Age at Sexual Maturity in Icelandic Stocks of Atlantic Salmon (*Salmo salar*)

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For Icelandic stocks of Atlantic salmon (*Salmo salar*) in 77 rivers, the combination of June ocean temperature, length of river ascended by the salmon, discharge of the river in July–September, and latitude explained much of the variation in percentages of grilse — 72% for females and 62% for males. For both sexes, percentage of grilse was directly related to ocean temperature but inversely related to length of river, discharge of river, and latitude. For stocks in 23 Southwest Coast rivers, length of river explained 72% of the variation in percentage of females that were grilse. Females in stocks south of the thermal gradients separating Atlantic from Arctic or Polar water tended to return as grilse; females north of the gradients tended to return after more than one winter at sea. The decline in percentages of grilse clockwise from southwestern to northeastern rivers corresponded closely with the decline in June ocean temperatures between these areas. I hypothesize that the salmon stocks have adapted their age at sexual maturity to the length and discharge of the rivers, natural mortality rates during their second year at sea, and average expected ocean temperatures, reflecting conditions for growth and survival, that the smolts encounter. Age at maturity appears not to be a direct causal response to any of these physical factors, and appears best understood only with reference to the entire life history pattern of each stock.

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Pour la plupart des stocks islandais de saumons atlantiques (*Salmo salar*) dans 77 rivières, une combinaison des facteurs suivants : température de l'océan en juin, longueur de la rivière remontée par le saumon, débit de la rivière en juillet–septembre et latitude expliquent une bonne partie de la variation du pourcentage de castillons — 72 % pour les femelles et 62 % pour les mâles. Chez les deux sexes, le pourcentage de castillons est en relation directe avec la température de l'océan mais en relation inverse avec la longueur de la rivière, son débit et la latitude. Dans le cas de stocks de 23 rivières de la côte méridionale, on peut relier à la longueur de la rivière 72 % de la variation du pourcentage de femelles castillons. Les femelles dans les stocks situés au sud des gradients de température séparant l'eau atlantique de l'eau arctique ou polaire tendent à retourner en rivière comme castillons; au nord de ces gradients, les femelles ont tendance à retourner en rivière après plus d'un hiver en mer. La diminution des pourcentages de castillons depuis les rivières du sud-ouest dans le sens des aiguilles d'une montre vers le nord-est correspond étroitement à l'abaissement des températures océaniques de juin de cette région à l'autre. J'émets l'hypothèse que les stocks de saumons ont adapté leur âge de maturité sexuelle à la longueur et au débit des rivières, au taux de mortalité naturelle durant leur deuxième année en mer et aux températures océaniques moyennes anticipées, reflétant les conditions, pour la croissance et la survie, que rencontrent les smolts. L'âge de la maturité ne semble pas être une réponse directe à aucun de ces facteurs physiques, mais s'expliquerait le mieux en fonction seulement des caractéristiques du cycle de vie entier de chaque stock.

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IN some Icelandic stocks of Atlantic salmon (*Salmo salar*), most fish return to their natal rivers after spending one winter in the sea;[1] in other stocks most fish return after two or more winters at sea. Similar variations are observed around the world between stocks of salmon inhabiting different rivers or different portions of the same river (Rounsefell 1958; Ricker 1972; Gardner 1976). Biologists have long sought the causes of these variations in life history. Dahl (1916) observed that northern Norwegian rivers had more large, older salmon and southern rivers had more small, younger salmon. Because, as a rule, salmon from the northern rivers spent more years in both freshwater and in the sea than did those of southern rivers, he speculated that "the whole life cycle of the salmon requires a longer period of development in the north than in the south."

More recently, Schaffer and Elson (1975) found significant positive correlations between mean weight of salmon, which indicated how long they had been at sea, and the length of the river that the salmon ascended for Canadian rivers in the Bay of Chaleur, the North Shore of the Gulf of St. Lawrence, and Nova Scotia. They argued that salmon required more energy to ascend longer rivers, and because of these energy requirements, selection would favor fish that stayed longer in the sea. They concluded that the observed relations beween length of river and mean weight of salmon were adaptive.

For salmon stocks in Quebec, Newfoundland, and Labrador, Power (1981) found a positive relation between discharge of river and the number of years a salmon from that river remained in the sea before maturing. He also stressed the adaptive nature of observed variations in age at maturity.

