

Variation in Male Parr Maturation Within and Among Populations of Atlantic Salmon, *Salmo salar*

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The covariation of growth and maturation in male Atlantic salmon parr, *Salmo salar*, produces a relationship characterized by a size threshold below which individuals generally do not mature. The threshold of 70–72 mm fork length is evident both within and among populations. Parr maturation can reduce growth during the second year of life by an average of 4.0%. Among-year variation in growth rate affects the yearly incidence of maturation for males at age 1+ but has no detectable effect on the total proportion of male parr maturing in a population. Increases in the proportion of mature parr in the Matamek River, Quebec, can be explained by variation in growth alone; there is no evidence for genetic changes in this population.

La covariation de la croissance et de la maturation chez les tacons de saumon de l'Atlantique, *Salmo salar*, produit une relation caractérisée par un seuil de taille au-dessous duquel les mâles n'atteignent généralement pas la maturité. Un seuil variant de 70 à 72 mm de longueur à la fourche est évident au sein de populations et entre celles-ci. La maturation des tacons peut réduire la croissance par un moyen de 4 % de la deuxième année du cycle vital. La variation du taux de croissance d'une année à l'autre influe sur la fréquence annuelle de la maturation des mâles à 1+ an, mais n'a aucune incidence discernable sur la proportion totale de tacons mâles d'une population que atteignent la maturité. La variation de la croissance peut, à elle seule, expliquer les augmentations de la proportion de tacons matures présents dans la rivière Matamek (Québec); il n'ya aucune évidence de changements génétiques dans cette population.

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The sexual maturation of male Atlantic salmon parr, *Salmo salar*, is a common phenomenon throughout the geographical range of this species, occurring at varying levels of incidence among populations (Jones 1959; Schiefer 1971; Dalley et al. 1983). This early maturation can have profound demographic consequences on salmon populations (Saunders and Schom 1985). High mortality and delayed smoltification associated with parr maturation reduces male salmon production by 60% in Newfoundland (Myers 1984). There is evidence from laboratory (Alm 1959; Leyzerovich 1973; Saunders et al. 1982; Thorpe et al. 1983) and field (Schiefer 1971; Dalley et al. 1983) research that males destined to mature as parr initially have a faster mean growth rate than male parr that do not mature before migration to sea. Although studies on hatchery Atlantic salmon have shown that maturing parr grow faster at first (Murphy 1980) and then at a slower rate than immature parr after the commencement of gonadal development, i.e. in the late summer and autumn before spawning (Leyzerovich 1973; Saunders et al. 1982), there has been no attempt to quantify this effect for naturally occur-

ring populations.

The purpose of this study is to collate and analyze systematically all available data on parr maturation among North American populations of Atlantic salmon to determine the degree to which growth and maturation covary within and among natural populations. It is necessary to have this information to determine whether differences in such maturation among populations, and changes within populations over time, can be attributed to variation in growth rate alone.

Furthermore, we wish to determine whether between-year variation in growth affects the proportion of a cohort that matures as parr. Although yearly variations may affect the age at maturation, there are no data to indicate whether yearly changes in growth affect the total proportion of males that mature as parr over the lifetime of a cohort. This information is important to the theoretical development of stock-recruitment relationships for Atlantic salmon because of the high mortality associated with parr maturation.

Our objectives in this paper are fourfold. First, we estimate the reduction in growth associated with maturation of male

TABLE 1. Heterogeneity factors computed for Little Codroy River and Miramichi River.

