Computing expected reproductive success of female Atlantic salmon as a function of smolt size

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A method is described for determining the expected reproductive success (gonadal mass of a returning fish times the probability of surviving to return) and expected fecundity of salmonids as a function of smolt size. Application of the method requires data relating (i) return weight and smolt size; (ii) probability of survival and smolt size; (iii) probability of return after one or two sea winters and smolt size; and (iv) gonads and return weight. Although there exists no published data set that contains all of this information, it is possible to piece together enough information from published sources on female Atlantic salmon to demonstrate the feasibility of the method, with the goal of encouraging the publication of datasets that will allow meaningful calculations for a single river. Thus, one should not expect general predictions about Atlantic salmon, but once local conditions are taken into account, it will be possible to predict the relationships between smolt size and expected fecundity or expected reproductive success.

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INTRODUCTION

The computation of the relationship between smolt size and expected gonadal mass (i.e. expected reproductive success) for salmonids is interesting for at least three reasons. First, life history models that focus on the pre-reproductive stages require an ' end condition ' (*sensu* Mangel & Clark, 1988) that relates smolt size to future fitness, determined by survival and reproduction. Second, managers of fish farms can use information relating smolt size and the timing of reproduction and ultimate somatic size of the fish to plan their product (Heen *et al.*, 1993). Third, restoration projects—with the goal of self-sustaining populations in the wild—often target a certain density of eggs (J. Armstrong, pers. comm.) as a measure of success. To do this, one needs to know the relationship between smolt size and fecundity of returning adults.

This note describes a conceptual method that can be used to compute the expected reproductive success, defined as gonadal mass of a returning female times the probability of surviving to return, for Atlantic salmon *Salmo salar* L. Currently published information on all components, for even one river system, that allows a completely confident calculation is lacking. Hence, the requisite data were collected from a number of sources, in order to illustrate how the computations will work. Once the logic is in place, with new data the calculations are routine.

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TABLE I. Estimates of b_s, relating smolt size and survival probability

Source	Species	Estimate of b_s
Ward & Slaney (1988)	Steelhead trout *Oncorhynchus mykiss* (Walbaum)	$0.037\,\mathrm{cm}^{-1}$
Ward *et al.* (1989)	Steelhead trout	$0.056\,\mathrm{cm}^{-1}$
Holtby *et al.* (1990)	Coho salmon *O. kisutch* (Walbaum)	$0.027\,\mathrm{cm}^{-1}$
Koening *et al.* (1993)	Sockeye salmon *O. nerka* (Walbaum)	$0.03{-}0.05\,\mathrm{cm}^{-1}$
Lundqvist *et al.* (1994)	Atlantic salmon	$0.05\,\mathrm{cm}^{-1}$

For definiteness, fish are assumed to spend either one or two winters in the sea, but this is not crucial for the method. The components of the calculation are the relationships between (i) return weight and smolt size; (ii) probability of survival and smolt size; (iii) probability of return after one or two sea winters and smolt size; and (iv) gonads and return weight. These are analysed singly and then used to compute expected reproductive success and expected fecundity.

MATERIALS AND METHODS

RETURN WEIGHT AND SMOLT SIZE

Assume that the return weight $W_i(L)$ of a smolt of size L that spent i winters in the sea is (alternatives are discussed in the last section):

$$W_i(L) = w_i + b_w L, \quad i = 1 \text{ or } 2 \tag{1}$$

where, w_1, w_2 and b_w are constants. The slope of the weight–smolt length relationship in Fig. 6 of Skilbrei (1989) is $0.125\,\mathrm{kg\,cm}^{-1}$, so that $b_w = 0.125$. Shearer (unpublished M.Sc. thesis, 1972) reported that the average length of North Esk smolts was $12.3\,\mathrm{cm}$, the average weight of one sea winter fish was $2.6\,\mathrm{kg}$ and of two sea winter fish was $4.1\,\mathrm{kg}$. From these data, $w_1 = 1.06\,\mathrm{kg}$ and $w_2 = 2.56\,\mathrm{kg}$.

