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Source: *Ecology*, Vol. 56, No. 3 (May, 1975), pp. 577-590

Published by: Ecological Society of America

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## THE ADAPTIVE SIGNIFICANCE OF VARIATIONS IN LIFE HISTORY AMONG LOCAL POPULATIONS OF ATLANTIC SALMON IN NORTH AMERICA<sup>1</sup>

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**Abstract.** In this paper variations in life history data among local populations of Atlantic salmon have been examined. The following patterns emerge: (1) The mean age of first spawning increases with the difficulty of upstream migration as estimated by the distance the fish ascend into freshwater. Other indices of river harshness yield similar results. (2) The effect of commercial fishing has been to eliminate larger and older fish from the run. Available evidence suggests that this has selected for an early age of first return on the Miramichi River and that the frequencies of genes coding for different ages of first spawning have been altered. (3) The mean age of first spawning is positively correlated with marine growth rates after the grilse stage. Rapid growth at sea subsequent to the grilse stage is associated with delayed reproduction; slower growth with an earlier age of first breeding. This result suggests different paths of high-seas migration. (4) The variability about the mean age of first spawning first increases and then decreases as one moves north over the salmon's range from Maine to Ungava.

In addition, we have observed that these results are in accord with predictions made by recent theoretical analyses of the optimal reproductive response to differing environmental conditions. We, therefore, conclude that the observed patterns of variation in life history are adaptive. We further take the agreement between theory and nature as a validation of the hypothesis that populations will in general differ from each other in the manner of their respective optima.

**Key words:** Atlantic salmon; evolution; life history, salmon; reproductive strategies, salmon; spawning age, salmon; theoretical ecology.

### INTRODUCTION

Early studies (Cole 1954, Lewontin 1965) of the evolutionary consequences of life history phenomena stressed the importance of high fecundity and early maturation as efficient means of increasing an organism's Malthusian (Fisher 1930) fitness. More recently, Gadgil and Bossert (1970) have observed that optimal life histories often involve delaying the age of first reproduction beyond the physiological minimum. Specifically, (Schaffer 1974a) environmental factors reducing the fecundity of adults per unit reproductive effort or the survival of their progeny will have this effect. Conversely, reductions in post-breeding survival and growth per unit effort will select for increased reproductive investment at all ages and a lowering of the age of first breeding. We test these predictions using data compiled for various local populations of Atlantic salmon (*Salmo salar*, L.) in eastern North America. (Fig. 1 is a map of the salmon's distribution and the locations of some of the salmon rivers referred to in this paper.)

Most populations of Atlantic salmon are anadromous (Jones 1959). Spawning occurs in freshwater streams where the young (fry and parr) grow to the smolt stage. However, the adult phase of the life cycle is spent feeding at sea. Recent tagging studies (Elson 1969, 1970, Stasko et al. 1973) suggest a path of migration that takes many of the fish from the American coast north and east to the Davis Strait off Greenland and then south and west back to the parent streams. Preliminary evidence also suggests that local populations are at least partly isolated from each other genetically (Møller 1970), this resulting from the fishes' tendency to spawn in the stream of their origin (Jones 1959). Straying is relatively infrequent (Elson 1969, 1970), and what is perhaps more remarkable, the adults appear to home to that part of the river in which they resided as juveniles (Saunders 1967). Thus, there appears to have been opportunity for local populations to have become differentiated from each other as a result of natural selection. We believe that such selection has contributed to the great variations in the mean age of first spawning as well as the variance about this figure that exist among the different river stocks. For example, nearly all the fish of the

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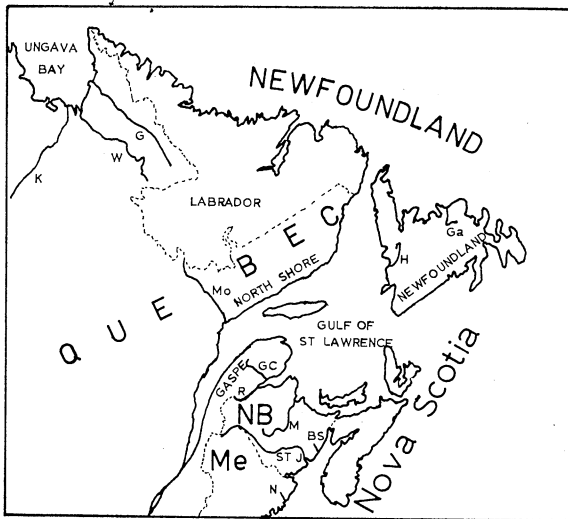


FIG. 1. Distribution of Atlantic salmon in North America, showing major salmon rivers discussed in text. BS, Big Salmon; G, George; Ga, Gander; GC, Grand Caspédia; H, Humber; K, Koksoak; M, Miramichi; Mo, Moisie; N, Naraguag; R, Restigouche; St. J, St. John; W, Whale.

Naraguag River in Maine spend 2 yr at sea before returning to spawn (Meister and Cutting 1967). On the other hand, the bulk of the first spawners on the Big Salmon River in New Brunswick are grilse—fish that have been in the ocean for a single winter; but in this river the standard deviation about the mean age of first spawning is much higher (0.45 vs. 0.18). Taking still a third river, the Moisie, in Québec, we find that the most abundant class of virgin fish have spent 3 yr at sea (Schiefer 1971). Here again there is considerable variation ( $\sigma = 0.58$ ) about the mean age which is 2.6 sea-years.

These differences appear real and not simply the result of differential exploitation by fisheries. Commercial fishing, however, has had profound effects upon some stocks both with regard to total population and to the age composition of spawners (Saunders et al. 1965, Allen and Saunders 1966, Kerswill 1971, Elson 1972, Paloheimo and Elson 1974), and we shall present data suggesting that in at least one river, the Miramichi, in New Brunswick, this has resulted in changes in the frequencies of genes affecting the age of first spawning.

#### THEORY AND PREDICTIONS

Since Cole (1954) first suggested that ecologists might profitably search for adaptive meaning in life history variations among related populations, considerable attention has been focused on predicting the manner reproductive rates should vary with environmental circumstance if breeding is adjusted to

maximize individual fitness (for example, Gadgil and Bossert 1970, Schaffer 1974a). Briefly, as first suggested by Cody (1966), the problem is one of best allocating an organism's finite resources—time and energy—to growth, maintenance and reproduction.<sup>3</sup> The optimal proportion of resources allocated to breeding—reproductive effort—depends on the return to fitness, measured in offspring that themselves survive to reproduce, relative to the returns in survival and increased future fecundity resulting from increased allocations to maintenance and growth. Specifically, an optimal life history maximizes, for all ages  $i$ , the sum

$$B_i + p_i (V_{i+1}/V_0) \quad (1)$$

(Schaffer 1974a) where  $B_i$  is the effective fecundity of an  $i$ -yr-old;  $p_i$  is the probability of survival from age  $i$  to  $i+1$ ; and  $(V_{i+1}/V_0)$  the reproductive value (Fisher 1930) of an  $i+1$ -yr-old. Analysis (Schaffer 1974a) of this condition yields two relevant results. First, environmental factors increasing reproductive success,  $B_i$ , per unit reproductive effort will select for greater reproductive effort at all ages and at the same time an earlier age of first reproduction. This is true if the effect is the same for all age classes, or, as is likely in the case we will consider, if younger individuals are more sensitive to such changes than older ones. Conversely, increased post-breeding survival and growth per unit effort will favor reduced effort at all ages and a later age of first reproduction.

