

A SPURIOUS CORRELATION IN AN INTERPOPULATION COMPARISON OF ATLANTIC SALMON LIFE HISTORIES¹

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Abstract. We tested two hypotheses concerning geographical variation in Atlantic salmon (*Salmo salar*) life histories: (1) mean age at first reproduction is positively correlated with growth rate at sea and (2) within-population variation in age at first reproduction first increases and then decreases with latitude. Data on growth and age at first reproduction were compiled from 41 populations in eastern North America. Data reliability was checked by a redetermination of ages based on scale examination. The proportion of fish that were incorrectly aged was small ($\approx 0.7\%$); however, aging errors were primarily of one kind; salmon that had previously spawned were misclassified as virgin fish of an older age class.

Growth rate at sea was found not to be positively correlated with age at maturation. Schaffer and Elson's (1975) positive correlation between growth and age at first reproduction can be attributed to a subtle statistical artifact caused by aging errors. We also found that within-population variation of age at maturation was not related to latitude.

We conclude that tests of life history theories should not assume constancy in life history traits, such as mortality, among populations.

Key words: Atlantic salmon; evolution; geographical variation; life history; reproductive strategies; *Salmo salar*; spawning age; spurious correlation; statistical artifact.

INTRODUCTION

Life history theory predicts that increased growth rate should lead to delayed maturation, all other factors remaining constant (Schaffer 1974a). However, high growth rates are usually associated with early maturation for fish and invertebrates (Alm 1959, Kanep 1974, Myers and Runge 1983, Policansky 1983, Hutchings and Morris 1985). This implies either that the theory is wrong or that there is a general covariation of other life history factors with growth rate such that the predictions of the theory are usually reversed.

A notable exception to the general pattern for fish was reported for the Atlantic salmon, *Salmo salar*, the anadromous form of which spends 1-3 yr at sea before returning to its natal stream to spawn (Jones 1959). Schaffer and Elson (1975) found a strong positive correlation between time spent at sea prior to maturation and growth rate at sea in North American populations of Atlantic salmon. This result supported their application of optimal life history theory to Atlantic salmon.

We investigated this inconsistency by examining the data upon which Schaffer and Elson (1975) based their correlation and by analyzing a more extensive data base to test their prediction. We found no evidence of

a correlation between growth rate at sea and sea age at maturation in Atlantic salmon. Furthermore, we could not verify their conclusion that within-population variation in age at maturation increases and then decreases with increasing latitude. Schaffer and Elson's (1975) result can be attributed to a subtle statistical artifact that is of general interest.

METHODS

For simplicity, one-sea-year (1SY) salmon refers here to fish that had spent 13-16 mo (encompassing one winter) at sea before maturing and returning to their natal streams to spawn. Similarly, 2SY and 3SY salmon had spent two and three winters at sea, respectively. Sea age at maturation refers to time spent at sea prior to spawning.

The rate of growth in length during the 1st 3 yr at sea decreases with age in Atlantic salmon (Allen et al. 1972). Hence, the unweighted linear regression of mean length on virgin sea age employed by Schaffer and Elson (1975) was inappropriate for this concave relationship. Growth rate at sea is more appropriately estimated as the difference between mean fork lengths of successive year classes. Fork length is the distance from the tip of the snout to the mid-fork of the tail.

Published data were compiled for salmon populations from rivers in eastern North America (Table 1).

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Age determinations had been based on scale analyses. Records from counting fences were used in preference to sport angling statistics when both kinds of data existed. We did not use commercial catch records and included data in our analysis only if information on the variation of length at a given age was available.

We examined the age-specific frequency distributions of length for populations in which the original scales were available for age verification. Data reliability was assessed by checking for outliers. We re-examined scales for individuals having lengths over two standard deviations (SD) from the population mean. Aging errors were primarily (over 70%) caused by interpretation of spawning marks as annuli (for details see Myers and Hutchings 1987); salmon that had previously spawned were often misclassified as virgin fish of an older sea age class. For example, the rate at which 1SY salmon (including those that had previously spawned) were misclassified as 2SY salmon in the Exploits River, Newfoundland, was 0.7%. These aging errors resulted in a systematic underestimation of the age-specific mean lengths for multi-sea-year salmon.

