Reconstructing the lengths of juvenile Atlantic salmon from atlas bones: estimating the parr to smolt ratio from regression analyses revisited

S. J. MIDDLEMAS*†‡ AND J. D. ARMSTRONG*

Fisheries Research Service Freshwater Laboratory, Faskally, Pitlochry, Perthshire, PH16 5LB Scotland, U.K. and †University of Aberdeen, Department of Zoology, Lighthouse Field Station, Cromarty, Rossshire, IV11 8YJ Scotland, U.K.

Analyses of regressions of atlas bone width against fish length (mixed regressions) of Atlantic salmon *Salmo salar* can be used to infer the parr:smolt ratio of the source populations. Analyses of mixed regressions have been used to infer that, contrary to previous reports, sawbill ducks *Mergus* spp. eat only a few smolts. Here a Monte Carlo simulation model is presented which quantifies the effect of variation in the smolt:parr ratio on the form of the mixed regression. Based on published mixed regressions, the model predicts 95% CI of 1–36% and 1–42% smolts in diets of sawbill ducks, which are broadly consistent with results of earlier studies. However, other large inconsistencies still exist between results of previous studies and these are briefly discussed.

Key words: *Salmo salar*; predation; diet; sawbill ducks; *Mergus* spp.

INTRODUCTION

A common method of assessing the diets of piscivorous birds is to examine their gut contents. Few intact fishes are recovered from carcasses because the soft tissue is digested rapidly. However, hard parts of fishes, such as bones and otoliths, are more resistant to digestion and have been used to identify individual prey to the level of species and to estimate their lengths (Fortunatova, 1951; Popova, 1978). The first vertebra (atlas bone) has been used to investigate the occurrence and size of Atlantic salmon *Salmo salar* L. in the diets of avian predators (Feltham & Marquiss, 1989; Carss & Marquiss, 1991; Marquiss *et al.*, 1998).

Sawbill ducks *Mergus* spp. prey on both the parr and smolt stages of Atlantic salmon (Feltham, 1990). The impact of predation on Atlantic salmon populations may vary depending on whether parr or smolts are consumed and it is important to distinguish between these life stages in the diets of birds (Carss & Marquiss, 1991; Armstrong *et al.*, 1998). Because salmon elongate as they metamorphose from parr to smolt (Hoar, 1976) the intercepts of the relationships between fork length (L_F) and atlas width (W_a) for the two life stages differ (Armstrong & Stewart, 1996). However, currently it is impossible to determine whether an individual atlas bone originates from a smolt or parr.

‡Author to whom correspondance should be addressed. Tel.: +44 (0) 1796 472060; fax: +44 (0) 1796 473523; email: s.middlemas@marlab.ac.uk

The percentage contribution of smolts to the Atlantic salmon component of the diet has been estimated to be *c.* 17% in goosanders *Mergus merganser* (Feltham, 1995*a*) and 14–38% in mergansers *Mergus serrator* (Feltham, 1995*b*) foraging in north-east Scotland. These studies used the premise that, in spring, Atlantic salmon <90 mm in length were parr and those >90 mm in length were smolts. Marquiss & Carss (1998) and Carss & Marquiss (1999) suggested that the form of the mixed regression (which included both parr and smolts) of atlas width on Atlantic salmon length could provide information on the ratio of the two life stages. On this basis they suggested that the diets of sawbill ducks in Scotland contained only a few smolts. Here, quantitative estimates and errors are derived using the best available information, and the conclusions of Carss & Marquiss (1999) are reconsidered.

MATERIALS AND METHODS

A simple model was constructed to explore how variation in the numbers of smolts and parr in a sample (e.g. the diet of birds) affects the form of the mixed regression. The model considered groups of parr and smolts, each with normally distributed length. The length distributions and the relationships between W_a and L_F for the two life stages were taken from Armstrong & Stewart (1996) (parr: $L_F = 57.1 W_a - 3.47$; smolt: $L_F = 56.9 W_a + 7.96$). There was uncertainty in the exact forms of these regressions, which was incorporated into the mixed regression using a Monte Carlo procedure.

The proportion of parr in a nominal population of 84 parr and smolts (the number of fish used to produce the mixed regressions) was varied between 0 and 100% in steps of 1 smolt. At each step, fish were selected at random from the distributions of lengths for each life stage. An estimate of W_a of each of these fish was then selected at random from the error distributions around the regressions relating W_a to L_F of parr and smolts. A regression relating L_F to W_a was then fitted to the mixed data using the least squares method. This process was repeated 1000 times at each step.

