of Atlantic salmon floy-tagged in each month.

excluded from the study. Five floy-tags were recovered from the river bed the following spring. The five fish were not excluded from the study as the losses appeared to have occurred after the end of the angling season as result of post-spawning mortality. In total, 38 Atlantic salmon were recaptured by anglers before the end of the angling season. Figure 2 shows the proportion of Atlantic salmon that were recaptured by the end of the season according to the month of tagging. Seventeen of the 38 recaptured salmon were re-released; none was captured a third time.

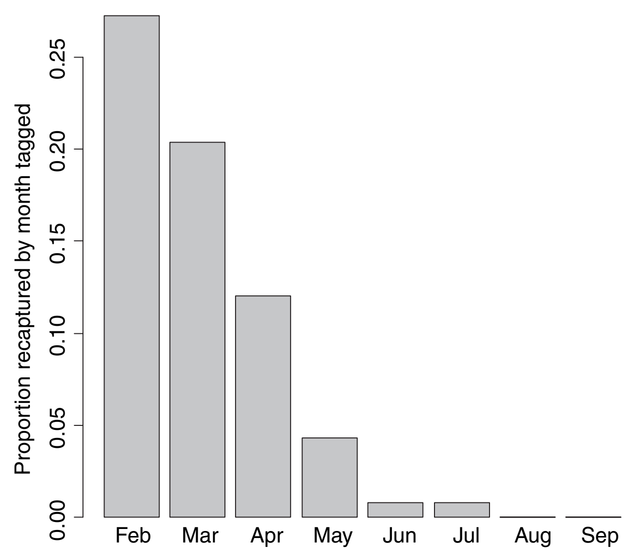

Figure 2. The proportion of floy-tagged Atlantic salmon that were recaptured by the end of the season by the month of tagging.

Fish tagged later in the season had less time to be recaptured. To ensure the probability of recapture was not influenced by the time available for capture, fish were only considered to have been recaptured in the statistical analyses if they were recaptured within a fixed period. Atlantic salmon are typically most readily exploitable by rod anglers during two intervals: after they first enter fresh water and before spawning (Beaumont *et al.* 1991; Clarke, Purvis & Mee 1991; Laughton 1991). Fish tagged from July onwards were excluded from the analyses since only one of the 267 individuals tagged after 30 June was recaptured. The pre-spawning period of exploitability occurs from September onwards on the Spey (Laughton 1991). To ensure recaptures during the pre-spawning interval were excluded, the time period for recapture was set at 61 days (the number of days from 1 July to 31 August). In summary, the analysis was restricted to fish tagged before July with recaptures within 61 days.

The vast majority of the Atlantic salmon caught on the Spey before July had spent two or more winters at sea and are referred to as multi-sea winter (MSW) salmon (MacLean, Smith & Laughton 1996). Only 12, one-sea winter (1SW) grilse were reported tagged before the end of June; none of which was recaptured. The 12 grilse were excluded from the analyses to standardise the results on MSW salmon. A total of 504 MSW Atlantic salmon were tagged before the end of June; 26 of which were recaptured within 61 days.

An information-theoretic approach

The standard frequentist approach to statistical inference is to estimate the relationship between the response and explanatory variables based on a single model. The model itself is selected according to whether or not the probability values of the explanatory variables are below a pre-specified threshold. Although commonly used, this approach produces biased estimates if, as is often the case, there is substantial support for one or more alternative models (Burnham & Anderson 2002).

The approach detailed by Burnham & Anderson (2002) uses a Kullback–Leibler (K–L) information theoretic criterion, such as Akaike's Information Criterion (AIC) to rate a set of candidate models according to their simplicity and fit to the data. The relationships of interest are then estimated based on the complete set of candidate models whose contributions are weighted according to their Akaike weight (w_i), a measure of relative support based on the information theoretic criterion.

To avoid producing models that include spurious relationships, the set of candidate models should be identified prior to model comparison (Burnham & Anderson 2002). The candidate model set should include the global model: the model which incorporates all relevant measured biological effects. If the global model adequately fits the data then all the candidate models with comparable or greater support will also fit the data (Burnham & Anderson 2002).