We used the following procedure to assess data reliability for populations in which original scales were not available. If length at a given age is normally distributed, then the expected percentage of individuals lying 2 SD below the population mean is 2.28. If more than twice this percentage of any age class was more than 2 SD below the population mean, the population was excluded from further analyses. This criterion excluded the data from the West River, Nova Scotia. Fifty percent of the fish classified as 2SY salmon in the West River were <65 cm in length, well within the size range characteristic of repeat-spawning 1SY fish. The robustness of our results was tested by including this river in the analysis.

Individual age-specific length data were not available for the Narraguagus River, Maine, and the Koksoak River in Ungava Bay, Québec. Means from these rivers were included because they represent Atlantic salmon near the northern and southern extremities of its range. Exclusion of these data did not affect the results.

RESULTS AND DISCUSSION

Growth at sea and sea age at maturation

Forty-one rivers satisfied our criteria for acceptance (Table 1). Our analyses (Fig. 1) failed to support a relationship between sea age at maturation and growth rate at sea ($r = 0.12$; $P > .05$; $n = 41$). Similar results were obtained by estimating growth rate at sea as the difference between mean lengths of fish that matured after 3 and 1 yr at sea ($r = -0.37$; $P > .05$; $n = 21$), and 3 and 2 yr at sea ($r = -0.12$; $P > .05$; $n = 21$). Exclusion of rivers with small sample sizes ($n < 5$ fish per age class) yielded similar correlations. The correlation was not significant when the suspect data from the West River were included.

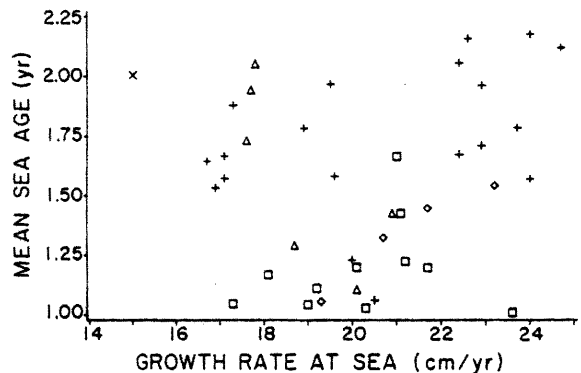


FIG. 1. Mean sea age at maturation (from sample sizes in Table 1) plotted against growth rate at sea as measured by the difference in mean lengths of fish that matured after 2 yr at sea and those that matured after 1 yr at sea; $r = 0.12$; $P(r) > .05$. Symbols refer to Newfoundland (□); Nova Scotia (Δ); New Brunswick (◇); Québec (+); and Maine (×).

We also tested Schaffer and Elson's hypothesis within geographic regions by regressing mean sea age at maturation against growth rate at sea for each province. The regression for New Brunswick salmon was positive and nominally significant at the .05 level. That one test should appear to be significant of the 14 performed in our analysis was likely due to chance alone (the probability of obtaining at least one significant result by chance at the .05 level from 14 independent tests is 0.51). Furthermore, it is questionable whether New Brunswick comprises a reasonable geographic region for such an analysis; two of the rivers considered empty into the Bay of Fundy, whereas two empty into the Gulf of St. Lawrence.

Statistical artifacts

In the original Exploits River data, a 0.7% error in aging resulted in >50% of the alleged 2SY salmon being misclassified. Under what circumstances can a 0.7% classification error rate be responsible for a correlation that appears to be highly significant (e.g., $P < .001$)? If measurement errors associated with the variations in question are not independent, then even a relatively small error rate can have serious statistical consequences. In this case, age misclassifications affect estimated mean age as well as growth rate. This effect will be small if the number of observations in each class, for example age class, are approximately equal, but can become important if there is great disparity in sample sizes.