RESULTS

A plot of the mean slope and intercept values for each of the different parr : smolt ratios was curved to the degree that most of the dependent variables (in this case the gradient) could be ascribed to either of two values of the explanatory variable (intercept) (Fig. 1). There was variation around the mean, which, for any given parr:smolt ratio, could be quantified as the area which included 95% of the observations. The bounds of this area were those intercept and slope combinations giving a χ^2 of 5·991 (the threshold 95% value at 2 d.f.) from the equation:

$$\chi^2 = (n-1) \left[(sumgg.sumii) - sumgi^2 \right]^{-1} \{ [(g - \bar{g})^2 \, summi] - [2(g - \bar{g})(i - \bar{\imath})sumgi] + [(i - \bar{\imath})^2 sumgg] \}$$

where: g = known slope, i = known intercept, n = number of observations, $\bar{g}$ = mean slope, $\bar{\imath}$ = mean intercept, $Sumgg = \Sigma(g - \bar{g})^2$, $Sumii = \Sigma(i - \bar{\imath})^2$ and $Sumgi = \Sigma(g - \bar{g})(i - \bar{\imath})$.

These 95% CI were elliptical (Fig. 1). The equation was used to calculate the probability that each of a number of possible parr:smolt ratios gave rise to published mixed regressions. A value for χ^2 was calculated for each ratio and
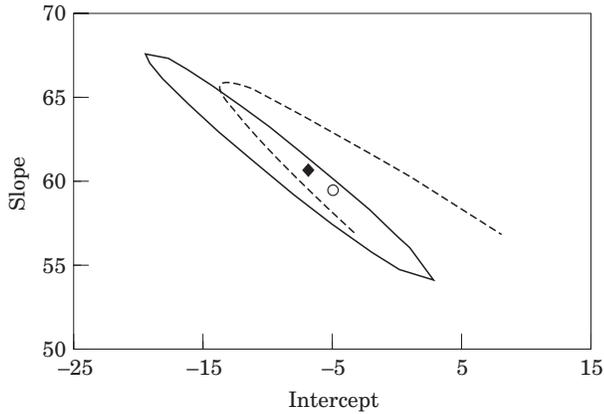
Fɪɢ. 1. Possible combinations of intercept and slope from a mixed regression of Atlantic salmon fork length on first vertebra width (– – –, mean values). The form of the regression depends on the proportions of parr and smolts in the population. Variation, modelled by Monte Carlo simulation, is shown for populations containing 10% smolts (——). The position of the two mixed regressions are also shown [Marquiss & Carss, 1998 (◆); Carss & Marquiss, 1999 (○)].
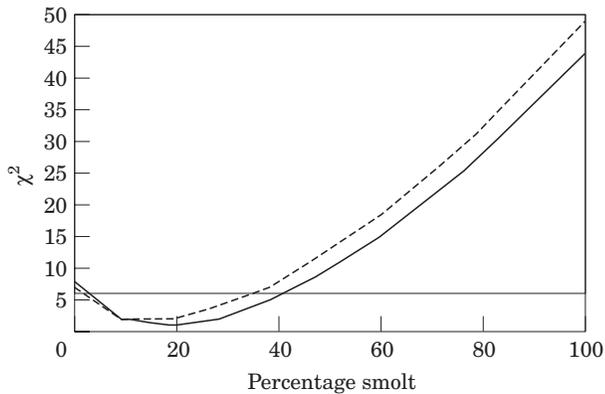

Fɪɢ. 2. Plot showing how the probability (χ^2) of the combination of slope and intercept in the two mixed equations changes with the percentage of smolts in the sample [Marquiss & Carss, 1998 (——); Carss & Marquiss, 1999 (– – –); critical value at $P = 0.05$ (——)].

compared with the threshold level (5·991) (Fig. 2). Using this method, the 95% CI are 1–36% and 1–42% smolts for the Carss & Marquiss (1999) and Marquiss & Carss (1998) data respectively.

DISCUSSION

The model suggests that the incidence of smolts in the diets of sawbill ducks is potentially much larger than implied by Marquiss & Carss (1998) and Carss & Marquiss (1999) and consistent with previous diet studies (Feltham 1995a,b). However, there is an inconsistency because the samples of Carss & Marquiss (1999) were mainly fish >90 mm, which by Feltham's definition were smolts. There are several possible explanations for this inconsistency. First, the forms for the regressions of atlas width on length of parr and smolts are from only a

few populations but have been applied to data sets from across Scotland. It is possible that between-site and -year variation in these regressions is sufficient to cause substantial inaccuracies in the approach (Carss & Marquiss, 1999). Secondly, sawbill ducks may consume primarily large parr that, if they survived, would have remained in the river rather than emigrating. Existing surveys suggest that few fish >90 mm in autumn and winter remain in the river as parr during the following year (Egglishaw, 1967, R. Gardiner, pers. comm.). However, it is possible that sawbill ducks and other predators feed selectively on large parr, many of which may have been males that spawned in the previous autumn, to the extent that that few of them survive. Finally, the mixed regressions of Marquiss & Carss (1998) and Carss & Marquiss (1999) included fish consumed in the winter and it is possible that although they were destined to smolt they had not yet elongated and would therefore retain a parr-like relationship between atlas width and fork length.