The extent to which the day of the year of tagging (DoY) and reported weight are related to the probability of recapture was estimated using two closely related but complementary methods (Doksum & Gasko 1990): logistic regression (Collet 2003) and event (survival) analysis (Hosmer & Lemeshow 1999). Within each method, models were compared and inferences made using the information theoretic framework detailed by Burnham & Anderson (2002). The information theoretic criterion used was the bias-corrected form of AIC referred to as AICc. All analyses were conducted using R 2.2.1 (R Development Core Team 2005).

Logistic analysis

Logistic regression attempts to model the log odds of a binary response variable (Collet 2003). Two of the key assumptions of logistic regression are that (1) the log odds are a linear function of the explanatory variables (assumption of linearity); and that (2) the errors follow a binomial distribution (binomial assumption).

In the case of the floy-tagged Atlantic salmon, the binary response variable was whether or not each individual was recaptured with 61 days of tagging. The candidate model set consisted of three linear logistic models corresponding to all combinations of the explanatory variables DoY and weight (Table 2). Due to the relatively low number of recaptures which exploratory data plotting indicated were evenly spread between the three angling seasons, year was not included as an explanatory variable. In addition, neither the site of capture nor the distance from the river mouth were included as explanatory variables since >85% of the 504 MSW fish tagged before 1 July were caught from just three sites within 5 km of each other.

Table 2. The three candidate models in the logistic analysis with their log likelihoods given the data [$\ell(\hat{\theta})$], number of estimable parameters (K), AIC_c values, AIC_c differences (Δ_i) and Akaike weights (w_i). The sample size (n) was 493

Model	$\ell(\hat{\theta})$	K	AIC_c	Δ_i	w_i
DoY + weight	−88.46	3	182.96	0.00	0.54
DoY	−89.62	2	183.26	0.30	0.46
Weight	−95.88	2	195.78	12.81	0.00

The assumption of linearity was tested by comparison of the global logistic model to an additive logistic model (Hastie & Tibshirani 1990) with a cubic smoothing spline (Bowman & Azzalini 1997) on DoY and weight. The additive model received the majority of the support (w_i: 0.77). Examination of the residuals and splines revealed that none of the 11 MSW Atlantic salmon tagged in February were recaptured within 61 days (although three were recaptured by the end of the season: one at the end of May, one in June and one in September). Since the data points at the extreme ends of a smoother have a disproportionate influence on its shape (Bowman & Azzalini 1997), all 11 of the fish caught in February were excluded. As a result, the global model now provided a better fit to the 493 MSW salmon tagged between March and June than its additive alternative (w_i: 0.89). The binomial assumption was tested by comparing the global model's deviance (Collet 2003) when fitted to the observed data set with its deviance when fitted to 1000 parametric bootstrap replicate data sets (Manly 1997). The large probability value ($P > 0.4$) provided further confirmation of the global model's goodness-of-fit. The collinearity between DoY and weight was estimated from the variance inflation factor (Fox & Monette 1992).

Event (survival) analysis

Event analysis is concerned with the modelling and testing of hypotheses of the time to an event, which is often referred to as failure (Hosmer & Lemeshow 1999). One of the main challenges with the analysis of event data is that the time to failure for some individuals is often unknown (these observations are referred to as censored). Typically, the time to failure is unknown because an individual is lost from the study or the study ends before the individual fails. The only limitation on the use of censored data in event analysis is that the censoring is independent of the explanatory variables, i.e. the probability of censoring does not change with the value of an explanatory variable.

Cox's proportional hazards regression, a semi-parametric event model, assumes that (1) the log of the hazard function is a linear function of the explanatory variables (assumption of linearity); and that (2) the effects of the explanatory variables on the hazard function are constant over time (assumption of proportional hazards). The hazard function is the instantaneous probability that an individual fails given that they have survived to time t. The Cox's model is semi-parametric because even though the baseline hazard is unspecified the covariates enter the model linearly.