For salmon, we translate these results to predict first that long, fast rivers requiring a large expenditure of energy to reach the spawning grounds (Foerster 1968) will select for a longer period of feeding at sea and hence for delayed breeding, whereas short, easy rivers should be typified by reproduction at an earlier age. Consistent with this prediction are observations by Weaver (1963, also Hartman 1969) on several species of salmonids indicating that larger fish are able to swim further and for longer periods in a current than smaller individuals. Additionally, Kerswill has observed that late-run fish on the Miramichi River enjoy post-spawning survival rates substantially higher than those of their early-run counterparts. In this river early-run fish spawn mostly in the headwaters (Saunders 1967) and thus penetrate further into fresh

<sup>3</sup> Because these resources are limited, it is customary to assume an inverse relation between the intensity of breeding at a given stage in an organism's life cycle and subsequent growth and survival. Evidence consistent with this assumption has been summarized by Calow (1973) for a variety of species. In Atlantic salmon, post-spawning mortality is often high (Belding 1934) and repeat spawners are often smaller than virgin fish of the same age (Table 8).

TABLE 1. Comparison of scale data (age) and angling statistics (weight)

Province	River	Year	Sample <sup>a</sup>	$\bar{x}$ age 1st spawning (yr)	$\bar{x}$ wt angling catch (lb)
New Brunswick	St. John Big Salmon	1967	Trap (743)*	1.4	6.7
		1968	Fence (703)*	1.2	5.5
		1969	Fence (92)*	1.6	7.4
		1970	Fence (276)*	1.0	5.9
	N.W. Miramichi	1967	Fence (394)*	1.2	4.4
Nova Scotia	Petite	1970	Angling (75)	1.0	4.0
	West	1967	Fence (87)*	1.0	3.8
		1968	Fence (120)*	1.1	3.4
Quebec	Moisie P. Saguenay	1969	Angling (913)	2.6	18.4
		1967	Angling (119)	2.0	10.9
		1968	Angling (60)	1.6	6.2
		1969	Angling (62)	1.4	5.9
	Ste. Marguerite	1969	Angling (192)	2.0	7.8
Newfoundland	Exploits	1963	Trap (900)*	1.0	4.5
	Little Codroy	1954-1963	Fence (1218)	1.4	7.8

<sup>a</sup>\*: A significant (> 50%) sample of the run.

$r = .913$ ;  $P(r) < 0.0005$ —all data.

$r = .784$ ;  $P(r) < 0.01$ —"\*" data.

Numbers in brackets refer to sample size; fence—a counting fence that catches almost all the run; trap—fish trap such as on a fishway, takes most of the run; angling—a portion of the angling catch examined for scale readings.

water than late-run salmon, which generally spawn further downstream.

A second prediction is that stocks characterized by high rates of growth at sea subsequent to the age of first possible spawning should be characterized by higher ages of first spawning than populations exhibiting lower oceanic growth rates. On the other hand, highly exploited stocks should be characterized by early breeding because the commercial nets differentially take the larger (i.e., older) individuals (Murray 1968, Allen et al. 1972), as they enter the home river.

Finally, analysis of simple life histories neglecting age structure suggests that if the expectation of survival from egg to adult varies from year to year, selection will favor populations in which adults first spawn at different ages (Schaffer 1974b, Cohen 1966; a different point of view is found in Wynne-Edwards 1962). If all years are uniformly good or bad, there is no merit to this. However, if there is a mix, it may be advantageous for a fish having a life cycle similar to the salmon to produce progeny programmed to spend differing periods at sea. Intuitively, one might expect that the frequency of unfavorable years increases as one moves north along the salmon's range from Maine to the Ungava Peninsula, where, as Power (1969) observes, the gravel in which the fish spawn "are most susceptible to drying and freezing during the prolonged winter." Unfortunately, quantitative data bearing on this point are not available. On the other hand, in North America the mean number of years that juveniles reside in the river increases markedly with

latitude (Elson 1957), being about 2 yr in Maine (Meister and Cutting 1967) and 5 to 6 yr in Ungava (Power 1969). So even if the frequency of unfavorable years does not increase with latitude, the chances of a given fish's offspring being exposed to one do increase. Accordingly we expect the variance about the age of first spawning either to increase monotonically with latitude or to first increase and then decrease. The latter should be the case if at high latitudes the probability of a fish's progeny being exposed to a bad winter is very high.

#### MATERIALS AND METHODS

Two types of data were used for testing these predictions. The first, and most desirable, were obtained from records kept at counting fences and traps on fishways. In such cases, scale samples are taken from a significant proportion of the run, enabling a precise determination of the spawning history and growth rate of each fish. Unfortunately, such information was available to us for only about a dozen rivers.

Far more abundant, are the so-called "creel" censuses which annually give a minimal count of the salmon angled on nearly every Canadian river and their total weight. These data are clearly less desirable. However, because the percentage of repeat spawners is generally low, and because the weight of virgin fish dramatically increases with sea age, the mean weight of angled fish as determined from the creel censuses is generally well correlated with the mean age of first spawning on rivers for which both types of information are available (Table

TABLE 2. Angling statistics

River	Years	Fish/yr		Wt/fish (lb)		Nets	River length (mi)
		Mean	SD	Mean	SD		
Gaspé Peninsula <sup>a</sup>							
Grand	1964-69	109	51	10.9	1.4	11	20
Bonaventure		304	181	10.2	2.9	23	30*
York		174	74	11.0	1.3	45	40*
St. Jean		144	40	8.2	0.5	45	36*
P. Cascapedia		41	26	8.7	0.9	23	18*
G. Pabos Ouest		18	10	6.1	1.9	11	8
Dartmouth		84	27	10.3	2.6	45	13*
Mal Baie		16	12	4.9	1.3	11	11*
G. Cascapédia	1963-70	53	15	18.5	2.8	64	51*
South Shore, Gulf of St. Lawrence <sup>a</sup>							
Ste. Anne	1964-69	47	30	12.3	0.8	13	25
Madeleine		30	24	9.2	4.3	17	7
Cap-Chat		28	17	12.1	2.4	13	12
Matane	1965	755	—	8.4	—	20	31*
Mitis	1964-69	24	6	12.9	3.2	20	7
Anticosti Island <sup>a</sup>							
Jupiter	1964-69	1,781	347	6.4	0.4	0	35
Patate		44	32	6.7	0.9	0	9
Salmon		187	36	6.1	0.4	0	12
La Loutre		169	65	5.9	0.4	0	9
Becsie		55	22	5.7	0.4	0	6
MacDonald		135	44	5.0	0.7	0	9
Bay of Chaleur <sup>b</sup>							
Kedgewick	1949-60	504	438	16.0	2.5	119	85
Restagouche		2,680	1,515	14.5	2.5	119	72
Upsalquitch		722	434	8.0	2.5	119	51
Patapedia	1950-53	219	60	10.4	1.1	119	55
Jacquet	1949-60	151	123	4.2	0.8	93	24
Charlo	1962	20	—	5.0	—	93	30
Matapedia	1965-69	184	98	9.2	0.8	119	45
North Shore, Gulf of St. Lawrence <sup>a</sup>							
Watshishou	1964-69	245	84	8.2	0.2	39	20
Natashquan		353	88	10.0	0.7	39	63
Etamamiu	1967-68	377	—	5.4	—	67	30
P. Watshishou	1964-69	146	79	5.3	1.0	39	18
Washicoutai		162	65	9.4	1.9	67	21
Corneille		161	56	5.7	0.6	39	14
Romaine		57	22	11.8	1.3	20	40
Mingan		142	39	8.9	0.6	20	33
St. Jean		537	73	9.9	0.7	20	53
Jupitagon		104	61	5.1	0.8	20	6
Moisie		667	214	18.1	1.6	36	81
Ste. Marguerite <sup>c</sup>		485	151	10.6	2.1	52	43
Godbout		70	41	6.9	1.4	42	45
English		25	29	5.4	1.2	42	3
Mistassini		173	62	5.2	0.7	42	8
Trinite		446	115	5.1	0.3	42	29
P. Trinite		11	7	4.1	0.4	42	7