Why do most salmon in some Icelandic stocks return to their rivers after 1 yr at sea but most salmon in other stocks return after 2 or more yr at sea? This question relates to variations between stocks and their underlying causes. The answer to this question is sought by biologists who want to explain variations in life history patterns, by anglers who want to know why they catch mostly big salmon in one river and small salmon in another, by commerical fisherman who get different prices per unit weight for salmon of different sizes, and by aquaculturists and salmon ranchers who want to manipulate return rates of younger and older salmon for maximum profit.

If the observed variations in age at maturity are primarily adaptive, some long-term environmental factors must be inducing these adaptations. The problem is to separate the environmental factors that have led to adaptations by fish of particular stocks from the factors that merely produce short-term physiological responses by individual fish. Assuming sufficient nondominance genetic variability on which selection can act, differences in environments between stocks will lead to adaptive variations, especially if the environmental differences persist over time.

To attempt to determine which environmental factors may have led to adaptations in age at maturity in Iceland's stocks of salmon, I investigated the correlation between percentage of male grilse and female grilse in the salmon catch of 77 rivers and four factors: the length of the river ascended by the salmon; the discharge of the river when the adult salmon migrate upstream (July–September); the latitude of the river; and ocean temperature when the smolts enter the ocean (June–August).

[1]In this paper, salmon that have matured or are about to mature after one winter in the sea (having one ocean annulus) are called grilse; salmon with two or more ocean annuli are called multi-sea-winter salmon.

Methods

SALMON LIFE HISTORY DATA

Salmon ascend about 80 rivers in Iceland and most of these rivers support carefully managed angling with rods (Gudjónsson 1978). River owners and fishing clubs keep accurate statistics on weight (at intervals of 0.5 kg) and sex of individual salmon caught. There is no significant fishery for salmon in the ocean by Icelanders and my preliminary analysis indicates that, unlike some North American stocks (Paloheimo and Elson 1974), slight or no changes in age composition have occurred in most stocks over the last 20 yr. Harvesting with fishing rods is less size selective than harvesting with gill nets, and because of the significant cost of permits, anglers keep most fish they catch regardless of the fish's weight.

For 76 rivers I determined the number of years the salmon had spent at sea by analyzing weight-frequencies of rod-caught salmon separately by sex. For one other river, Thjorsá (No. 73 in Fig. 1), which is a large glacial river fished mainly by gill nets, I used weight–frequency data of gill-netted salmon of known sex. In most stocks, most females weighing more than 3.5 kg and most males over 4 kg had spent 2 or more years at sea. For selected stocks, I analyzed scales to verify ages of females of 3.0–3.5 kg and males of 3.5–4.0 kg weight ranges within which grilse and multi-sea-winter salmon often overlapped. To lessen the possibility of changes in age composition over time biasing the data, I calculated where possible the average percentage of grilse in the catch for a constant period of several years, usually 1967–73. For rivers where few salmon were caught or the data were not separated by sex over all years, I used whatever data were available for any years before 1974. The effects of introduced hatchery fish on stock composition were small during this pre-1974 period. The final statistics I obtained from these calculations were the average percentages (over several years) of males that were grilse (hereafter called percent male grilse) and the percentages of females that were grilse (hereafter called percent female grilse).

LENGTH AND DISCHARGE OF RIVERS

Rivers in Iceland were classified by Rist (1956) as glacial (J), direct runoff (D), spring-fed (L), and lake-fed (S), and each type has distinct discharge characteristics. Glacial rivers, e.g. upper tributaries of Blanda (No. 49) and Thjorsá (No. 73), are typically brownish to whitish, at least in summer, because of fine sediments in the water. Many large rivers receiving glacial water have clear water tributaries (such as Blanda's tributary Svartá, No. 50), in which adult salmon spawn and young salmon rear. The discharge of glacial rivers is typically highest in July and August because the glaciers are then melting rapidly (Rist 1956). Because

TABLE 1. Summary of percent male and female grilse, ascendable length, discharge, latitude, and offshore ocean temperatures for 77 Icelandic rivers classified by type according to Rist (1969). (J = glacial, D = direct runoff, L = spring-fed, S = lake-fed; types listed in combinations in order of decreasing importance.