A simplified example will demonstrate this principle. Consider populations that consist only of 1SY and 2SY salmon. The mean sea age at maturation will be $1 + q$, where q is the proportion of the population returning after 2 yr at sea. Let e be the proportion of 1SY salmon misclassified as 2SY salmon. If all 1SY salmon are of length l_1 , and 2SY salmon of length l_2 , then growth as estimated by the apparent difference between the mean length of the two age classes is

TABLE 1. Relationship between length (cm) and number of years spent at sea (SY) for virgin Atlantic salmon in North America.

| River | Latitude °N | Fork length* (sample size) | | | Collection method† | Year | Reference |
|---------------------|-------------|----------------------------|-------------|------------|--------------------|----------------------------|----------------------------|
| | | 1SY | 2SY | 3SY | | | |
| Newfoundland | | | | | | | |
| Exploits | 49.0 | 52.0 (846) | 75.6 (10) | | F | 1963 | Myers and Hutchings (1987) |
| Hunt | 55.0 | 57.8 (8) | 76.6 (24) | | A | 1980 | Myers and Hutchings (1987) |
| North Harbour | 47.0 | 55.1 (38) | 76.3 (11) | | F | 1970, 1971, 1973, 1974 | Lear and Day (1977) |
| Pinware | 52.0 | 53.2 (748) | 74.3 (142) | | A | 1980, 1981 | Myers and Hutchings (1987) |
| Sand Hill | 54.0 | 53.9 (3196) | 73.0 (389) | 98.1 (2) | A | 1967, 1969-1974 | Myers and Hutchings (1987) |
| Eagle | 54.0 | 54.4 (302) | 74.7 (9) | | A | 1971, 1979 | Myers and Hutchings (1987) |
| Forteau | 51.5 | 54.2 (353) | 72.9 (11) | | A | 1979-1981 | Myers and Hutchings (1987) |
| Highlands | 48.0 | 53.3 (16) | 73.4 (4) | | F | 1982 | Myers and Hutchings (1987) |
| Humber | 49.0 | 55.0 (297) | 73.5 (9) | 86.5 (17) | F | 1967, 1976, 1979-1981 | Myers and Hutchings (1987) |
| Little Codroy | 47.5 | 54.1 (197) | 75.1 (163) | 89.6 (35) | F | 1957-1963 | Myers and Hutchings (1987) |
| Lomond | 49.5 | 51.4 (108) | 70.7 (7) | | A | 1975, 1978-1981 | Myers and Hutchings (1987) |
| New Brunswick | | | | | | | |
| Miramichi | 47.0 | 52.1 (8604) | 72.8 (4016) | 82.4 (48) | F | 1971-1983 | ‡ |
| Saint John | 46.5 | 56.3 (583) | 78.0 (474) | | F | 1977-1979 | Myers and Hutchings (1987) |
| Big Salmon | 45.0 | 53.2 (1654) | 70.8 (139) | | F | 1965-1973 | Jessop (1986) |
| Restigouche | 48.0 | 53.2 (1488) | 76.4 (701) | 92.6 (335) | F | 1972-1980 | Randall (1984) |
| Nova Scotia | | | | | | | |
| LaHave | 44.0 | 53.8 (68) | 72.5 (28) | | F | 1982 | Myers and Hutchings (1987) |
| Liscomb | 45.0 | 52.3 (770) | 72.4 (82) | 91.7 (5) | F | 1979-1982 | Myers and Hutchings (1987) |
| Margaree | 46.0 | 53.5 (17) | 71.1 (23) | 81.7 (5) | F | 1973 | Myers and Hutchings (1987) |
| North | 46.0 | 54.6 (2) | 72.3 (35) | | F | 1972 | Myers and Hutchings (1987) |
| Philip | 44.5 | 56.6 (22) | 74.4 (167) | 86.7 (34) | A | 1978 | Myers and Hutchings (1987) |
| St. Mary's | 44.0 | 54.0 (60) | 74.9 (20) | 91.1 (9) | A | 1974 | Myers and Hutchings (1987) |
| Québec | | | | | | | |
| Bouleau | 50.0 | 50.6 (15) | 74.6 (20) | | G | 1972, 1973 | Randall and Power (1979) |
| Pigou | 50.0 | 53.1 (5) | 72.7 (7) | | G | 1972, 1973 | Randall and Power (1979) |
| Cap-Chat | 49.0 | 56.3 (16) | 78.9 (73) | 93.4 (36) | A | 1974, 1975, 1977 | Myers and Hutchings (1987) |
| Corneille | 50.0 | 53.3 (203) | 70.0 (369) | | A | 1964-1968 | Myers and Hutchings (1987) |
| Grande | 48.0 | 54.9 (12) | 74.4 (76) | 90.9 (9) | A | 1983 | Myers and Hutchings (1987) |
| Koksoak | 57.0 | 61.7 (221) | 78.6 (253) | | G | 1980 | Robitaille et al. (1984) |
| Leaf | 58.5 | 62.4 (6) | 79.7 (44) | | G | 1968 | Lee and Power (1976) |
| Madeleine | 49.0 | 51.5 (172) | 75.2 (334) | 92.1 (53) | A | 1972, 1975-1979 | Myers and Hutchings (1987) |
| Matamek | 50.0 | 52.9 (20) | 72.9 (6) | | G | 1974 | Myers and Hutchings (1987) |
| Matane | 49.0 | 54.8 (186) | 71.9 (149) | 90.3 (56) | A | 1969 | Myers and Hutchings (1987) |
| Matapédia | 48.0 | 56.8 (66) | 80.0 (354) | 94.6 (171) | A | 1973 | Myers and Hutchings (1987) |
| Nabisipi | 50.0 | 54.5 (61) | 77.4 (1252) | 87.6 (14) | G | 1960-1962, 1963, 1965-1967 | Myers and Hutchings (1987) |
| Pt. Saguenay | 48.0 | 56.7 (182) | 79.1 (39) | 92.3 (83) | A | 1978, 1979 | Myers and Hutchings (1987) |
| Ste. Anne | 49.0 | 56.1 (19) | 80.8 (107) | 95.8 (39) | A | 1973, 1974 | Myers and Hutchings (1987) |
| Ste. Marguerite | 48.0 | 52.8 (63) | 75.2 (70) | 90.1 (75) | A | 1969, 1976 | Myers and Hutchings (1987) |
| St. Jean | 50.0 | 53.0 (35) | 75.9 (73) | 89.3 (3) | A | 1977 | Myers and Hutchings (1987) |
| St. Jean (Gaspésie) | 48.5 | 54.4 (60) | 73.3 (157) | 90.7 (11) | F | 1978, 1979, 1983 | Myers and Hutchings (1987) |
| Trinité | 49.0 | 54.2 (319) | 74.7 (21) | | A | 1981 | Myers and Hutchings (1987) |
| Watshishou | 50.0 | 53.3 (189) | 70.4 (254) | | A | 1981-1983 | Riley et al. (1984) |
| Maine | | | | | | | |
| Narraguagus§ | 44.5 | 54.8 (13) | 69.8 (964) | 81.7 (19) | F | 1962-1966 | Meister and Cutting (1967) |