	Sites	\bar{n}	α	β	ϵ	Heterogeneity factor
Little Codroy						
57	11	6.4	56.90	20.10	0.013	1.1
58	10	8.4	4.10	1.43	0.180	2.1
59	14	4.8	5.96	3.80	0.091	1.4
60	31	11.0	2.17	0.77	0.340	3.5
61	22	4.8	0.30	0.32	1.610	5.2
62	23	6.7	5.50	1.74	0.140	1.7
63	27	7.4	4.90	1.90	0.150	1.8
Total	138	7.9	1.82	0.84	0.380	2.9
Miramichi	14	12	0.60	1.09	0.59	5.2

parr. Second, we compare patterns of growth and parr maturation among and within populations. Third, we determine whether significant differences exist in the incidence of mature male parr among populations, once growth effects have been statistically controlled. Fourth, we test for increases in the incidence of male parr maturity within populations that cannot be accounted for by changes in growth rate alone.

Statistical Preliminaries

Before assessing the variation in male parr maturity, we determined the accuracy with which estimates of such maturation were made. We tested the hypothesis that mature male parr were randomly distributed within a river. We examined data on the numbers of 1+ males maturing in the Little Codroy River, Newfoundland, collected by A. R. Murray from 1957 to 1963 (Murray 1968a, 1968b). Each sampling site was placed in one of five categories based upon the modal gravel size at the site (group A < 2.5 cm, 2.5 cm ≤ group B < 7.6 cm, 7.6 cm ≤ group C < 15.2 cm, 15.2 cm ≤ group D < 30.5 cm, 30.5 cm ≤ group E). A χ^2 test showed that maturation status was not independent of gravel type ($\chi^2 = 18.3$, $df = 8$, $P = 0.02$). Mature male parr were more common in sites with gravel size suitable for spawning (group B). Similar results were obtained if samples were taken only in August. Thus, the proportion of males that mature at a particular sample site was not an appropriate estimate of male parr maturity for the entire population.

A better estimate can be obtained by considering the male parr that do not mature. Because Atlantic salmon have a 1:1 sex ratio at hatching (Vladimirovskaya 1958; Mitans 1973) and mortality before maturation is independent of sex (Myers 1984), the proportion of age 1+ male parr that mature is 1 - (number of immature age 1+ male parr/number of age 1+ female parr). A χ^2 test on the Little Codroy data showed immature males and females to be distributed independently of stream bed type ($\chi^2 = 1.04$, $df = 4$, $P = 0.90$). We used this new criterion for estimating the proportion of males that mature.

However, within-river heterogeneity still existed (χ^2 test for independence of Little Codroy data, sites with expected cell size less than five eliminated, $\chi^2 = 68.6$, $df = 26$, $P = 0.0001$). Thus, it is still necessary to account for within-river heterogeneity in any analysis.

The usual assumption in the analysis of binary data, such as maturation of male parr, is that the number of animals in a class, e.g. those that mature, follows a binomial distribution.

This is, for example, one of the assumptions of probit models (Finney 1971). This assumption is not valid for the incidence of parr maturation because there is significant within-river variation in this characteristic. To analyse this heterogeneity, we assume that at any one site in a river, the number of sampled males that are mature follows a binomial distribution with parameter p , and that the binomial parameter p varies as a beta distribution with parameters (α, β) . That is, the variation in incidence of male parr maturation follows a beta-binomial distribution (Paul and Plackett 1978). If there are n males sampled at m sites, then the variance in mature males is

$$(1) \quad \frac{p(1-p)(n\epsilon+1)}{mn(\epsilon+1)}$$

where $\epsilon = 1/(\alpha + \beta)$. Thus, the variance for the beta-binomial distribution is $(n\epsilon + 1)/(\epsilon + 1)$ times the variance of the binomial distribution. If α and β are estimated for a population, then this heterogeneity factor $(n\epsilon + 1)/(\epsilon + 1)$ can be used to adjust the variance computed using the binomial assumption, to the appropriate value needed for meaningful significance tests (Paul and Plackett 1978).

Data were available from the Little Codroy River and the Miramichi River (Schofield and Peppar 1982) to assess within-river heterogeneity. Maximum-likelihood estimates of α and β were obtained using the Nelder-Mead simplex algorithm as described by Griffiths (1973). A heterogeneity factor was computed using the mean sample size per site, \bar{n} (Table 1). The binomial assumption underestimates the variance by as much as one tenth its true value.