River	Type	Male grilse (% of all males)	Female grilse (% of all females)	Length of river (km)	Discharge of river (m^3/s)	Latitude (minutes N of 63°N)	Ocean temperature (°C)
1 Ellidaár	L+S+D	91	86	6	2.9	67	8.05
2 Úlfarsá	S+D+L	95	91	7	1.1	68	8.05
3 Leirvogsá	D+L	87	84	8	1.9	72	8.05
4 Laxá í Kjós	D+S	74	67	18	4.8	78	8.05
5 Bugda	D+S	81	81	4	1.2	79	8.05
6 Brynjudalsá	D	91	85	10	1.0	81	8.05
7 Laxá í Lsveit	D+S	77	72	13	1.5	85	8.05
8 Leirá	D	92	94	4	0.4	84	8.05
9 Andakílsá	D+S	87	81	5	7.2	93	8.05
10 Hvítá	D+L+J	73	66	48	80.6	101	8.05
11 Grímsá/Tunguá	D+S	81	75	32	4.7	94	8.05
12 Flókadalsá	D	91	88	30	3.1	96	8.05
13 Reykjadalsá	D+L	77	77	47	1.8	99	8.05
14 Thverá	D	69	50	60	3.2	105	8.05
15 Nordurá	D	75	59	45	17.2	106	8.05
16 Gljúfurá	D	96	93	20	0.4	102	8.05
17 Langá	D+S	88	80	17	8.5	97	6.93
18 Álftá	L+D	82	66	10	2.4	97	6.93
19 Hítará	S+D	70	64	14	6.5	104	6.93
20 Haffjardará	L+D+S	72	54	16	5.1	110	6.93
21 Straumfjardará	D+S	68	49	11	2.3	110	6.93
22 Fródá	D+L	75	69	5	0.4	113	6.93
23 Laxá á Skógst	D	75	67	3	0.5	121	6.93
24 Hördudalsá	D	83	66	10	1.0	120	6.93
25 Midá í Dölum	D	78	65	12	2.3	120	6.93
26 Haukadalsá	D+S	72	57	6	4.4	123	6.93
27 Fáskrúd	D	77	64	8	1.4	132	6.93
28 Flekkudalsá	D	85	72	4	1.0	129	6.93
29 Krossá á Skardsst	D	85	74	5	1.5	136	6.81
30 Hvolsá/Stadarh	D	84	74	8	1.3	143	6.81
31 Laugardalsá	D+S	79	50	3	0.4	179	5.81
32 Ísafjardará	D	74	51	4	1.2	166	5.81
33 Langadalsá	D	57	26	20	1.6	170	5.81
34 Hvannadalsá	D	62	41	5	0.7	174	5.81
35 Selá, Stfirdi	D	80	37	12	2.2	170	5.09
36 Vídidalsá, Stfirdi	D	70	31	3	0.8	160	5.09
37 Hrófá	D	69	34	2	0.5	158	5.09
38 Vikurá	D	45	30	7	0.6	146	5.09
39 Bakkaá	D	64	29	5	0.4	138	5.09
40 Laxá á Hrútafirdi	D	57	45	2	0.5	134	5.09
41 Hrútafjardará/Siká	D	59	29	10	1.9	127	5.09
42 Midfjardará	D	60	31	33	4.0	133	5.09
43 Núpsá	D	64	32	33	0.5	128	5.09
44 Austurá	D	53	25	24	1.1	129	5.09
45 Vesturá	D	64	34	32	1.5	130	5.09
46 Vídidalsá/Fitjaá	D+S	50	19	45	10.0	142	5.09
47 Vatnsdalsá	D+L+S	54	35	43	6.4	149	5.09
48 Laxá á Ásum	S+D	80	61	15	2.3	157	5.09
49 Blanda	D+J	33	18	100	56.2	140	5.09
50 Svartá	D	57	25	41	5.9	149	5.09
51 Laxá-Ytri	D	69	47	15	6.0	163	5.09
52 Fossá í Laxárdal	D	70	21	2	1.1	177	4.44
53 Sæmundará	D	60	6	28	1.1	158	4.44
54 Húseyjarkvísl	D+L	56	31	27	8.6	158	4.44
55 Hofsá í Vesturdal	D+J	61	25	2	4.0	174	4.44
56 Fljótaá	S+D	74	34	7	6.4	182	4.44
57 Fnjóská	D	50	20	34	32.7	169	4.44
58 Skjálfandafljót	D+L+J	69	15	28	88.3	171	4.44
59 Laxá í Adaldal	L+S	41	17	27	49.2	174	4.44

TABLE 1. (*Concluded*)