\* Length determined by survey; other lengths taken from ASA map.

<sup>a</sup> Dep. Tourism, Fish and Game, Fish and Game Branch, Québec, P.Q.

<sup>b</sup> Dep. Environ. Canada, Fisheries, Resource Development Branch, Halifax, N.S.

<sup>c</sup> Sacre-Coeur.

<sup>d</sup> Murray and Harmon (1969).

<sup>e</sup> Data not taken.

<sup>f</sup> Data not available.

<sup>g</sup> Notre Dame Day.

TABLE 2. Continued

River	Years	Fish/yr		Wt/fish (lb)		Nets	River length (mi)
		Mean	SD	Mean	SD		
Nova Scotia <sup>b</sup>							
Margaree	1949-60	332	131	10.2	1.5	34	30*
North (Victoria Co.)		137	90	8.1	0.7	15	9
Grand (Richmond Co.)		72	43	4.4	0.6	9	9
St. Mary's		538	336	8.9	1.2	40	32
Ecum Secum		88	39	4.7	0.6	40	8
Liscombe		64	63	5.1	0.8	40	5
Mosers		193	98	4.6	0.4	59	12*
Tangier		34	20	5.5	1.2	59	8
Quoddy		24	15	4.7	0.5	59	3
Port Dufferin		102	49	4.8	0.6	59	4
Kirby		41	24	5.0	0.8	59	*3
Ship Harbor		73	55	6.0	1.1	59	5
Musquadoit		63	40	10.7	2.1	33	32
Ingram		69	39	6.2	1.4	33	5
Gold		93	61	7.1	1.1	45	22
La Have		384	255	7.5	1.2	76	25*
Petite		56	27	5.5	1.1	50	8*
Medway		594	257	7.4	1.3	140	20
Mersey		87	98	7.1	1.3	90	13
Tusket		77	52	8.6	1.0	1	20
Salmon (Digby Co.)		40	20	9.6	0.8	0	10*
Nictaux		87	58	7.8	1.0	0	33
Round Hill		58	39	8.2	0.4	0	7
Lequille		25	18	8.3	1.1	0	9
Annapolis		69	48	8.2	0.7	0	38
West (Sheet Harbor)		332	147	4.9	1.2	59	6*
New Brunswick <sup>b</sup>							
Hammond	1961-62	78	—	6.1	—	149	18
Kennebecassis	1949-60	77	82	6.6	1.7	149	58
Nashwaak		213	194	6.9	1.1	149	60
St. John		1,380	521	6.6	0.8	149	133
Tobique		1,059	704	9.3	2.0	149	213
Big Salmon		71	97	6.7	0.9	44	18
Digdeguash		8	—	7.2	—	4	26
Petit Codiac		29	19	4.3	0.6	44	40
Coverdale		116	82	3.7	0.5	44	42
Millstream		14	7	6.5	1.2	42	20
Middle & Little		99	56	8.4	1.6	42	25
Bartibog		115	67	6.2	1.9	291	28
Tabisintac		1,926	2,085	8.2	0.7	16	32
Tetagouche		46	26	7.8	1.7	42	40
Nipisiquit		609	31	7.2	0.9	42	68
S.W. Miramichi		21,132	7,949	6.1	0.6	373	124
L.S.W. Miramichi		2,371	1,576	5.4	0.2	373	70
N.W. Miramichi		3,524	1,851	5.7	1.9	373	70
Cains		1,548	1,306	6.3	0.9	373	80
Dungarvon		380	231	5.8	0.8	373	70
Renous		1,148	594	5.9	0.8	373	68
Newfoundland <sup>d</sup>							
Anchor Brook	1953-66	1,365	— <sup>e</sup>	4.5	— <sup>e</sup>	— <sup>f</sup>	5
Barachois Bk.		3,073	—	4.3	—	—	7
Baie de l'Eau		855	—	3.8	—	—	5
Biscay Bay		2,685	—	4.1	—	—	13
Branch		1,388	—	5.0	—	—	15
Burnt Is. Bk.		2,471	—	4.3	—	—	8

TABLE 2. Continued

River	Years	Fish/yr		Wt/fish (lb)		Nets	River length (mi)
		Mean	SD	Mean	SD		
Newfoundland <sup>d</sup>							
Castors	1953–66	2,949	— <sup>e</sup>	4.9	— <sup>e</sup>	— <sup>f</sup>	18
Cinq Cerf		747	—	4.4	—	—	12
Conne		588	—	3.7	—	—	20
Crabbes Bk.		457	—	5.4	—	—	27
Exploits		577	—	4.5	—	—	42
Fishels Bk.		231	— <sup>e</sup>	4.8	— <sup>e</sup>	— <sup>f</sup>	25
Flatbay Bk.		883	—	4.1	—	—	47
Fox Island		139	—	6.0	—	—	15
Gambo		207	—	4.6	—	—	33
Gander		1,813	—	4.9	—	—	75
Garnish		23	—	3.6	—	—	7
G. Codroy		554	—	5.5	—	—	20
Grey		152	—	4.8	—	—	20
Harry's		1,288	—	4.5	—	—	38
Highlands		72	—	8.7	—	—	20
Humber		2,496	—	4.7	—	—	68
Indian Arm Bk.		263	—	4.3	—	—	12
Isleaux Morts		125	—	4.5	—	—	8
Lomond		216	—	4.4	—	—	11
L. Barachois		151	—	4.2	—	—	10
L. Codroy		22	—	7.8	—	—	8
Northern Arm <sup>e</sup>		30	—	3.9	—	—	12
Portland Crk.		541	—	5.9	—	—	5
River of Ponds		1,340	—	4.6	—	—	15
Serpentine		210	—	6.3	—	—	18
Southeast		184	—	5.0	—	—	6
S.W. and Bottom		489	—	4.8	—	—	20
Ste. Genevieve		316	—	4.2	—	—	8
Terra Nova		195	—	4.2	—	—	18
Tommy's Arm		57	—	3.6	—	—	4
Torrent		76	—	6.2	—	—	0.5*
Trout		67	—	5.7	—	—	12
Western Bk.		48	—	5.9	—	—	5
Windmill		59	—	4.2	—	—	5

1). Consequently, our strategy is to use the angling data (Table 2) to as great an extent as possible, supplementing this with information from counting fences (Table 3) where appropriate.