Reduction in Growth Caused by Maturation

We estimated the reduction in growth resulting from maturation as parr, taking care to include the observation that males destined to mature as parr have a higher mean growth rate than other males during early gonadal maturation. The fundamental assumption in our estimate was that there would be no difference in growth between male and female parr in the absence of parr maturation. This was tested by examining growth, before maturation occurs, as recorded in the first year scale growth. A two-way analysis of variance, considering yearly variations as well as possible differences between sexes, on 2600 1+ parr yielded no significant variation in growth between males and females ($P > 0.05$).

We wish to estimate λ , the proportional reduction in length resulting from maturation. Thus, on average, a male that ma-

TABLE 2. Fork lengths and reduction in length associated with parr maturation in the Little Codroy River (calculated from Eq. 1).

	Year						
	1957	1958	1959	1960	1961	1962	1963
Mean fork length (mm)							
(sample size)							
Immature males (m_i)	87.5 (18)	82.9 (25)	85.2 (29)	78.3 (82)	82.5 (89)	82.8 (35)	83.4 (68)
Mature males (m_p)	85.3 (70)	87.8 (93)	86.7 (76)	84.9 (289)	85.7 (120)	88.6 (123)	86.7 (136)
Females (f)	87.1 (70)	88.2 (84)	89.3 (67)	86.6 (338)	87.2 (171)	92.5 (155)	85.4 (199)
Proportion 1+ males maturing (q)	0.795	0.788	0.724	0.776	0.658	0.812	0.677
Proportional reduction in length (λ)	0.019	0.020	0.045	0.046	0.045	0.065	-0.003
Reduction in second year growth (mm)	1.65	1.76	4.02	3.98	3.92	6.01	—

TABLE 3. Relationship between growth and sexual maturation in salmon parr (sample size in parentheses). See text for explanation of how "% mature" was calculated (for "% mature", sample size equals total number of females plus total number of immature males).

River	Fork length (mm) at 1+	% mature	Fork length (mm) at 2+	% mature	Collection method ^a	References ^b
Newfoundland						
Bay de l'Eau	73.1 (52)	72.4 (35)		80.0 (6)	E	1,2
Come By Chance	72.2 (70)	78.6 (34)			E	1,2
Lomond	72.7 (79)	48.6 (56)		100.0 (2)	E	1,2
North Harbour	84.3 (44)	11.8 (32)		80.0 (6)	E	1,2
Rocky	85.4 (45)	16.0 (41)	104.4 (71)	25.6 (68)	E	1,2
Salmon	73.6 (37)	24.0 (31)	100.8 (64)	89.0 (20)	E	1,2
Rushoon	97.2 (18)	100.0 (18)	108.0 (54)	100.0 (33)	E	1,2
Tote	62.5 (6)	80.0 (6)	82.8 (49)	37.5 (39)	E	1,2
Highlands	82.7 (82)	55.0 (58)	109.8 (64)	52.4 (31)	E	3
Little Codroy	85.9 (2574)	71.5 (1654)	115.6 (877)	84.0 (526)	E	3
Northwest	90.5 (45)	95.2 (22)			E	3
Southwest	78.3 (43)	84.0 (29)			E	3
Wings	76.3 (55)	79.3 (35)			E	3
Western Arm	75.4	3.9 (214)	109.0	41.1 (170)	E	3
Quebec						
Bouleau	83.6 (48)	13.0 (86)	112.9 (80)	35.9 (84)	S	4
Pigou	96.2 (53)	37.5 (39)	133.8 (32)	63.1 (26)	S	4
Matamek	85.9 (158)	62.6 (239)	125.6 (292)	64.7 (209)	F,S,A	5,6,7
Corneille	98.9 (39)	38.3 (76)	148.5 (16)	80.0 (36)	S,A	6
Manitou	76.3 (3)	36.0 (3)	114.9 (41)	82.3 (20)	S,A	6
Mistassini	76.1 (47)	9.7 (59)	108.9 (29)	100.0 (26)	S,A	6
Moisie	63.1 (36)	0.0 (388)	89.9 (25)	0.7 (580)	S,A	6
Puyjalon	71.3 (46)	0.0 (45)	117.1 (17)	100.0 (10)	S,A	6
Ste. Marguerite	66.3 (8)	16.7 (11)	93.5 (32)	35.0 (33)	S,A	6
St. Jean	54.2 (23)	0.0 (23)	74.3 (29)	11.1 (34)	S,A	6
Watshishou	89.3 (64)	40.8 (58)	120.2 (35)	25.0 (28)	A,G	8
Nova Scotia						
Margaree	85.8 (82)	75.0 (45)	110.8 (32)	90.9 (12)	E	3
New Brunswick						
Miramichi	93.9 (380)	60.5 (276)	114.4 (210)	63.4 (153)	E	9
Restigouche	82.0 (212)	22.0 (178)	111.0 (30)	68.4 (25)	E	10