Many of the problems associated with studying the interactions between populations of piscivorous birds and salmonids, and suggestions for further work, have been the subject of recent reviews (Russell *et al.*, 1996; Marquiss *et al.*, 1998). This study illustrates the value of incorporating errors into modelling processes. A useful next stage in developing predatory bird consumption models will be to derive error distributions for parameters that are currently taken as fixed values, for example, the assumption of a cut-off between smolts and parr at 90 mm.

References

Armstrong, J. D. & Stewart, D. C. (1996). The relationship between first vertebra width and body length of Atlantic salmon differs between parr and smolts. *Journal of Fish Biology* **49,** 1038–1040.

Armstrong, J. D., Gardiner, R. & Laughton, R. (1998). Potential responses by juvenile salmonid populations to predation. In *Fish-eating Birds and Salmonids in Scotland* (Marquiss, M., Carss, D. N., Armstrong, J. D. & Gardiner, R., eds), pp. 61–70. Edinburgh: The Scottish Office Agriculture, Environment and Fisheries Department.

Carss, D. N. & Marquiss, M. (1991). Avian predation at farmed and natural fisheries. In *Interactions between Fisheries and the Environment, Proceedings of the Institute of Fisheries Management 22nd Annual Study Course* (Lucas, M. C., Diack, I. & Laird, L., eds), pp. 179–196. Aberdeen: Aberdeen Xpress Print.

Carss, D. N. & Marquiss, M. (1999). Skeletons in the cupboard? Quantifying bird predation on Atlantic salmon: atlas vertebra: fish length equations revisited. *Journal of Zoology, London* **248,** 272–276.

Egglishaw, H. J. (1967). The food, growth and population structure of salmon and trout in two streams in the Scottish Highlands. *Freshwater and Salmon Fisheries Research* **38,** 1–38.

Feltham, M. J. (1990). The diet of red-breasted mergansers (*Mergus serrator*) during the smolt run in north-east Scotland: the importance of salmon smolts and parr. *Journal of Zoology, London* **222,** 285–292.

Feltham, M. J. (1995*a*). Consumption of Atlantic salmon smolts and parr by goosanders: extrapolation from doubly-labelled water measurements of captive birds released on two Scottish rivers. *Journal of Fish Biology* **46,** 273–281.

Feltham, M. J. (1995*b*). Predation of Atlantic salmon, *Salmo salar* L., smolts and parr by red-breasted mergansers, *Mergus serrator* L., on two Scottish rivers. *Fisheries Management and Ecology* **2,** 289–298.

Feltham, M. J. & Marquiss, M. (1989). The use of the first vertebrae in separating and estimating the size of trout (*Salmo trutta*) and salmon (*Salmo salar*) in bone remains. *Journal of Zoology, London* **219,** 113–122.

Fortunatova, K. R. (1951). Methods of studying feeding of predaceous fishes. *Zoologicheskiyi Zhurnal* **30,** 562–571 (in Russian).

Hoar, W. S. (1976). Smolt transformation: evolution, behaviour and physiology. *Journal of the Fisheries Research Board of Canada* **33,** 1234–1252.

Marquiss, M. & Carss, D. N. (1998). The diet of sawbill ducks and cormorants in Scotland. In *Fish-eating Birds and Salmonids in Scotland* (Marquiss, M., Carss, D. N., Armstrong, J. D. & Gardiner, R., eds), pp. 28–51. Edinburgh: The Scottish Office Agriculture, Environment and Fisheries Department.

Marquiss, M., Carss, D. N., Armstrong, J. D. & Gardiner, R. (1998). *Fish-eating Birds and Salmonids in Scotland.* Edinburgh: The Scottish Office Agriculture, Environment and Fisheries Department.

Popova, O. A. (1978). The role of predaceous fish in ecosystems. In *Ecology of Freshwater Fish Production* (Gerking, S. D., ed.), pp. 215–249. New York: John Wiley.

Russell, I. C., Dare, P. J., Eaton, D. R. & Armstrong, J. D. (1996). *Assessment of the Problem of Fish-eating Birds in Inland Waters in England and Wales.* Lowestoft: MAFF.