River	Type	Male grilse (% of all males)	Female grilse (% of all females)	Length of river (km)	Discharge of river (m^3/s)	Latitude (minutes N of 63°N)	Ocean temperature (°C)
60 Ormarsá	D+L	45	35	7	9.2	203	3.26
61 Deildará	D+S	47	38	6	0.4	205	3.26
62 Svalbardsá	D	49	24	13	15.7	191	2.97
63 Sandá	D+L	54	22	10	11.5	190	2.97
64 Hölkná	D	42	34	10	10.3	189	2.97
65 Hafralónsá	D	37	20	25	9.0	185	2.97
66 Midfjardará/Kverká	D	65	21	5	13.3	181	3.36
67 Selá í Vopnafirdi	D+L	64	36	7	12.2	170	3.36
68 Vesturdalsá	D	68	43	28	0.9	161	3.36
69 Hofsá	D	70	21	31	5.9	158	3.36
70 Breiddalsá	D	90	72	10	6.9	108	2.98
71 Geirlandsá	D	71	71	5	4.1	50	8.22
72 Eldvatn	L	89	86	10	31.0	37	8.22
73 Thjórsá	D+J+L	41	27	48	428.0	56	8.46
74 Stóra-Laxá	D	56	21	96	6.6	65	8.46
75 Bruará	L+S	68	7	72	60.6	70	8.46
76 Sogid	L+S	71	61	39	102.0	63	8.46
77 Hvitá	D+J+S+L	70	33	95	120.7	65	8.46

upstream migration of salmon is from June to August, fish migrating up glacial rivers to spawn in clear-water tributaries do so when discharge from the rivers is near the annual peak.

Direct runoff rivers (e.g. Nordurá, No. 15, and Hofsá, No. 69) are formed by the confluence of smaller streams. Because of water-tight bedrock, the discharge of these rivers depends on season and weather, and tends to be high in early spring or summer when snowmelt is greatest. In most of the best direct runoff rivers of salmon, discharge usually peaks before June and is low by July when salmon begin their migration upstream. Because direct runoff rivers are frequently small as well, salmon ascending these rivers usually are confronted with much lower discharges than are those ascending rivers fed by glaciers.

Spring-fed rivers (e.g. tributaries of Bruará, No. 75, and Sogid, No. 76) frequently originate in gushing springs located beneath younger parts of the Móberg Formation. The flows of the springs and the rivers fed by them are stable. Salmon ascending either large or small spring-fed or lake-fed rivers encounter stable, predictable flows. In general, Iceland's largest rivers in their main stems are combinations of the four types. For example, the main stem of Blanda is of two types and Thjorsá is of three types.

For one-third of the rivers, the Icelandic National Energy Authority Hydrological Survey operates gauging stations that measure mean daily discharge. Rist and Sigurdsson (1981) summarized the average monthly discharges at these gauging stations over periods from 1 to 48 yr, depending on the river. For these rivers, I estimated mean discharge from July to September by averaging the monthly mean discharges for these months.

For another one-third of the rivers, only spot measurements of discharge were available during the 3-mo period (Rist 1967, 1968). If more than one estimate existed, these estimates were averaged to get the best available estimate of mean discharge.

For the last one-third of the rivers, there were no direct discharge measurements. For these rivers, I estimated the average discharge during July–September by assuming that discharge per square kilometre of drainage area (Rist 1969) for rivers of unknown discharge was the same as that for neighboring rivers of known discharge and of the same or similar combination type according to Rist's (1956) classification (Table 1).

For each river I determined the maximum distance that salmon ascended before their migration was blocked by waterfalls or other physical or thermal obstructions. This information came from data compiled by Einar Hannesson of the Iceland Institute of Freshwater Fisheries and from my own surveys of about 10 rivers. For most rivers, the distance that the salmon ascended was precisely known (Table 1).

LATITUDE AND OCEAN TEMPERATURE

I estimated the latitude of each of 77 rivers (Geodetic Institute Maps of Iceland, Scale 1 : 100 000) as being midway between the mouth of the river and the uppermost point where salmon were known to ascend (Table 1).