^aE = electrofishing; S = seining; G = gill netting; A = research angling; F = fyke netting.

^b1, Dalley 1979; 2, Dalley et al. 1983; 3, L. Marshall, Department of Fisheries and Oceans, Halifax, N.S.; 4, Randall and Power 1979; 5, Schiefer 1969; 6, Schiefer 1971; 7, R. J. Gibson, unpubl. data; 8, Riley et al. 1984; 9, Schofield and Peppar 1982; 10, R. Randall, Department of Fisheries and Oceans, Moncton, N.B.

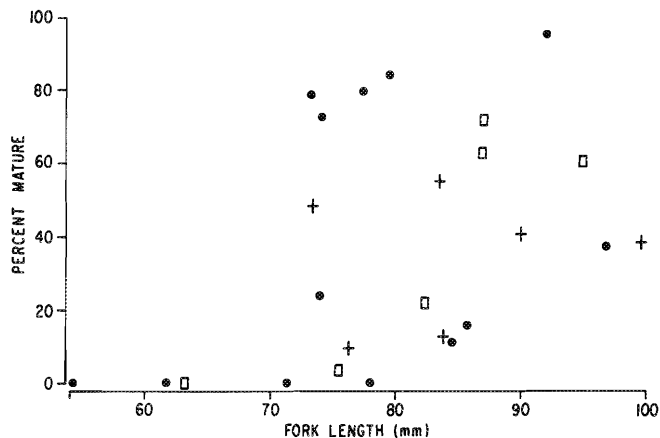


FIG. 1. Proportion of 1+ male parr that mature as a function of mean length of 1+ fish in August for North American rivers listed in Table 3 (populations with sample size between 20 and 50 (●), between 50 and 100 (+), and over 100 (□)).

tures would be $1-\lambda$ as long as it would be were it not to mature. If our assumption holds, the mean size of male and female parr at the time some males are maturing is the same, and

$$(2) f = (1 - q) m_i + \frac{q}{(1 - \lambda)} m_p$$

where f = mean fork length of 1+ female parr, m_i = mean fork length of 1+ immature male parr, m_p = mean fork length of 1+ mature male parr, and q = proportion of mature parr within the male population. Note that $m_p/(1 - \lambda)$ is the mean fork length 1+ mature males would have achieved if they had not matured. The reduction in length was thus estimated to be

$$(3) \lambda = 1 - \frac{q m_p}{f - (1 - q) m_i}$$

Data from seven years (1957–63) were available from the Little Codroy River to calculate growth reduction. A comparison of the cumulative distribution of fork lengths of males and females showed that these distributions were significantly different in six of seven years (Kolmogorov–Smirnov test, $P < 0.05$). All years except 1963 showed a reduction in growth of mature males (Table 2). There was an average 4.0% (1.9–6.5%) reduction in length (~3.6 mm) associated with male parr maturation. Since this reduction took place only during the second year of life, the reduction in yearly growth during the year the parr matured was approximately 8%.