Table 3. The three candidate models in the event analysis with their log likelihoods given the data [$\ell(\hat{\theta})$], number of estimable parameters (K), AIC_c values, AIC_c differences (Δ_i) and Akaike weights (w_i). The sample size (n) was 493

Model	$\ell(\hat{\theta})$	K	AIC_c	Δ_i	w_i
DoY + weight	−144.46	2	292.95	0.00	0.53
DoY	−145.61	1	293.23	0.28	0.47
Weight	−151.88	1	305.77	12.82	0.00

Consequently, the model optimises the coefficients using partial likelihood (Lp) as opposed to maximum likelihood (ML). Although the baseline hazard is ignored while estimating the coefficients it can be determined from the fitted model together with the observed data.

Cox's proportional hazards regression models were fitted to the same data set as the logistic regression models, i.e. the 493 MSW Atlantic salmon tagged between March and June. An individual was deemed to have failed if it was recaptured. Observations were censored after 61 days. For simplicity and because none of the re-released fish was caught a third time it was assumed that once an individual was recaptured it was no longer available for capture. The candidate model set contained the equivalent of the three models in the logistic analysis (compare Tables 2 & 3). The assumption of linearity was checked through comparison of the global model against an additive Cox's proportional hazards model with penalised smoothing splines on DoY and weight (Venables & Ripley 2002). The proportional hazards assumption was checked by plotting the Schoenfeld residuals of the global model against the log of time (Hosmer & Lemeshow 1999). Neither assumption was violated.

Results

Early running Atlantic salmon on the River Spey experienced much higher rod recapture rates than later-running individuals. Whereas over 25 % of the MSW fish tagged early in March were recaptured by anglers within 2 months, only 2 % of the MSW fish tagged in June were recaptured within the same time period (Figs 3 & 4). Only one of the 267 fish (0.37 %) tagged from July onwards was recaptured by the end of the September.

In contrast to season, weight at tagging was not an important predictor of a MSW Atlantic salmon's recapture probability. Although the analyses suggested a moderate decline in the probability of recapture with weight (Figs 5 & 6), the confidence intervals around

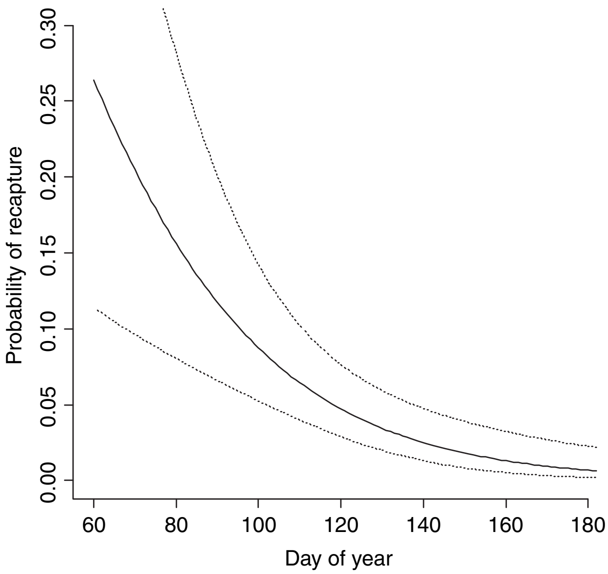

Figure 3. The multi-model inference of the probability of recapture within 61 days by day of the year of tagging based on the three logistic models in Table 2. The solid line is the predicted relationship for a MSW Atlantic salmon of weight 4 kg. The broken lines are the 95% confidence intervals.