Along the submarine ridge connecting Scotland and Greenland on which Iceland is located, a strong thermal gradient exists between Eystrahorn and Vestrahorn, between the warmer, more saline (>35‰) water of the North Atlantic and the colder, less saline (<35‰) water of the Iceland Sea (Thomsen 1938; Stefánsson 1962; Fig. 1). Off northwestern Iceland, along the Iceland–Greenland part of the ridge, there is another abrupt thermal gradient where warm North Atlantic water (the Irminger Current) meets the cold water of the Iceland Sea and the East Greenland Current (Stefánsson 1962). This gradient extends east to 66°N 26°W and then stretches northeastward. Between this gradient and the northwestern peninsula of Iceland, the Irminger Current penetrates northward and eastward throughout summer. The water temperature at a 20-m depth may be one Celsius degree lower off Kögur than off Latrabjarg. East of Kögur the ocean temperatures from June to August vary greatly between years. In warmer years the North Icelandic winter water stratifies

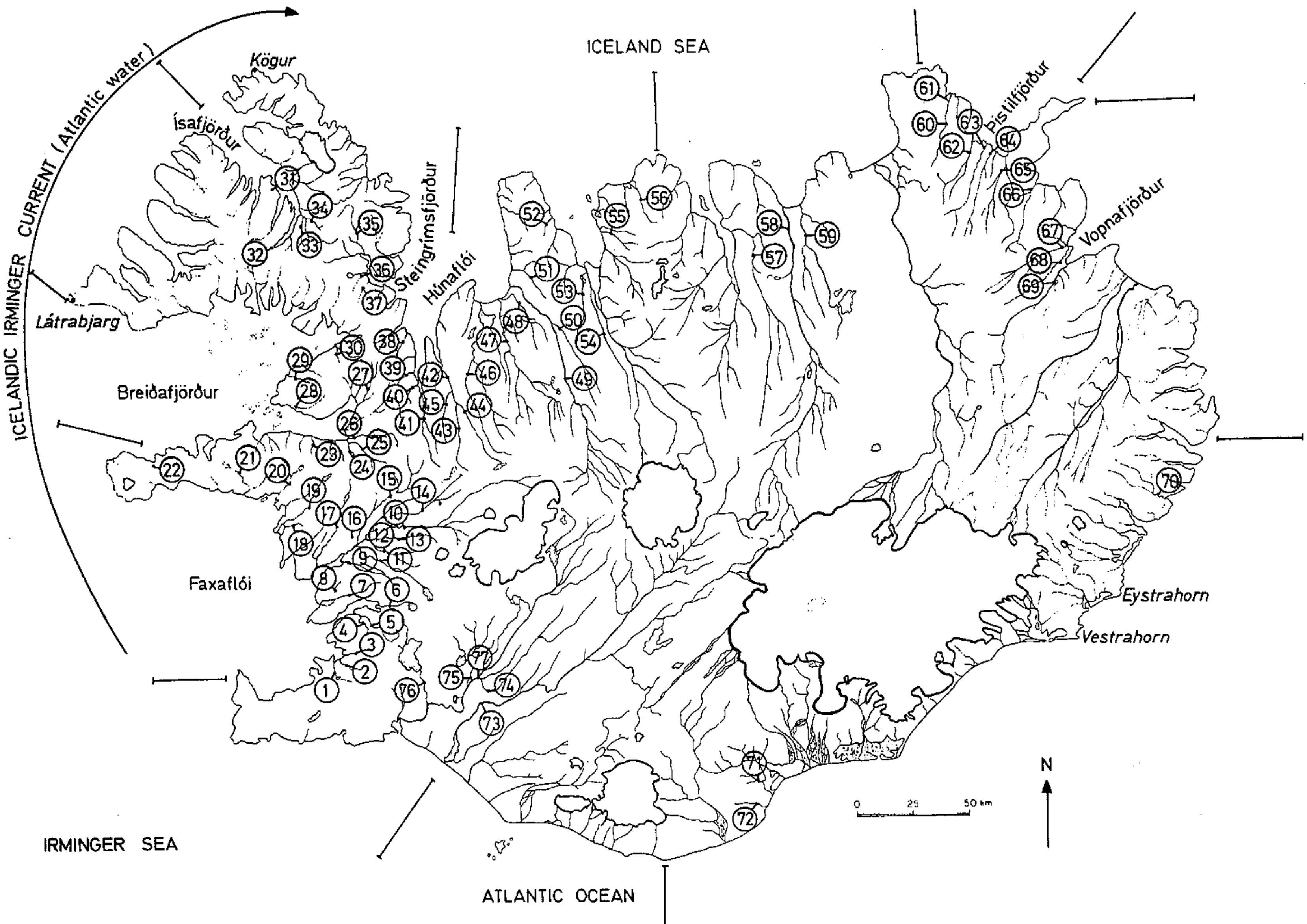

FIG. 1. Map showing 77 major and minor salmon rivers and geographical features of Iceland. Ocean temperature transects are shown by black lines. See Table 1 for names and characteristics of the rivers.