It is possible that parr maturation alters some other feature of the distribution of fork lengths. To test this hypothesis, each mature 1+ male fork length was multiplied by $1/(1-\lambda)$ and then combined with the distribution of immature male parr. This modified distribution of male fork lengths was compared with the female distribution by quantile–quantile plots (Wilk and Gnanadesikan 1968) and Kolmogorov–Smirnov tests. There was no systematic or significant ($P > 0.05$) deviation of the modified male lengths from the female distribution.

Among-Population Comparisons of Parr Maturation

The purpose of this analysis was to describe the covariation in growth and maturation of male parr among 27 salmon populations in eastern North America (Table 3) and to determine if there were any significant differences among populations in

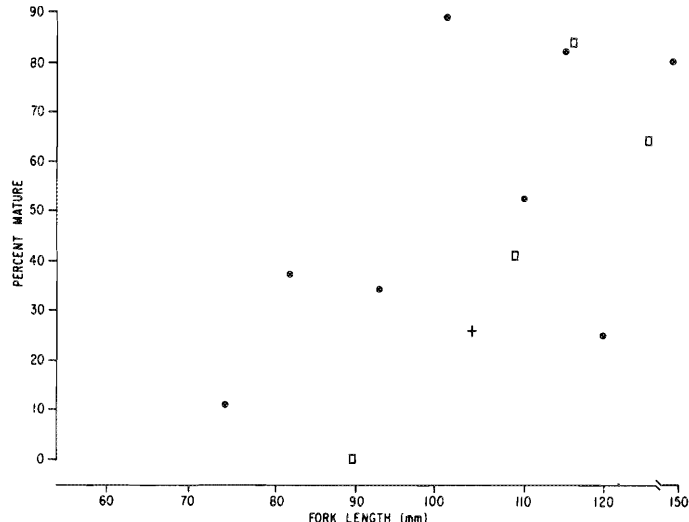


FIG. 2. Proportion of 2+ male parr that mature as a function of mean length of 2+ fish in August for North American rivers listed in Table 3 (populations with sample size between 20 and 50 (●), between 50 and 100 (+), and over 100 (□)).

the incidence of male parr maturity once the effect of growth rate had been removed.

To avoid the confounding bias of reduced growth caused by maturation, mean female length was used in the analysis if it was available. If not, then the mean lengths were modified by using the estimated mean proportion of the males maturing, q , observed in the population and the proportional reduction in length caused by maturation, λ . Let the mean length observed in a population be X . We need a coefficient that when multiplied by the mean length observed in the population, X , approximates the mean length of females in the population. If we make the simplifying assumption that immature males grow at approximately the same rate as females, we have

$$(4) X = \frac{1}{2}f + \frac{1}{2}\{(1 - q)f + qf(1 - \lambda)\}$$

where, as before, we have assumed a 1:1 sex ratio. A coefficient, γ , is required such that

$$(5) \gamma X = f.$$

Rearranging the above two equations yields the correction factor

$$(6) \gamma = \frac{2}{2 - q\lambda}.$$

There appears to be a size threshold (≈ 72 mm at the end of the second year of life) below which males are not likely to mature (Fig. 1). Data were log-transformed and analysed using a probit regression (Finney 1971). The slope of the regression was significant ($P < 0.05$), indicating a positive covariation between growth and maturation among rivers. However, the fit of the data to the model was not good ($\chi^2 = 1153.0$, $df = 21$, $P < 0.0001$). The χ^2 was recalculated after excluding the St. Jean River population (the only population with an expected cell frequency less than five) and was still highly significant ($\chi^2 = 1152.0$, $df = 20$, $P < 0.0001$). The among-population variation remained high significant ($P < 0.0001$) following application of the maximum heterogeneity factor (5.2).