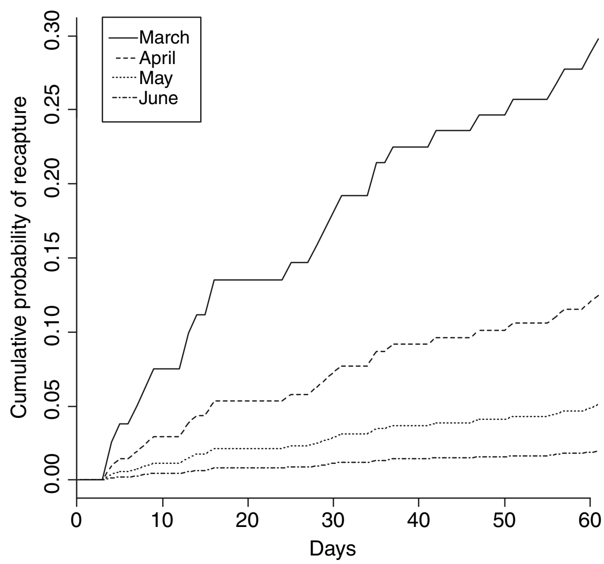

Figure 4. The multi-model inference of the cumulative distribution function of the probability of recapture based on the three Cox's proportional hazards models in Table 3. The four lines are the predicted functions for cohorts of MSW Atlantic salmon of weight 4 kg tagged on the first day of each month.

the logistic regression were extremely broad indicating a great deal of uncertainty about the actual relationship (Fig. 5). The low variance inflation factor of the logistic global model (VIF: 1.15) indicated that the

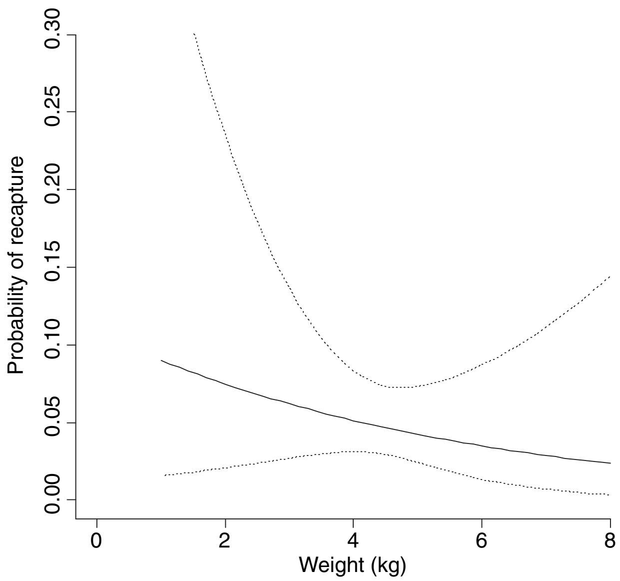

Figure 5. The multi-model inference of the probability of recapture within 61 days by weight based on the three logistic models in Table 2. The solid line is the predicted relationship for a MSW Atlantic salmon tagged on 1 May. The broken lines are the 95% confidence intervals.

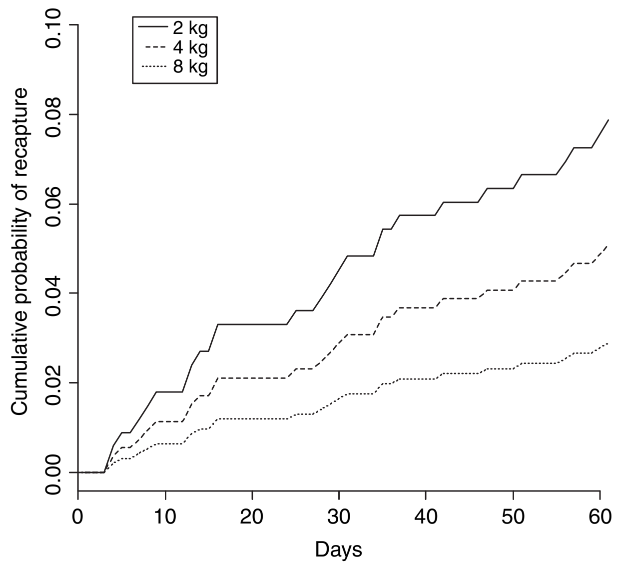

Figure 6. The multi-model inference of the cumulative distribution function of the probability of recapture based on the three Cox's proportional hazards models in Table 3. The three lines are the predicted functions for cohorts of MSW Atlantic salmon of weight 2, 4 and 8 kg released on 1 May.

uncertainty in the weight estimate was a property of the explanatory variable and was not due to collinearity between DoY and weight.