PROBABILITY OF SURVIVAL AND SMOLT SIZE

Assume that the probability $S_i(L)$ that a smolt of length L survives the ith sea winter is:

$$S_i(L) = s_i + b_s L, \quad i = 1 \text{ or } 2 \tag{2}$$

where s_1, s_2 and b_s are constants. The slope, relating increased length and increased survival probability, is very difficult to measure. However, there is remarkable commonality among different estimates (Table I). For computations reported here, the conservative value $b_s = 0.03\,\mathrm{cm}^{-1}$ was used. Shearer's (unpublished M.Sc. thesis, 1972) data suggest about a 10% survival in the first sea winter and a 70% survival in the second sea winter. Consequently, $s_1 = -0.269$ and $s_2 = 0.331$. Thus, for example, for a 19-cm smolt $S_1(19) = 0.3$ and $S_2(19) = 0.9$, so that the probability that a 19-cm smolt survives to return after one sea winter is 0.3 and after two sea winters is $0.3 \times 0.9 = 0.27$.

PROBABILITY OF RETURNS AFTER ONE OR TWO SEA WINTERS

Assume that $P(L)$ is the probability that a smolt of length L is a one sea winter (1SW) fish. Since all fish are assumed to return after one or two years, the probability that a smolt of length L is a two sea winter (2SW) fish is $1 - P(L)$. Imagine that n smolts of length L are released. Then $nP(L)S_1(L)$ fish will return as 1SW fish and

$n(1 - P(L))S_1(L)S_2(L)$ fish will return as 2SW fish. Consequently, the ratio $R(L)$ at return of 1SW to 2SW fish of smolt length L is

$$R(L) = \frac{nP(L)S_1(L)}{n(1 - P(L))S_1(L)S_2(L)} = \frac{P(L)}{(1 - P(L))S_2(L)} \qquad (3)$$

If $R(L)$ is known, equation (3) can be solved for $P(L)$

$$P(L) = \frac{S_2(L)R(L)}{1 + S_2(L)R(L)} \qquad (4)$$

Nicieza & Braña (1993) give data on $R(L)$ for the Rivers Narcea, Esva and Cares that can be used to estimate $P(L)$ from equation (4).

GONADS AND RETURN WEIGHT

Return weight includes both gonads and soma. In some cases, they can be separated directly from data on body mass and gonad mass. Otherwise, the following method can be used. Sutterlin & MacLean (1984) give relationships between absolute fecundity (number of eggs), individual egg volume and body weight for two Atlantic salmon populations in Newfoundland. Fecundity (F, eggs) and weight (W, g) are related by

$$F = c_1 W^{k_1} \qquad (5)$$

where $c_1 = 4.832$ and $k_1 = 0.8697$. The volume (cm^3) of a single egg and adult weight are related by

$$V = c_2 + c_3 \ln(W) \qquad (6)$$

where $c_2 = 0.01158$ and $c_3 = 0.01232$. Suppose that the weight W of a fish is composed of gonadal mass G and somatic mass B, so that $W = G + B$. Assuming that the density of eggs is 1 g cm^{-3}, it is also true that $G = FV$. Thus

$$G = c_1(B + G)^{k_1}(c_2 + c_3 \ln(B + G)) \qquad (7)$$

If B is specified, equation (7) is a nonlinear equation for G that can be solved by Newton's method (Appendix).

Using this approach gives a virtually linear relationship between gonadal mass and weight

$$G(W) = -0.3255 + 194.45W \qquad (8)$$

where gonadal mass $G(W)$ is measured in g and mass W is measured in kg.

EXPECTED REPRODUCTIVE SUCCESS

Expected reproductive success of a smolt of length L, $R_e(L)$, is the gonadal mass of a returning fish times the probability of survival to return

$$R_e(L) = P(L)S_1(L)G(W_1(L)) + (1 - P(L))S_1(L)S_2(L)G(W_2(L)) \qquad (9)$$

Similarly, the expected fecundity $F_e(L)$ of a smolt of length L is

$$F_e(L) = P(L)S_1(L)c_1 W_1(L)^{k_1} + (1 - P(L))S_1(L)S_2(L)c_1 W_2(L)^{k_1} \qquad (10)$$