There was a significant correlation between size and maturation for parr maturing at age 2+ although a size threshold

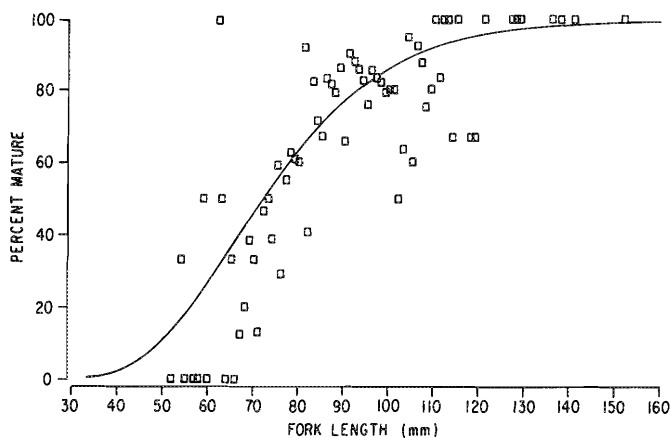


FIG. 3. Maturation versus length relationship of male parr within the Little Codroy population (line represents probit regression of log-transformed data).

was not apparent (Fig. 2). These data should be interpreted with caution, however, because many parr smoltify at age 2.

Within-Population Variation

Size before maturation was estimated for 1275 male parr of the Little Codroy River population (1957–63 years combined). For χ^2 goodness of fit tests, fork length (millimetres) classes were combined such that expected cell frequencies of males exceeded five.

The pattern of length-specific maturation for 1+ parr in the Little Codroy was similar to that observed for the among-population data. The probit analysis indicated a size threshold of ≈ 70 mm, below which males were not likely to mature (Fig. 3). There was a much better fit of the within-population data to a probit regression on log-transformed length ($\chi^2 = 122.1$, $df = 58$, $P < 0.0001$) than there was in the among-river comparison.

Yearly Variation in Parr Maturity and Growth

We examined data from the Matamek (1967–78) and Little Codroy (1957–63) rivers, the only two North American populations with time series of data on parr maturation, to determine the degree to which the incidence of parr maturity has varied over time within populations. In both rivers, maturation first occurs at 1+ and smolt ages are predominately 2, 3, and 4 (Murray 1968a, 1968b; Gibson 1978; Myers 1984). Parr used in the Matamek analyses were collected in the areas below the third and fourth falls of this river. Before the successful introduction of non-Matamek salmon fry into the river in 1978 and 1979, only one 1+ mature male parr was collected below the second falls. Furthermore, spawning does not occur below these falls (R. J. Gibson, pers. obs.), and their 7-m height (Power et al. 1973) precludes upstream migration of parr to the spawning grounds. Parr collected below the second falls, then, were excluded from the analyses. Post-1978 data from the Matamek River were excluded because of the successful introductions of non-Matamek salmon fry into the river in 1978 and 1979.

The among-year pattern of variation in parr maturation (Fig. 4) is similar to the within-year pattern for the Little Codroy River (Fig. 3) and the among-population pattern