As an index of the difficulty of upstream migration, we used the distance the fish ascend into freshwater given by the Atlantic Salmon Association's (ASA) 1967 map of salmon distribution. Where possible this information was supplemented by surveys of the major spawning localities and discussions with local fishery scientists and wardens. The ASA map was also used to estimate the intensity of commercial fishing outside the various rivers in Maine, Nova Scotia, New Brunswick, and Québec. (In Newfoundland, neither the map nor local fisheries officials could provide sufficient detail to make such estimates meaningful and this information was not used.) The angling statistics, river lengths, and the

number of nets associated with each stream are presented in Table 2. For those populations for which scale data were available, growth rates at sea were estimated by comparing the fork lengths (head to notch in tail) of the different age classes of virgin spawners (Table 4).

## RESULTS

### *River length and commercial fishing*

Plotting the mean weight of the angled fish against river length (Fig. 2A, B, C, D) yields mixed results. In some regions (e.g., Bay of Chaleur, North Shore of the Gulf of St. Lawrence, Gaspé Peninsula) the correlation is very high (.87-.98), and the regression line quite steep (0.14-0.20 lbs/mile). In Nova Scotia, a lesser ( $r = .69$ ) but still highly significant ( $P(r) < .001$ ) correlation is observed, and the re-

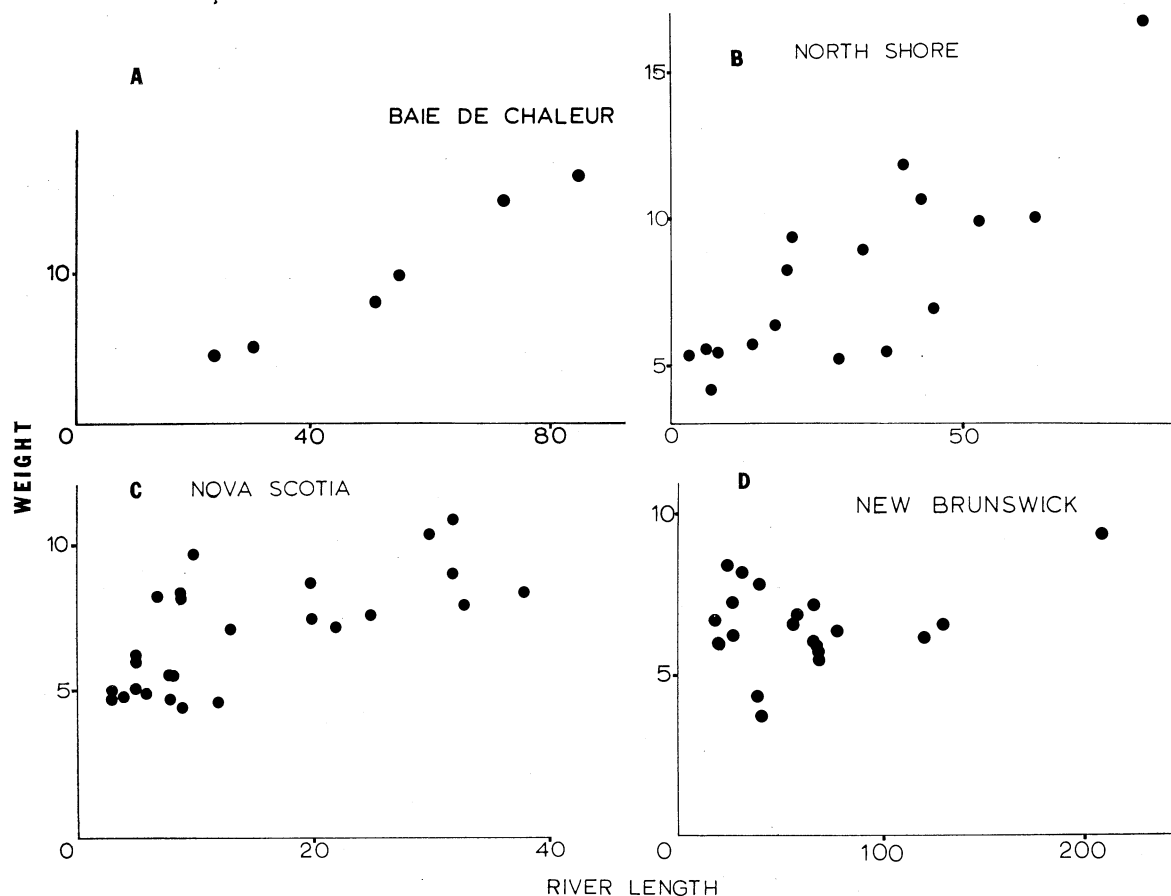


FIG. 2. The mean weight of angled fish plotted against river length for four regions: (A) Bay of Chaleur (1949–1960).  $r = .98$ ;  $P(r) < .001$ . Slope of regression line,  $m = .20$  lbs/mile. (B) North Shore of Gulf of St. Lawrence (1964–1969).  $r = .87$ ;  $P(r) < .001$ ;  $m = .14$  lbs/mile. (C) Nova Scotia (1949–1960).  $r = .69$ ;  $P(r) < .001$ ;  $m = .12$  lbs/mile. (D) New Brunswick (1949–1960).  $r = .29$ ;  $P(r) > .10$ ;  $m = .01$  lbs/mile. Data from Table 2.

gression line is less steep (0.12 lbs/mi). On the other hand, a positive, but not significant correlation ( $r = .29$ ;  $P(r) > .10$ ) was observed in New Brunswick, and in Newfoundland, there is no correlation at all ( $r = .02$ ;  $P(r) \gg .10$ ). These results are not wholly unexpected since the Québec stocks have probably been less seriously exploited than those of other regions and the rivers themselves not so disturbed. Schiefer (1971) has reproduced long-term angling records kept by the Moisie Salmon Club. These indicate little change in the age composition of the spawning runs on the Moisie from 1930 to 1970. Such is probably not the case in southern and central New Brunswick. Recent studies indicate a drastic reduction in the abundance of 2- and 3-yr virgin fish on the Miramichi (Elson 1972), and this trend probably holds in some degree for all the rivers in the region. We can only infer, since commercial fishing has been prosecuted with great vigor for nearly two centuries, that in its primeval state,

the Miramichi had an even greater abundance of larger fish than Huntsman (1939) noted in the 1930's. Similarly, it is possible that the current extremely high ratio of grilse to older fish in the longer rivers of Newfoundland (e.g., Humber—68 miles long, Gander—75 miles) is a consequence of preferential removal of the larger (older) fish by the commercial fishery.