* Fork length = distance from tip of snout to mid-fork of tail.

† F = Counting fence; A = recreational angling; G = research gill nets within river/estuary.

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§ Lengths given in Schaffer and Elson (1975) are total length, not fork length.

$$\frac{ql_2 + e(1-q)l_1}{q + e(1-q)} - l_1,$$

or equivalently

$$(l_2 - l_1) \frac{q}{q + e - eq} \quad (1)$$

The growth in length is greatly underestimated if q is small. If e and q are both small, then Eq. 1 can be approximated by

$$(l_2 - l_1) \frac{q}{q + e} \quad (2)$$

Thus, if $q = e$ and both are small, then growth rate would be underestimated by $\approx 50\%$.

Now let 2SY salmon also be misclassified at rate e . The estimated annual growth rate is

$$\frac{(1-e)ql_2 + e(1-q)l_1}{(1-e)q + e(1-q)} - \frac{eq l_2 + (1-e)(1-q)l_1}{eq + (1-e)(1-q)} \quad (3)$$

If q and e are both small, Eq. 3 can again be approximated by Eq. 2. Thus, growth rates would be greatly underestimated when q is small even if aging errors occurred in both age classes. However, if aging errors occurred in both age classes, then growth rate would also be underestimated for populations with q close to 1.

Schaffer and Elson's (1975) spurious correlation was amplified by their use of an unweighted linear regression to estimate growth rate. For example, in their analysis of Sand Hill River, Newfoundland, data, the weight given to >1700 1SY fish was equal to that attributed to two fish classified as 3SY salmon. Similarly, 955 1SY salmon were weighted equally with two 3SY fish from the Exploits River. Scale analyses revealed the alleged 3SY fish from both the Sand Hill and Exploits rivers to be previous spawners, not virgin 3SY salmon.