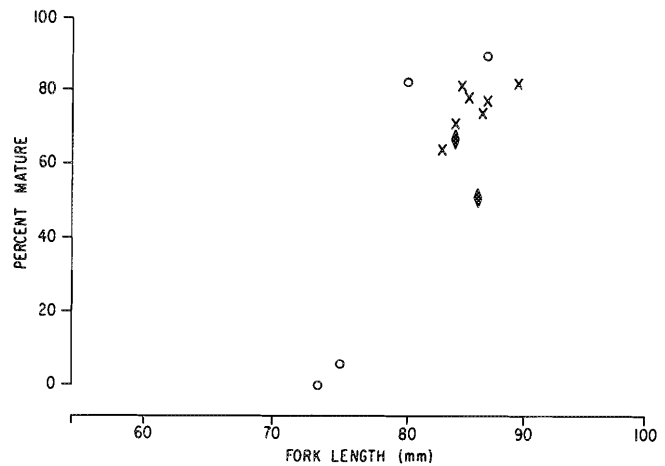


FIG. 4. Proportion of 1+ male parr that mature versus fork length of male parr in the population (Little Codroy River (x), Matamek River below third falls (O), and below fourth falls (◆)). Years in which sample size was less than 10 were not plotted.

(Fig. 1). Again there appears to be a threshold level of size required for maturation as a parr.

For the Little Codroy River population we could also calculate the proportion of 2+ males that mature as parr for four cohorts because Myers (1984) was able to estimate the mortality associated with parr maturation and the proportion of 1+ and 2+ parr that smolted and matured. Thus, we could determine if there was evidence that yearly changes in growth rate affected the proportion of *all* males that mature as parr within a cohort. We found no evidence that increased growth during the first year of life increased the total proportion of male parr that mature. In fact, the data suggest that increased growth during the first year of life is associated with a decreased proportion of males maturing at age 2 (Fig. 5).

Evolutionary Changes in Parr Maturation

It has been suggested that the proportion of mature male parr increases within populations that experience high mortality at sea (Gibson 1978; Montgomery 1983). One explanation for this increase is that intense fishing pressure should favour those genotypes that mature in freshwater, thereby avoiding mortality at sea (Myers 1983; Caswell et al. 1984). We examined the residuals of the probit regression of percent parr maturity on growth from the Matamek (1967–78) and Little Codroy (1957–63) rivers to determine if that percentage has increased independent of changes in growth rate. A plot of the residual variation in parr maturation, using the probit regression generated from the Little Codroy River population, shows no obvious pattern with time for the Matamek population (Fig. 6). Similarly, there was no apparent trend with time in the residuals in the Little Codroy River population. The robustness of our conclusions were tested by calculating the residuals from the among-river (Fig. 1) and within-population (Fig. 4) probit regressions of maturity on length. Again, no relationship with time was evident.

Discussion

There is a common pattern in the covariation of maturation and growth in salmon parr within and among populations and among years; few male parr mature below 70–72 mm in

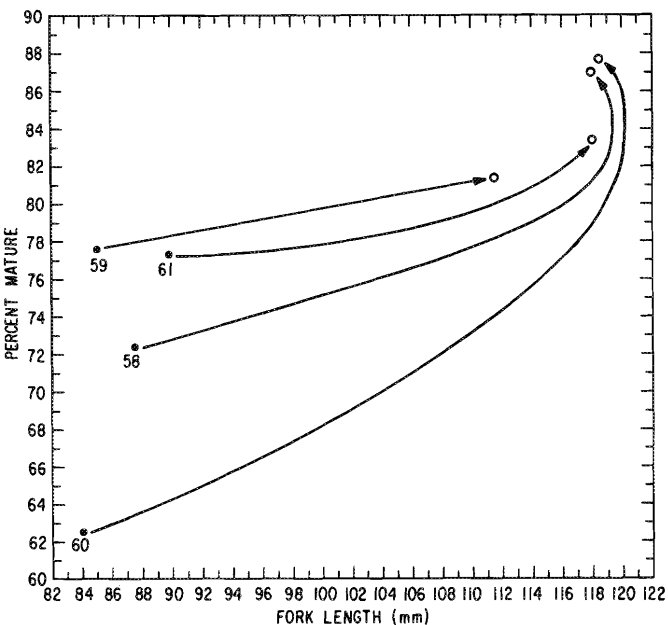


FIG. 5. Incidence of maturity for 1+ male parr (●) and the incidence for 1+ and 2+ parr (○) versus the mean length of 1+ and 2+ parr for the Little Codroy population. Data are plotted by year of hatching.