The importance of commercial fishing is made more apparent by noting that the slope of the regression line (mean weight of angled fish vs. river length) varies inversely with the intensity of estuarial netting (Fig. 3). To better assess the joint effects of river length and fishing pressure, we performed bivariate regression analyses (Table 5) comparing the mean weight of the angled fish with these two variables. In Québec and Nova Scotia, river length accounted for roughly half of the observed variance with fishing pressure adding another 4% or 5%. In New Brunswick, on the other hand, the number



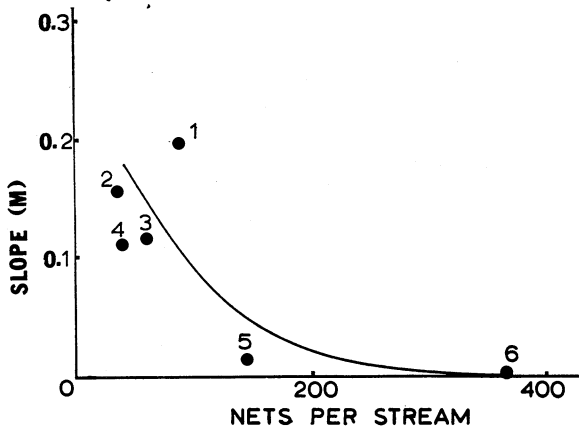


FIG. 3. Slope,  $m$ , of regression line: mean weight angled fish vs. river length plotted against the number of estuarial nets for six regions: (1) Bay of Chaleur; (2) South Gaspé (Québec); (3) North Shore Gulf of St. Lawrence; (4) Nova Scotia; (5) St. John river system (New Brunswick); (6) Miramichi river system (New Brunswick). Data from Table 2.

of commercial nets accounted for 17% of the cumulative variance whereas river length only added 8%.

#### Post-grilse growth rates at sea

Table 4 summarizes the sizes for different age classes of virgin fish for all the rivers for which

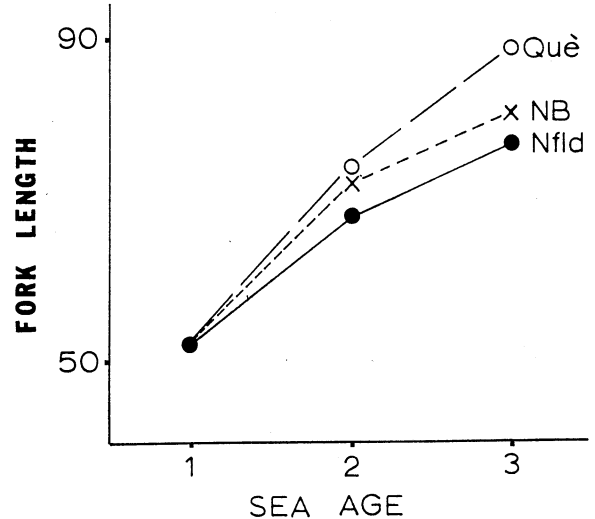


FIG. 4. Fork length vs. sea age for rivers of different regions. Slopes of regression lines are—Québec, 18.5 cm/yr; New Brunswick, 14.8; Newfoundland, 12.5. New Brunswick measurements adjusted to grilse fork length = 52 cm by subtracting 2 cm from average fork length of each age class. Data from Table 4.

we were able to obtain data. Because salmon first spawning at different ages grow at approximately the same rate in the ocean (Jones 1959, cf. our discussion), we can estimate the rate of sea growth

TABLE 3. Composition of spawning runs

River	State or province	Latitude (°)	Method of capture	Sample	Grilse (%)	Percent composition of spawning runs				SD*
						2 Sea-yr (%)	3 Sea-yr (%)	Repeats (%)		
Naraguagus <sup>a</sup>	Maine	44½	Fishway trap	1,045	1	88	2	9	.18	
Machias <sup>a</sup>	Maine	44½	Fishway trap	531	3	84	3	10	.26	
Petite <sup>b</sup>	Nova Scotia	44	Angling	143	94	2	0	4	.14	
West <sup>b</sup>	Nova Scotia	45	Counting fence	206	93	6	0	1	.24	
Big Salmon <sup>b</sup>	New Brunswick	45	Counting fence	1,680	33	5	1	61	.45	
St. John <sup>b</sup>	New Brunswick	46½	Trap	1,762	61	32	1	6	.51	
N.W. Miramichi <sup>c</sup>	New Brunswick	47	Counting fence	394	73	22	1	3	.46	
P. Saguenay <sup>d</sup>	Québec	48	Angling	252	52	36	12	0	.70	
Grand <sup>d</sup>	Québec	48	Angling	58	59	40	1	0	.52	
Ste. Marguerite <sup>d, e+</sup>	Québec	48½	Angling	636	21	44	32	4	.73	
Mistassini <sup>e</sup>	Québec	49	Angling	158	30	70	0	0	.46	
Mingan <sup>e</sup>	Québec	50	Angling	949	9	82	6	3	.39	
Romaine <sup>e</sup>	Québec	50	Angling	253	17	60	19	4	.62	
Godbout <sup>e</sup>	Québec	50	Angling	633	20	78	0	2	.41	
Corneille <sup>d, e</sup>	Québec	50	Angling	345	27	70	0	3	.45	
Matamek <sup>e</sup>	Québec	50	Angling	327	67	32	0	1	.47	
St. Jean <sup>e</sup>	Québec	50	Angling	101	2	81	15	2	.39	
Moisie <sup>e</sup>	Québec	50½	Angling	913	4	26	58	12	.58	
Whale <sup>f</sup>	Québec (Ungava)	57	Commercial ±	169	16	84	0	0	.37	
George <sup>f</sup>	Québec (Ungava)	57	Commercial ±	118	5	92	0	3	.22	
Koksoak <sup>f</sup>	Québec (Ungava)	57	Commercial ±	106	4	96	0	0	.20	
Exploits <sup>g</sup>	Newfoundland	49	Fishway trap	963	88	2	0	10	.15	
L. Codroy <sup>h</sup>	Newfoundland	47½	Counting fence	1,218	63	26	5	6	.59	
Sandhill <sup>g</sup>	Newfoundland (Labrador)	54	Fishway trap	1,989	90	9	0	1	.29	

<sup>a</sup> At Sacre-Coeur.

<sup>b</sup> These data biased against grilse.

<sup>\*</sup> Standard deviation of mean age of first spawning.

<sup>a</sup> Meister and Cutting (1967).

<sup>b</sup> Dep. Environ. Can. Fisheries, R.D.B., Halifax, N.S.

<sup>c</sup> Dep. Environ. Can. Fisheries, F.R.B., St. Andrews, N.B.

<sup>d</sup> Dep. Tourism, Fish & Game, Fish & Game Branch, Quebec, P.Q.

<sup>e</sup> Schiefer (1971).

<sup>f</sup> Power (1969).

<sup>g</sup> Dep. Environ. Can. Fisheries, R.D.B., St. John's Nfld.

<sup>h</sup> Murray (1968).