Our results demonstrate how the misclassification of a few fish can create spurious correlations in life history comparisons when measurement errors are not independent. Even a relatively small error rate, such as that found for the Exploits River data (0.7%), can lead to a result that appears to be significant.

Latitude and variation in sea age at maturation

A second prediction of life history theory that Schaffer and Elson (1975) attempted to test was that variation in life history traits should increase and then decrease with increasing latitude (Schaffer 1974b). We tested this prediction using the data in Table 1. We hypothesized that the second-order term of the polynomial regression of the coefficient of variation of sea age at maturation y on latitude of river mouth x should be negative (Fig. 2). The resulting regression, $y = \beta_0 + \beta_1 x + \beta_2 x^2$ ($\beta_0 = -183$; $\beta_1 = 9.04$; $\beta_2 = -0.095$), did not support the hypothesis [$P(\beta_2 = 0) = .37$]. There also was no evidence for a linear trend with latitude [$P(\beta_1 = 0) = .41$]. Similar results were obtained if the standard deviation was used in the regression instead of the coefficient of variation. We also reanalyzed the data presented by Schaffer and Elson (1975), using the coefficient of variation as a measure of variation, and found β_2 to be significant [$P(\beta_2 = 0) < .05$]. However, this result was due to the inclusion of three rivers of Ungava Bay, in which the fish were collected using highly size-selective commercial gill nets. If these points

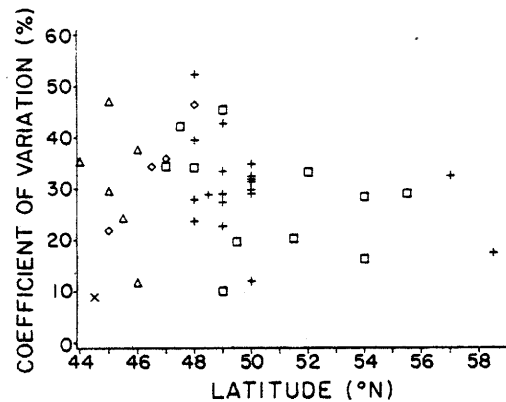


FIG. 2. Coefficient of variation (%) of sea age at maturation plotted against latitude ($^{\circ}$ N). Symbols refer to Newfoundland (\square); Nova Scotia (Δ); New Brunswick (\diamond); Québec (+); and Maine (\times).

were replaced by research data (Robitaille et al. 1984), or eliminated, the significant result again disappeared.

Schaffer and Elson's (1975) conclusion that the variability in Atlantic salmon sea age at maturation peaks in the midlatitudes was due to a simple error; standard deviation was used as a measure of variation instead of the coefficient of variation. The standard deviation in this case is proportional to the mean and cannot be used to compare variation.

COMPARATIVE LIFE HISTORY STUDIES

Schaffer's (1974a) predictions on the evolution of individual life histories are not borne out in interpopulation comparisons for Atlantic salmon. However, this is neither evidence for nor against the applicability of optimal life history theory to Atlantic salmon, although this theory may not be an adequate approximation to the evolution of salmonid life histories (Gross 1984, 1985, Myers 1984, 1986, 1987). Life history theory predictions are often "tested" by comparing the covariation of two life history traits (one of which is a component of fitness), e.g., growth rate and age at maturity, among populations (see Stearns 1977). An implicit assumption in such studies is that other traits known to be of great importance, e.g., mortality, remain constant among populations. This assumption is simply not consistent with a vast amount of available data (e.g., Pauly 1980). For example, life history theory predicts that individuals with rapid growth rate should have delayed maturation, all other factors remaining constant. However, when individuals among populations are compared, this is rarely the case. On the other hand, quantitative tests of life history theory using growth and mortality data have yielded predictions that are consistent with observed ages at maturation (Bell 1980, Myers and Doyle 1983, Myers and Runge 1983, Roff 1984, Stearns and Crandall 1984), suggesting that mortality and growth generally covary.

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