The three rivers give similar, but not identical relationships between smolt length and expected reproductive success or expected fecundity (Fig. 1) and in the most common range of smolt sizes (about 10–16 cm), the three forms of $R_e(L)$ yield virtually identical predictions. The expected gonadal mass 'averages' the gonadal mass of all smolts of
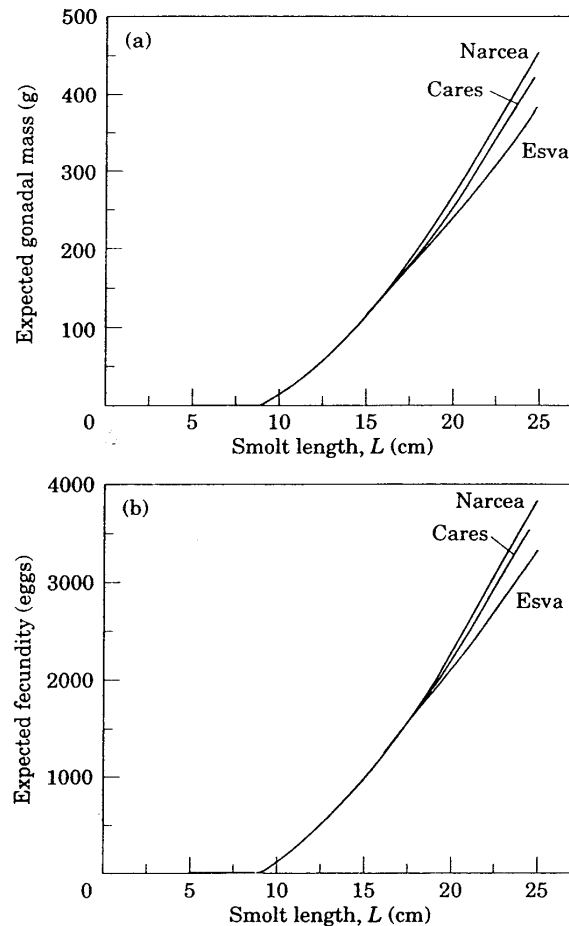
Fig. 1. The relationship between (a) expected reproductive success or (b) expected fecundity and smolt length. For ease of presentation, smolt sizes are shown over a range larger than typically observed.

that size, regardless of whether they were 1SW or 2SW and implicitly includes those which do not survive to return (and thus have reproductive output equal to 0). Thus, the expected gonadal mass of a smolt of a given size is considerably less than the gonadal mass, given that a fish has survived to return.

DISCUSSION

Because the sources of data used for this computation varied, the results (Fig. 1) should not be interpreted literally. Instead, they are a demonstration of the feasibility of the method summarized in equations (9) and (10). To apply the method with confidence, one should use data from a single river and apply it only to females.

Three comments can be made about the method. First, linear relationships between $W_i(L)$ and $S_i(L)$ were assumed. These are not required for application of the method; if sufficient data exist to parametrize a nonlinear relationship, then one can be used; alternatively, with enough data the empirical relationship

itself can be used. The components that are to some sense 'data free' are the details of the computation of the probability of 1SW or 2SW [equation (4)], which can be generalized for stocks with more than two sea winters, and the determination of gonadal mass as a function of body weight [equations (5)–(8) and Appendix A]. Second, variance estimates were not computed for any of the parameters. In a real application of this method, clearly one should do so, in order to obtain reasonable confidence bounds about expected reproductive success and expected fecundity. It is likely that if variability in parameter estimates were included, the small differences between the three rivers (Fig. 1) would be swamped by the uncertainty in the parameters. Third, there is clear evidence that size and fecundity relationships differ between river stocks (Thorpe & Mitchell, 1981) and that younger females produce smaller eggs (Thorpe *et al.*, 1984), which means that the relationship between egg volume and adult weight may, in principle, depend upon whether the fish returns after one or two sea winters. That is, predictions must take local conditions into account; but once this is done, the method illustrated in this paper can be used to relate fecundity, expected reproductive success, and smolt size.

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APPENDIX A: DETERMINATION OF GONADAL MASS FROM BODY WEIGHT

Equation (7) can be solved by Newton's method (Press *et al.*, 1986), which is an iterative procedure for solving nonlinear equations. Rewriting equation (7) as

$$H(G) = G - c_1(B+G)^{k_1}(c_2 + c_3\ln(B+G)) = 0 \qquad \text{(A1)}$$

The derivative $H'(G)$ is

$$H'(G) = 1 - c_1 k_1(B+G)^{k_1-1}(c_2 + c_3\ln(B+G)) - c_1(B+G)^{k_1}c_3/(B+G) \qquad \text{(A2)}$$

Beginning with an initial guess for gonadal mass $G = G_1$ (which was set at $0{\cdot}05B$) subsequent values are determined by

$$G_{n+1} = G_n - \frac{H(G_n)}{H'(G_n)} \qquad \text{(A3)}$$

Equation (A3) is used until the difference $|G_{n+1} - G_n|$ is very close to 0 (10^{-5} gm was used in this paper). For the parameters in this paper, the method converged very quickly (typically 5–10 iterations).