Discussion

The extent to which the estimated seasonal recapture probabilities (Figs 3 & 4) reflect exploitation depends on the extent to which the following five assumptions (adapted from Pollock *et al.* 2001) are met: (1) there is no natural and angling mortality; (2) there is no non-reporting of recaptures and no tag loss; (3) the tagged sample is representative of the target population; (4) the probability of capture (and recapture) is homogenous within run-timing groups; and (5) the fate of each tagged fish is independent of the fate of other tagged fish.

Assumption (1) was likely to have been closely met. Studies that have examined the effect of catch and release on Atlantic salmon have concluded that provided the fish are handled correctly and the water temperature is below about 22 °C, mortality is minimal (Wilkie, Davidson, Brobbel, Kieffer, Booth, Bielak & Tufts 1996). The fish were tagged and released by trained guides and the water temperature on the Spey rarely exceeds 20 °C.

Similarly, the assumption (2) of no non-reporting and no tag loss was also likely to have been closely met. Due to the publicity campaign and reward scheme (Pollock *et al.* 2001) it was felt that reporting was close to 100%. Although the lack of double-tagging prevented estimation of tag loss, a previous study on the Welsh Dee found that after an average of 100 days just one of 16 double-tagged Atlantic salmon (6%) had lost its floy tag (Davidson *et al.* 1996).

For assumption (3) to be met, the tagged fish must have been fresh-run and their behaviour must have been unaltered by capture and tagging. The size of successive run-timing groups increases from February to July (Smith, Laughton & Dora 1996). Consequently, the majority of tagged fish were expected to have been relatively fresh-run. In addition, radio-tracking studies found that migratory and spawning behaviour of Atlantic salmon is not demonstrably affected by catch and release (Webb 1998; Whoriskey *et al.* 2000).

The assumption (4) that the capture (and recapture) probability is homogenous was supported because controlling for run-timing neither sea-age (Davidson *et al.* 1996) nor weight (current study) is an important predictor of the probability of recapture.

As Pollock *et al.* (2001) stated, the assumption (5) of the independence of tagged fish is likely violated in all real studies. However, as reporting was felt to be close to 100% and because angling effort on the River Spey is constrained by the private beat system, any independence should not cause model bias; although it may mean that the uncertainty is under-estimated (Pollock *et al.* 2001).

Overall recapture rates probably underestimate the actual exploitation rates although the general pattern of higher rod exploitation of earlier-running Atlantic salmon is likely robust. There are at least three possible explanations for this pattern. Firstly, early-running fish ascend a river more slowly than later-running fish (Laughton 1991). Since Atlantic salmon are most readily exploitable during this initial period of in-river activity (Clarke *et al.* 1991; Davidson *et al.* 1996), the prolonged duration of the upstream migration can at least partly explain the higher exploitation rates. Secondly, river flows tend to be higher earlier in the year (Clarke *et al.* 1991; Laughton 1991) and higher flows are generally associated with greater catchability (Clarke *et al.* 1991; Davidson *et al.* 1996). Thirdly, the catchability of salmonids is often greater at lower abundances (Peterman & Steer 1981; Beaumont *et al.* 1991) and earlier-running Atlantic salmon are currently less abundant than other run-timing groups (Smith *et al.* 1996; Youngson *et al.* 2002).