TABLE 2. Variation in percentages of male and female grilse explained by stepwise regression of ocean temperature and length, discharge, and latitude for 77 Icelandic rivers. (** $P < 0.01$; * $P < 0.05$.)

Sex of grilse, and variable	Additional % explained by adding this variable to model	% of total variation explained
Males		
Ocean temperature	34**	34**
Length of river	21**	54**
Discharge of river	6**	60**
Latitude	2*	62**
Percent grilse = 3.9201 (ocean temperature)−0.2659 (length)−0.7862×10⁻¹ (discharge) −0.1006 (latitude)+65.3585.		
Females		
Ocean temperature	43**	43**
Length of river	24**	67**
Discharge of river	3**	70**
Latitude	2**	72**
Percent grilse = 6.5955 (ocean temperature)−0.5044 (length)−0.9225×10⁻¹ (discharge) −0.2033 (latitude)+47.4314.		

and dominates the surface layer; in colder years a layer of cold Polar water (<34‰ salinity) overlies the North Icelandic winter water (Malmberg 1972). Salmon smolts leaving southern and western rivers in June would thus swim into warm (6−9°C at 20 m) saline Atlantic water, whereas smolts leaving northern and northeastern rivers would swim into cool north Icelandic winter water mixed with penetrating Atlantic water. During cold years the smolts would swim into a surface layer of cold Polar water (<2°C at 20 m).

Ocean temperatures off Iceland have been measured at several depths for many years at standard stations along standard transects by the Marine Research Institute, Reykjavík. For 12 transects around the coast (Fig. 1), I combined the June temperatures at 20- and 25-m depths over the first four stations and averaged these values for each transect over a 33-yr period (1946−78). Because data were unavailable for many transects and years, I had only from 2 to 24 temperatures from which to calculate mean long-term June temperatures. Fortunately, the data along the more variable north coast were more nearly complete (data for 8−24 yr along each transect) than those along the much less variable south coast (data for 2−7 yr). Consequently the resulting mean relationships between transects for long-term June temperatures agreed closely with Stefánsson's (1960) regional 1950−60 mean estimates at 20 m. There were too few data to be analyzed for July and August, but because average surface water temperatures in July and August are closely related to temperatures in June (Stefánsson 1969, fig. 1), I had excellent evidence that June temperature relationships between transects at 20 m were maintained through August. I assigned each river a value for June ocean temperature based on where it entered the sea in relation to the 12 transects and on Stefánsson's (1960) charts of temperatures at a 20-m depth from 1950 to 1959. Each river was assigned 1 of 12 ocean temperatures (Table 1).[2]

[2]More detailed data used to calculate mean values for percentages of grilse, discharge of rivers, and ocean temperatures are available from the author.

I chose the 20-m depth because salmon are believed to feed near the surface (Stasko et al. 1973). Although the 20-m depth is within the surface layer, the temperature does not fluctuate as much as that at the surface in response to sudden changes in weather.

STATISTICAL ANALYSES

I investigated relations between percent of grilse (males and females separately as dependent variables) and length of river, discharge of river, latitude, and ocean temperature (independent variables) with linear, multiple, and stepwise regression analyses. I also computed partial correlation coefficients to assess the effect of one independent variable while controlling for the effect of one or more other variables (Nie et al. 1975).

Results

VARIATIONS IN PERCENT GRILSE

For female salmon, the combination of ocean temperature, length of river, discharge of river, and latitude explained 72% of the variation in percentage of grilse. All four independent variables made a significant contribution to explaining this variation (F-test, $P < 0.01$; Table 2). Individually, percentage of grilse was directly related to ocean temperature ($r = 0.66$; $P < 0.01$), inversely related to length of river ($r = -0.34$; $P < 0.01$) and latitude ($r = -0.60$; $P < 0.01$), but not significantly related to discharge ($r = -0.18$; $P > 0.05$). Ocean temperature and length of river, which were the first two variables to enter the stepwise model, explained 67% of the variation in percentage of grilse; discharge and latitude explained an additional 5%.

Ocean temperature and latitude were closely correlated with each other, but overall the correlations between independent variables were weak, even though some were statistically significant (Fig. 4).