length. Although the idea that there is a "critical length" for maturation is clearly simplistic, it is an adequate first approximation in describing parr maturation. Perhaps this critical length is required before sufficient energy stores are available for maturation and subsequent winter survival. This hypothesis could be tested by examining the distribution of sizes of mature males before reproduction, e.g. in August, and after winter survival in the spring. If there is size-dependent overwinter survival, then there should be a shift in the size distribution of summer-to-spring samples. An alternative hypothesis is that parr size is crucial in the establishment of the dominance hierarchy among male parr downstream of a spawning sea-run pair (Myers and Hutchings 1986). This hypothesis could be tested by examining the proportion of eggs fertilized by mature male parr of different sizes using electrophoretic markers.

Although growth has a great effect on the proportion of males that mature at 1+, it is clearly not the only factor involved. The highly significant χ^2 values from the probit regressions, which resulted after accounting for length effects and data heterogeneity, suggest that a large amount of the variation in maturation cannot be explained by length alone. The significant heterogeneity within populations is consistent with evidence for additive genetic variation in parr maturation (Naevdal et al. 1976). Similarly, the great among-population variation in parr maturation suggests either that the evolutionary pressures on parr maturation vary among populations or that alternative evolutionarily stable strategies exist within populations (Myers 1986). The evolutionary mechanism leading to this among-river variation warrants further study.

Although among-year variation in growth during the first year of life affects the proportion of 1+ males that mature, we found no evidence that increases in growth rates increase the total proportion of male parr that mature within a year-class, since a male parr not maturing at 1+ may mature later. Such factors need to be considered in constructing stock-recruitment models.

Changes in the proportion of male parr maturing in the

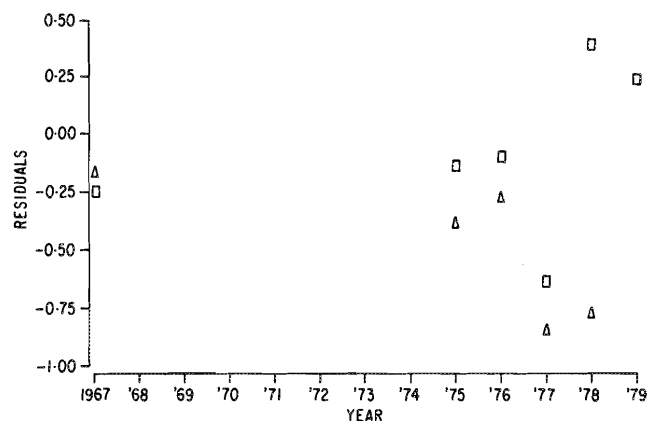


FIG. 6. Residuals from probit regression (from Little Codroy population, see Fig. 3) of proportion mature versus length in the first year, by year, in the Matamek River (□, third falls; △, fourth falls).

Matamek River population can be accounted for by changes in growth alone. There is no evidence that the proportion of mature parr in the Matamek that has been increasing in recent years is a genetic change caused by increased commercial fishing pressures as proposed by Montgomery (1983) and Caswell et al. (1984), who did not consider the relationship between growth and maturation. Given a generation time of 4–5 yr for Atlantic salmon, significant short-term (5–15 yr) increases in the proportion of mature parr in a population would reflect extremely high selection intensities and heritabilities for parr maturation.

It is difficult, or impossible, to achieve random sampling in rivers because of extreme among-site variation. We have mitigated this problem by estimating the degree of heterogeneity in the proportion of males maturing in two intensively sampled rivers, and using this "heterogeneity factor" to interpret the accuracy of our data. It was found that the assumption of simple random sampling was not appropriate for our data but that quantitative comparisons could be made once the heterogeneity was accounted for. Spurious results could arise from a failure to utilize such within-population information.

Acknowledgments

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