TABLE 4. Length-age class relations

River	Sample size	Fork length (cm)			M <sup>a</sup>	Mean age 1st spawning
		Grilse	2 Sea-yr	3 Sea-yr		
Newfoundland						
Sandhill	1,971	54	72	79	12.5	1.1
Exploits	961	52	66	79	13.5	1.0
L. Rattling Bk. <sup>b</sup>	156	51	66	73	11.0	1.1
Average		52	68	77	12.5	1.1
Québec						
Moisie	639	49	75	91	21.0	2.6
St. Jean <sup>c</sup>	97	53	79	84	15.5	2.1
Mingan	135	49	73	85	18.0	2.0
Ste. Marguerite <sup>d</sup>	169	49	75	88	19.5	2.2
Corneille	234	52	68	...	...	1.6
Mistassini	59	46	69	...	...	1.6
Matamek	189	51	72	...	...	1.3
P. Saguenay	219	56	79	92	18.5	1.6
Pt. Daniel	179	55	71	90	17.5	1.6
Carleton Fishery <sup>e</sup>	1,616	58	80	95	18.2	...
Average		52	74	89	18.5	1.8
New Brunswick						
Big Salmon	1,029	52	72	78	13.0	1.1
St. John	894	55	75	85	15.0	1.5
N.W. Miramichi	688	54	76	87	16.5	1.3
Average		54	74	83	14.8	1.3
Nova Scotia						
West	117	51	66	74	11.5	1.1
Maine						
Naraguagus	1,095	60	76	89	14.5	2.0
Ungava (Québec)						
George	112	56	79	...	...	2.0 <sup>f</sup>
Whale	169	59	72	...	...	1.8 <sup>f</sup>
Koksoak	106	60	82	...	...	2.0 <sup>f</sup>
Average		58	77			1.9 <sup>f</sup>

<sup>a</sup> Slope of regression line: Fork length vs. sea age.<sup>b</sup> Dep. Environ. Can. Fisheries, Resource Development Branch, Fisheries and Marine Service, St. John's, Nfld.<sup>c</sup> On North Shore, Gulf of St. Lawrence.<sup>d</sup> At Sacre-Coeur.<sup>e</sup> Bergeron and Gagnon 1962.<sup>f</sup> These estimates too high; sampling technique biased against grilse because of large mesh size of nets. Best estimates 1.6-2.0.

TABLE 5. Correlation of mean weight angled fish with river length and number of commercial nets

Region	Sample size	F-value	River length			No. of commercial nets		
			Regr. coef.	Partial corr. coef.	Proportion cum. var.	Regr. coef.	Partial corr. coef.	Proportion cum. var.
Québec	44	20.6*	.14	.69*	.46	-.02	-.27*	.04
Nova Scotia	26	12.7*	.11	.68*	.47	-.01	-.31**	.05
New Brunswick	21	3.1**	.01	.43*	.08	-.004	-.43*	.17
Newfoundland	41	...	-.00	-.02 <sup>a</sup>	.00	...	...	...
Québec + Nova Scotia	70	39.3*	.13	.73*	.51	-.02	-.26*	.03
Québec + Nova Scotia + New Brunswick	91	11.3*	.05	.43*	.08	-.01	-.37*	.13

\* Significant at .05 level (1-sided).

\*\* Significant at .10 level (1-sided).

<sup>a</sup> Regression was performed against river length only, hence a total correlation coefficient.

TABLE 6. Correlation of mean weight angled fish with river length, sea growth and number commercial nets

Sample	Sample size	F-value	River length			Sea growth			No. of commercial nets			Total proportion var. determined
			Regr. coef.	Partial corr. coef.	Proportion cum. var.	Regr. coef.	Partial corr. coef.	Proportion cum. var.	Regr. coef.	Partial corr. coef.	Proportion cum. var.	
Excluding Newfoundland	11 <sup>a</sup>	7.21*	.004	.53 <sup>c</sup>	.07	.11	.77*	.49	-.002	-.67*	.20	.76
Total	14 <sup>b</sup>	9.68*	.001	.15	.12	.13	.77*	.52	— <sup>d</sup>	— <sup>d</sup>	— <sup>d</sup>	.64

\* Significant at .05 level (1-sided).

<sup>a</sup> Rivers—Moisie, P. Saguenay, Ste. Marguerite, Port Daniel, Big Salmon, St. John, N.W. Miramichi, West, Nanguagas, St. Jean, Mingan.<sup>b</sup> The above plus Exploits, Sandhill, and L. Rattling Brook in Newfoundland.<sup>c</sup>  $P(t) < .10$ , one sided.<sup>d</sup> Bivariate analysis, fishing pressure not known for Newfoundland.

following the grilse stage by comparing the lengths of virgin fish of different age classes and calculating the slope,  $m$ , of the regression line: Fork length vs. sea age. This analysis (Table 4) not only reveals differences between rivers, but also suggests regional patterns of variation. Grilse from all three regions are approximately the same size, but following this stage, Québec stocks on average grow fastest, whereas Newfoundland fish grow slowest (Fig. 4). These results suggest that fish from different regions have different paths of high seas migration. They also suggest an explanation for the observed lack of correlation between the mean weight of angled fish and river length in Newfoundland. Delayed breeding will, after all, only be selected for if another summer at sea results in increased fecundity the following autumn. If post-grilse growth rates at sea are low, there will be little reason to opt for the additional year in the ocean no matter how long the native stream. Growth rates in New Brunswick stocks are intermediate between those observed in Québec and Newfoundland, and it is therefore suggestive that the correlation between the mean weight of angled fish and river length in this region is greater than that observed in Newfoundland, but less than in Québec.

One can also treat the populations detailed in Table 2 individually, comparing the calculated growth rate with the mean age of first spawning (Fig. 5). Here a substantial correlation ( $r = .81$ ) is highly significant ( $P(r) < .001$ ). Finally, to investigate the joint effects of river length, netting, and growth rates, we performed a multivariate regression comparing the mean age of first spawning to all three variables for 11 rivers from Québec, New Brunswick, Nova Scotia, and Maine, and then for these plus 3 Newfoundland streams, but omitting fishing pressure (Table 6). In both analyses, river length accounted for about 10% of the variance and post-grilse growth rates for about 50%. Netting added another 20% in the first sample. So for 11 rivers we can account for 76% of the cumulative variance with 3 variables and for 14 rivers, 64% with 2.

#### Variability about the mean age of first spawning

The standard deviations about the mean age of first spawning are listed for those rivers for which data were available in Table 3. Plotting these figures against latitude (Fig. 6), we observe that variability first increases and then decreases as one goes north from Maine to Ungava. This result is thus consistent with one of the two possible patterns based

TABLE 7. Interval between spawnings

River	Number of re-spawners	Mean age 1st spawning (sea-yr)	River length (mi)	Proportion repeat spawners with interval between spawning		
				1 yr	> 2 yr	Mixed
Petite	6	1.0	8	1.00	.00	.00
Big Salmon	331	1.1	18	.95	.03	.02
Ste. Marguerite <sup>a</sup>	7	2.0	43	.14	.86 <sup>b</sup>	.00
West	14	1.1	6	.79	.21	.00
St. John	138	1.5	133	.45	.51	.04
Exploits	96	1.0	42	.99	.01	.00
Moisie	98	2.6	81	— <sup>c</sup>	.97	...
N.W. Miramichi	339	1.3	20	.17	.83	...

<sup>a</sup> At Sacre-Coeur.<sup>b</sup> Confirmed in general by Schiefer (1971) as being similar to Moisie.<sup>c</sup> Schiefer (1971) does not give sample size.