Higher exploitation of early-running Atlantic salmon has at least three important implications for fishery management. Firstly, this study has shown that anglers are capable of catching a substantial proportion (>25%) of early-running MSW fish. Management measures such as catch and release will be correspondingly effective when used to increase spawning escapement to particular parts of catchments (Laughton 1991; Webb 1998; Whoriskey *et al.* 2000). Secondly, anglers appear to be exerting a large selection pressure against fish that are genetically predisposed (Stewart *et al.* 2002) to return to rivers early in the year. The potentially large, rapid and adverse effects of human selection pressures on fish populations have been well-documented (Ashley, Wilson, Pergams, O'Dowd, Gende & Brown 2003; Consuegra *et al.* 2005). Finally, the management of fishing effort on Atlantic salmon based on a single annual rod exploitation rate is inappropriate since, as has been demonstrated, different stock components experience large differences in exploitation.

Acknowledgements

We are extremely grateful to all the proprietors, guides (ghillies) and fisherman who participated in the project. We also thank John Webb (Atlantic Salmon Trust) and Iain McLaren (FRS Freshwater Laboratory) for their assistance with tagging training and Ted Castro-Santos, Robyn Irvine, Jason Godfrey and John Armstrong for their comments. The project was generously supported by Diageo and the Edinburgh Smoked Salmon Company Ltd.

References

Ashley M.V., Wilson M.F., Pergams O.R.W., O'Dowd D.J., Gende S.M. & Brown J.S. (2003) Evolutionarily enlightened management. *Biological Conservation* **111,** 115–123.

Beaumont W.R.C., Welton J.S. & Ladle M. (1991) Comparison of rod catch data with known numbers of Atlantic salmon (*Salmo salar*) recorded by a resistivity counter in a southern chalk stream. In: I.G. Cowx (ed.) *Catch Effort Sampling Strategies*. Oxford: Fishing News Books, Blackwell Scientific Publications, pp. 49–60.

Bowman A.W. & Azzalini A. (1997) *Applied Smoothing Techniques for Data Analysis: the Kernel Approach with S-Plus Illustrations*. Oxford: Clarendon Press, 208pp.

Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. New York: Springer, 488pp.

Clarke D., Purvis W.K. & Mee D. (1991) Use of telemetric tracking to examine environmental influences on catch effort indices. A case study of Atlantic salmon (*Salmo salar* L.) in the River Tywi, South Wales. In: I.G. Cowx (ed.) *Catch Effort Sampling Strategies*. Oxford: Fishing News Books, Blackwell Scientific Publications, pp. 33–48.

Collet D. (2003) *Modelling Binary Data*, 2nd edn. Boca Raton: Chapman and Hall/CRC, 387pp.

Consuegra S., García de Leániz C., Serdio A. & Verspoor E. (2005) Selective exploitation of early running fish may induce genetic and phenotypic changes in Atlantic salmon. *Journal of Fish Biology* **67**(Suppl. A)**,** 129–145.

Crozier W.W. & Kennedy G.J.A. (2001) Relationship between freshwater angling catch of Atlantic salmon and stock size in the River Bush, Northern Ireland. *Journal of Fish Biology* **58,** 240–247.

Davidson I.C., Cove R.J., Milner N.J. & Purvis W.K. (1996) Estimation of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) run size and angling exploitation on the Welsh Dee, using mark-recapture and trap indices. In: I.G. Cowx (ed.) *Stock Assessment in Inland Fisheries*. Oxford: Fishing News Books, Blackwell Scientific Publications, pp. 293–307.

Doksum K.A. & Gasko M. (1990) On a correspondence between models in binary regression analysis and in survival analysis. *International Statistical Review* **58,** 243–252.

Fox J. & Monette G. (1992) Generalized collinearity diagnostics. *Journal of the American Statistical Association* **87,** 178–183.

Goody N.P. (1988) The hydrology of the River Spey. In: D. Jenkins (ed.) *Land Use in the River Spey Catchment*.

Aberdeen: Aberdeen Centre for Land Use, Symposium No. 1, pp. 64–69.

Hastie T.J. & Tibshirani R.J. (1990) *Generalized Additive Models*. New York: Chapman and Hall/CRC, 336pp.

Hilborn R., Quinn T.P., Schindler D.E. & Rogers D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences* **100,** 6564–6568.