Combinations of variables were much better than any individual variable at explaining the variation in duration of sea

TABLE 3. Partial correlation coefficients for independent variables and percentages of male and female grilse for 77 Icelandic rivers (all significant at $P < 0.01$ level).

For a given:	The variable	Explained − % of the variation in % of male grilse	Explained − % of the variation in % of female grilse
Latitude	Length of river	31	42
Ocean temperature	Length of river	31	41
Lat. + ocean temp.	Length of river	33	45
Length of river	Ocean temperature	49	62
Discharge of river	Ocean temperature	45	52
Length + discharge	Ocean temperature	54	65
Latitude	Discharge of river	23	20
Ocean temperature	Discharge of river	22	18
Lat. + ocean temp.	Discharge of river	24	20
Length of river	Latitude	44	58
Discharge of river	Latitude	40	47
Length + discharge	Latitude	51	62

TABLE 4. Variation in percent of male and female grilse explained by stepwise model of length, discharge, and latitude for 23 Icelandic Southwest Coast rivers (Nos. 1–16, 71–77). (**$P < 0.01$; *$P < 0.05$.)

Sex of grilse, and variable	Additional % explained by adding this variable to model	% of total variation explained
Males		
Discharge of river	48**	48**
Length of river	21**	69**
Latitude	1	70**
Females		
Length of river	72**	72**
Latitude	6**	78**
Discharge of river	3	81**

TABLE 5. Variation in percent of male and female grilse explained by stepwise regression model of length, discharge, and latitude for 25 Icelandic North Coast rivers (Nos. 35–59). (**$P < 0.01$; *$P < 0.05$.)

Sex of grilse, and variable	Additional % explained by adding this variable to model	% of total variation variation
Males		
Length of river	39*	39**
Latitude	3	42**
Discharge of river	2	44**
Females		
Discharge of river	20*	20*
Length of river	2	22
Latitude	1	23

residence. For example, for a given length and discharge, ocean temperature explained 65% of the variation in percentage of grilse. Similarly, for a given latitude and ocean temperature, length of river explained 45% of the variation in percentage of grilse (Table 3).

For the males, ocean temperature, length of river, discharge of river, and latitude explained 62% of the variation in percentage of grilse. All four variables entered the model significantly (F-test, $P < 0.05$; Table 2). Percentage of male grilse was directly related to ocean temperature ($r = 0.58$; $P < 0.01$), but inversely related to length of river ($r = -0.32$; $P < 0.01$), discharge of river ($r = -0.26$; $P < 0.05$) and latitude ($r = -0.52$; $P < 0.01$). For a given length and discharge of river, ocean temperature explained 54% of the variation in percentage of grilse; for a given ocean temperature and latitude, length of river explained 33% of the variation (Table 3).

For both females and males the best two-variable combination for explaining percentage of grilse was ocean temperature and length of river (Table 2).

For Southwest Coast rivers (Nos. 1–16 and 71–77) considered separately, length of river explained 72% of the variation in percent of female grilse (Fig. 5). Latitude explained an additional 6% and discharge 3% for 81% of the total variation. For males, length and discharge together accounted for 69% of the variation in percentage of grilse (Table 4).

For North Coast rivers (Nos. 35–59) considered separately, the relations between length, discharge, and percentage of grilse were less close. For males, only length entered the stepwise model significantly, explaining 39% of the variation in percentage of grilse. For the females, discharge was the first variable entered and was the only variable closely related to percent of grilse (Table 5).

Other Results

In 75 of 77 rivers the percent of grilse was lower for females than males. For southwest coast rivers (Nos. 1–9) flowing into Faxaflói, percentages of both male and female grilse generally exceeded 80, whereas salmon returning to many northern and northeastern rivers (e.g. Sæmundará, No. 53; Skjálfandafljót, No. 58; Hofsá, No. 69) were mostly grilse males and multi-winter sea females (Table 1).