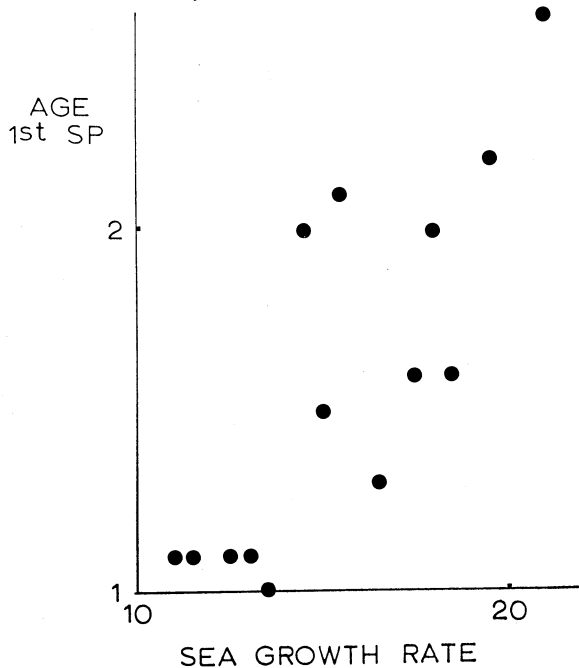


FIG. 5. Mean age first spawning (SP) plotted against rate of sea growth ( $m$ , Table 4), after the grilse stage;  $r = .81$ ;  $P(r) < .001$ .

on analysis of simple life history models (e.g., Cohen 1966, Schaffer 1974b).

#### DISCUSSION

##### *River length and other indices of river harshness*

Thus far, we have equated river length (as measured by the maximum distance that salmon penetrate into fresh water) with the energy that a fish must expend in order to ascend to the spawning grounds. Of course, this is only a very rough measure of the actual energetic cost of upstream migration and in specific cases may lead to totally erroneous predictions. Accordingly, we turn in this section to other indices of river harshness that may more accurately reflect the caloric demands of the spawning migration. First, we consider the number of years

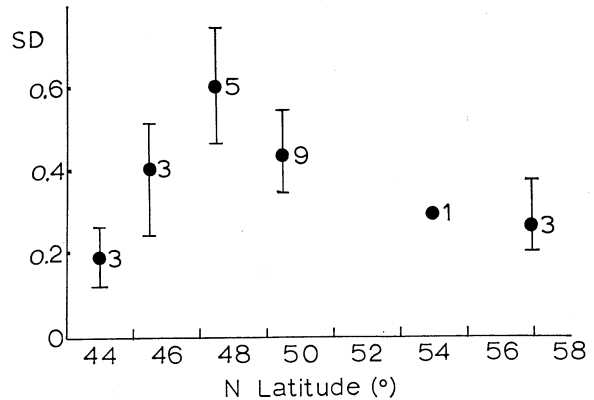


FIG. 6. Standard deviation (SD) about mean age first spawning plotted against latitude. Each point is the average for 2° of latitude, e.g., 45°–46°. Number to the right gives sample size; vertical lines give the range in all cases but the samples at north latitudes 47°–48° and 49°–50°, where it denotes the SE about the mean calculated for  $t = .95$ . Data from Table 3.

post-spawners spend in the ocean before returning to the river. All else being equal, an easy river should leave post-spawners in better condition than a difficult stream. Hence, we would expect a shorter inter-spawning interval on easy rivers, and thus a high degree of correlation between this figure and the age of first reproduction. Data relevant to this prediction are presented in Table 7. Two points are worth noting. First, the predicted correlation is highly significant ( $r = 0.83$ ;  $P(r) < .01$ ). Second, one river, the Northwest Miramichi, is exceptional (Fig. 7). Here, the bulk (77%–83%) of the fish spend two summers at sea between spawnings, yet the mean age of first spawners is low (1.3 sea-years). But we have previously suggested that in the Miramichi system commercial fishing has seriously distorted the natural age composition of the spawning runs by eliminating the older age classes of virgin fish. Hence, what we are seeing may not be an anomaly, but human interference.

The relative loss of growth that results from spawning may also be calculated. In Table 8, data are

TABLE 8. Loss of growth due to spawning

	Big Salmon			St. John (N.B.)			NW Miramichi		
	Grilse	2-Sea-yr virgin	2-Sea-yr repeat	Grilse	2-Sea-yr virgin	2-Sea-yr repeat	Grilse	2-Sea-yr virgin	2-Sea-yr repeat
N	522	112	563	781	1,157	7	425	235	47
$\bar{x}$ fork length	57.8 cm	71.6	63.5	55.3	74.4	62.3	54.1	75.8	58.7
SD	3.9 cm	4.1	3.7	4.3	4.3	5	2.3	1.1	5.3
Loss due to spawning*			44%			64%			79%

\* Percent loss due to spawning = [Fork length (2-sea-year virgins) – fork length (2-sea-year repeaters)]/[Fork length (2-sea-year virgins) – fork length (grilse)].

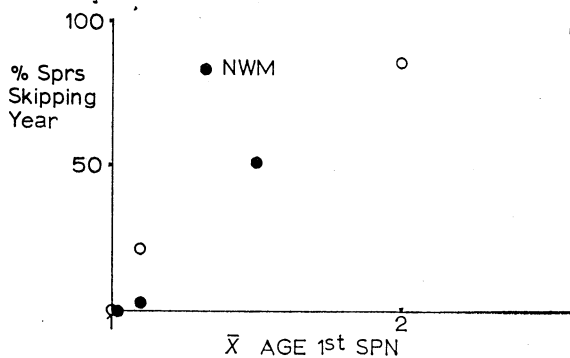


FIG. 7. Percent of repeat spawners (Sprs) spending one or more complete years at sea between spawnings plotted against mean age of first spawning. Hollow circles indicate small samples. NW Miramichi (NWM) exceptional to trend, discussed in text;  $r = .84$ ;  $P(r) < .005$ , one-sided.

given for the three rivers, all in New Brunswick, for which both lengths and scale readings were available. On the Big Salmon River (18 miles long) 2 sea-year fish that first spawned as grilse are 44% smaller than 2 sea-year virgins. On the much longer (133 miles) St. John, 7 fish (out of 1,945) were counted with this life history. These showed an average loss of 64%. For the Northwest Miramichi (70 miles) the figure is 79%. Though too few to warrant firm conclusions, these data appear to be well-correlated with the percent of fish that spend 2 yr in the ocean between spawnings. Again, the relatively large loss in growth observed among fish in the Miramichi suggests that it is a far more difficult river to ascend than the current age composition of the spawning runs would appear to indicate.

A final piece of evidence relating river harshness to the relative abilities of the different age classes to swim upstream comes from the seasonal pattern of entry into the river (Table 9). In general, larger fish are more abundant in the spring and fall when run-off is highest due to snow melt and rain. On

the other hand, grilse tend to predominate in the summer when water velocities are lowest. This pattern is quite general in North America and is also apparent in Great Britain (Jones 1959).