Hosmer D.W. & Lemeshow S. (1999) *Applied Survival Analysis: Regression Modelling of Time to Event Data*. New York: John Wiley & Sons, 386pp.

Inglis D.J., McEwen L.J. & MacLean A.G. (1988) Channel stability and flooding in the River Spey. In: D. Jenkins (ed.) *Land Use in the River Spey Catchment*. Aberdeen: Aberdeen Centre for Land Use, Symposium No. 1, pp. 70–78.

Laughton R. (1991) *The Movements of Adult Atlantic Salmon* (Salmo salar *L.*) *in the River Spey as Determined by Radio Telemetry during 1988 and 1989*. Scottish Fisheries Research Report 50, Edinburgh: The Scottish Office Agriculture and Fisheries in Association with The Spey District Salmon Fishery Board, 35pp.

MacLean J.C., Smith G.W. & Laughton R. (1996) An assessment of the grilse error associated with reported salmon, *Salmo salar* L., catches from two rod-and-line fisheries on the River Spey, Scotland, UK. *Fisheries Management and Ecology* **3,** 119–128.

Manly B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. New York: Chapman & Hall/CRC, 399pp.

Peterman R.M. & Steer G.J. (1981) Relation between sport-fishing catchability coefficients and salmon abundance. *Transactions of the American Fisheries Society* **110,** 585–593.

Pollock K.H., Hoenig J.M., Hearn W.S. & Calingaert B. (2001) Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* **21,** 521–532.

R Development Core Team (2005) *R: A Language and Environment for Statistical Computing*. Vienna: R Development Core Team. Available at: http://www.r-project.org.

Robards M.D. & Quinn T.P. (2002) The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. *Transactions of the American Fisheries Society* **131,** 523–536.

Smedbol R.K. & Stephenson R. (2001) The importance of managing within-species diversity in cod and herring fisheries of the north-western Atlantic. *Journal of Fish Biology* **59**(Suppl. A)**,** 109–128.

Smith G.W., Laughton R. & Dora S.J. (1996) Interpreting trends in adult Atlantic salmon (*Salmo salar* L.) populations from angling records: an analysis of catch and effort data from the River Spey. In: I.G. Cowx (ed.) *Stock Assessment in Inland Fisheries*. Oxford: Fishing News Books, Blackwell Scientific Publications, pp. 141–153.

Stewart D.C., Smith G.W. & Youngson A.F. (2002) Tributary-specific variation in timing of return of adult Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. *Canadian Journal of Fisheries and Aquatic Sciences* **59,** 276–281.

Venables W.N. & Ripley B.D. (2002) *Modern Applied Statistics with S*, 4th edn. New York: Springer, 495pp.

Webb J.H. (1998) *Catch and Release: the Survival and Behaviour of Atlantic Salmon Angled and Returned to the Aberdeenshire Dee, in Spring and Early Summer*. Scottish Fisheries Research Report 62, Edinburgh: Fisheries Research Services in Association with The Atlantic Salmon Trust, 16pp.

Whoriskey F.G., Prusov S. & Crabbe S. (2000) Evaluation of the effects of catch-and-release angling on the Atlantic salmon (*Salmo salar*) of the Ponoi River, Kola Peninsula, Russian Federation. *Ecology of Freshwater Fish* **9,** 118–125.

Wilkie M.P., Davidson K., Brobbel M.A., Kieffer J.D., Booth R.K., Bielak A.T. & Tufts B.L. (1996) Physiology and survival of wild Atlantic salmon following angling in warm summer waters. *Transactions of the American Fisheries Society* **125,** 572–580.

Youngson A.F., MacLean J.C. & Fryer R.J. (2002) Rod catch trends for early-running MSW salmon in Scottish rivers (1952–1997): divergence among stock components. *ICES Journal of Marine Science* **59,** 836–849.

Youngson A.F., Jordan W.C., Verspoor E., McGinnity P., Cross T. & Ferguson A. (2003) Management of salmonid fisheries in the British Isles: towards a practical approach based on population genetics. *Fisheries Research* **62,** 193–209.