#### *Implications of variation in growth rates*

We have already observed that post-grilse marine growth rates are well-correlated with the mean age of first spawning. These comparisons were made between rivers. However, the same relationship appears to hold for fish from the same river. Referring to the Northwest Miramichi, Allen et al. (1972) have recently observed that "of fish originating in the same river and from the same smolt class, those which mature after one sea winter grow more slowly during the spring and summer immediately preceding their return to the river than do those which do not return until they have spent 2 or more years at sea." They suggest that a similar relationship holds for fish returning after spending 2 and 3 yr in the ocean. These results, based on studies of fish tagged on leaving the home river and recovered in the ocean, parallel our own less elegant analysis. Taken together, both sets of data suggest variability in productivity of marine feeding grounds. They also suggest that fish from different rivers (and probably regions) have different paths of oceanic migration. Clearly, complex coevolutionary processes are involved here, the relevant factors being the difficulty of upstream migration and the rivers' proximity to feeding regions of high and low productivity. However, because the distribution of different stocks in the ocean is still not well defined, the precise nature of these interrelationships remains unclear.

#### *Heritable age of first spawning*

Our purpose has been to demonstrate the adaptive significance of variations in reproductive behavior among local populations of Atlantic salmon. We assume that life cycles, like morphological patterns can be inherited and are thus subject to selection. This point of view is not shared by all other students

TABLE 9. Seasonal distribution of angled large salmon and grilse

Month	Nova Scotia <sup>a</sup>			New Brunswick <sup>a</sup>			Québec <sup>b</sup>		
	S	G	% S	S	G	% S	S	G	% S
May	82	2	.98	8	40	.17	...	...	...
June	310	388	.44	1,005	1,506	.40	2,780	99	.97
July	175	733	.19	1,844	10,676	.15	4,066	1,715	.70
August	101	427	.19	820	6,469	.11	1,082	862	.56
September	193	380	.34	2,504	16,821	.13	160	25	.86
October	362	372	.44	742	1,537	.33	456	210	.69

<sup>a</sup> Mean number fish angled per month 1960–68; Dep. Environ. Can. Fisheries, Resource Development Branch, Halifax, Nova Scotia.

<sup>b</sup> Mean number fish angled per month 1964–69; Dep. Tourism, Fish and Game, Fish and Game Branch, Québec, P.Q.

of the salmon (e.g., Jones 1959, Schiefer 1971). Accordingly, we shall here summarize evidence supporting our position.

The best evidence suggesting that the age of first spawning is heritable has been reported by Elson (1970). (Ricker 1972 has also summarized evidence indicating the importance of heredity in other salmonids.) In the course of selective breeding experiments, it was observed that of the progeny of grilse- $\times$ -grilse matings, 73% of the tagged offspring returned as grilse; conversely, of the offspring of 2-sea-year- $\times$ -2-sea-year matings, 84% returned as 2 sea-year fish. The latter figure is especially impressive, since the extra mortality incurred in the ocean by the 2 sea-year fish will bias the results in favor of grilse. Furthermore, the crossings were made with stock from the same river (Northwest Miramichi), and the immature fish were reared under similar conditions.

A second line of evidence supporting the hypothesis that spawning age is heritable comes from records on the age composition of Miramichi salmon since 1954 by the Fisheries and Marine Service of the Department of the Environment of Canada. Since the early 1960's, the percent of older fish in the runs of many Canadian rivers has decreased markedly (Kerswill 1971, Saunders 1969). A similar decrease has been observed for the Miramichi as a whole. Thus from 1954 to 1960, half the fish taken in a research trap in the main estuary were grilse, the remainder being 2 sea-years or older. From 1961 to 1969, grilse represented about 84% of the run, and since 1969, the trend has continued (G. Turner, Department of the Environment of Canada, Fisheries and Marine Service, Resource Development Branch, Halifax, Nova Scotia, *pers. comm.*). Presumably, these figures reflect at least, to some extent, the effects of commercial netting both at home and as far off as Greenland. If differential removal alone were involved, one would expect only that the frequency of grilse would increase, not their actual number. In fact, the mean number of grilse netted per day in the traps increased from 38 to 53, whereas the number of larger fish dropped from 19 to 10. These changes suggest strongly that selection has altered the frequencies of the genes coding for different ages of return.

Despite these results, it is widely believed (e.g., Jones 1959) that growth rates in freshwater determine the age of first spawning—faster growing fish returning on average after a shorter stay in the ocean. This point of view is consistent with theoretical considerations, since fecundity per unit effort will be increased for all age classes and particularly for grilse. As an empirical hypothesis, it has been most articulately expressed by Schiefer (1971), who sug-

gested that fast growth rates in freshwater lead to high rates of precocious sexual maturation of male parr and that these fish then return to the river as grilse. Schiefer documents his hypothesis with data from several North Shore rivers, and we do not doubt that he has observed a real relationship. The question, however, is not whether or not freshwater growth rates can influence the age of first spawning, but whether or not this relationship is the same for all populations. The notion that environment affects the expression of heritable traits is neither new nor surprising. When we suggest that a trait has been selected for, we are merely abbreviating the statement that selection has favored a dose-response curve of a given shape and slope. Thus, while Schiefer's North Shore rivers fit his hypothesis, rivers from other regions do not, presumably because they have a different dose-response relationship. For example, on the North Shore, the mean age of smolts—which reflects freshwater growth rates (Elson 1957)—is about 3 yr on both the Matamek and Corneille rivers, and these have large grilse components in their spawning runs. The Moisie, on the other hand, has virtually no grilse and here the mean age of the smolts is 3.6 yr. However, the major salmon rivers of Maine, the Naraguagans and Machias, have mean smolt ages of about 2 yr, with perhaps 40%–60% of the male parr maturing (A. L. Meister, Atlantic Sea Run Salmon Commission. Univ. Maine, Bangor, *pers. comm.*), yet here the grilse component of the spawning runs is less than 10% (Meister and Cutting 1967). Furthermore, on the Ungava Peninsula, smolt ages are very high, and the percent of parr attaining sexual maturity seems to be fairly low (Power 1969). Yet the adult runs apparently lack the 3-sea-year virgin fish that predominate on the Moisie.

In order to properly assess the relevance of Schiefer's hypothesis, it will be necessary to determine the relation between sea age and freshwater growth rates for a variety of rivers, rather than to consider each river as a single point in a regression analysis. We suggest that although Schiefer's postulated relation probably exists for all stocks, its precise nature should vary from river to river and that higher or lower ages of first return should be associated with the same freshwater growth rates according to the principles set forth in this paper.

#### ACKNOWLEDGMENTS

It is a pleasure to acknowledge the assistance of the following members of the Fisheries and Marine Service, Department of Environment of Canada (DOE), the Quebec Department of Tourism, Fish and Game (PQ), and the International Atlantic Salmon Foundation (IASF) who willingly opened their files to us and made available much unpublished data: J. Bergeron (PQ), W. Carter (IASF), A. Ducharme (DOE), D. B. Lister (DOE), J. Pratt (DOE), B. Tetreault (PQ), L. Tremblay (PQ),

G. Turner (DOE), and C. Wyckes (DOE). We would also like to thank T. Carry, A. Meister, J. W. Saunders, and R. L. Saunders for useful discussions. John Bonner, Al Fischer, Henry Horn, Peter Larkin, Egbert Leigh, T. G. Northcote, and John Terborgh read various drafts of this paper and provided useful insights and criticisms. Robert MacArthur was a source of continuing encouragement and stimulation. This paper is respectfully dedicated to his memory.

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