As the regression analyses indicated, along the north coast the percentage of female grilse corresponded closely with oceanic temperatures off the rivers in summer. For example, for short rivers (<20 km, encircled in Fig. 2 and 3), representations of grilse dropped from 64 to 74% for the eight rivers (Nos. 22–25, 27–30) flowing into Breidafjördur (temperature 6.9°C) to 41 to 51% for the three short rivers (Nos. 31, 32, 34) in Ísafjördur (temperature 5.8°C), and to 29 to 45% for six rivers (Nos. 35–41) in western Húnaflói (temperature 5.1°C). For northeastern rivers (Nos. 60–64, 66, 67) for which temperatures were even lower (3.0–3.4°C), only 21 to 38% of the salmon were grilse. The drop in grilse from 64 to 74% in Breidafjördur to less than 50% in Ísafjördur and Húnaflói coincided closely with the position of the Iceland–Greenland Ridge and declining ocean temperatures between Breidafjördur and Húnaflói (Fig. 1, 2). Salmon in Breiddalsá (No. 70), which is 60 km north of the eastern thermal gradient, were mostly grilse. Unfortunately, there were too few salmon stocks in eastern Iceland to locate the point where the stocks again changed from mostly multi-sea-winter salmon to mainly grilse.

Although ocean temperature and latitude were closely correlated, there was clear evidence that ocean temperature off northwestern Iceland rather than latitude was affecting the percentages of grilse. In three short rivers in Ísafjördur (Nos. 31, 32, 34; temperature 5.8°C), the percentages of grilse were 41, 50, and 51, but in three rivers in Steingrímsfjördur (Nos. 35–37, temperature 5.1°C), which are farther south and originate near the same mountainous area, the percentages of grilse were 31, 34, and 37. Similarly, the salmon in rivers 27–30 in Breidafjördur (temperature 6.8°C) were 64–74% grilse but those in rivers 35–41 flowing into western Hunaflói (temperature 5.1°C) which are at a latitude similar to that of rivers in Breidafjördur were only 29–45% grilse (Fig. 2).

The long glacial rivers had lower percentages of female grilse than did surrounding, short nonglacial rivers. For example, Blanda (No. 49) and Skjálfandafljót (No. 58) each had fewer than 20% grilse. Svartá (No. 50), the large freshwater tributary of Blanda, had a higher percentage of grilse than Blanda as a whole.

The effects of river length and discharge were most clearly seen in the long, large rivers in the southwest (Nos. 73–77), which had a much lower percentage of female grilse than neighboring shorter, smaller volume rivers (Fig. 2). The northern rivers Fnjoská and Laxá (Nos. 57 and 59), which were both over 25 km long and had high discharges, also had low percentages of grilse (Fig. 1, 2).

The relations between ocean temperature, length, discharge and latitude, and grilse were not as well defined for males as for females, but most results for males agreed with results for females. The decline in percent of grilse from Breidafjördur to Vopnafjördur is evident in Fig. 3.

Discussion

In Iceland's stocks of Atlantic salmon, length of river, discharge of river, latitude, and ocean temperature are strongly correlated with, and appear to influence, the salmon's age at maturity. According to Schaffer's (1974, 1979) model, salmon from long, fast rivers should tend to remain in the sea longer than would those from short, easy rivers (Schaffer and Elson 1975). Because length and discharge are imperfect indicators of the work ($\int F \cdot dl$) a fish must do to reach its spawning grounds and to spawn, Schaffer and Elson suggested that long, large rivers would favor larger fish with greater energy reserves. That is, their increased size and fecundity would more than compensate for their extra year's mortality because their larger size would facilitate successful upstream migration and spawning. My analysis of Rist's unpublished data indicated that velocities generally increased with increasing discharge, which would further explain why large salmon might have an advantage in ascending larger, longer rivers. Ísaksson (1981) reported that most hatchery-reared salmon from Dalsá, an upper tributary of the long river Hvitá (No. 77), matured after 2 yr at sea, whereas most smolts of similar size from Kollafjördur hatchery stock reared under similar conditions returned as grilse. Ísaksson's results confirm the genetic tendency toward late maturation in an Icelandic salmon stock from a long river.

However, the Icelandic data and other published and unpublished information do not indicate that late age at maturity is necessarily an adaptive trait evolved by salmon in response to greater energy requirements for migration and spawning in long, large rivers. If such an adaptation existed, more large salmon should spawn in the upper parts of long rivers and more small salmon should spawn in the lower parts of rivers. The data do not support this expectation for either Atlantic or Pacific salmon. Killick and Clemens (1963) reported that most sockeye salmon (*Oncorhynchus nerka*) of the Fraser River's many discrete stocks returned after 2 yr at sea, but three-sea-winter salmon were most abundant compared to two-sea-winter fish in lower river stocks such as in Pitt and Harrison rivers, rather than in upper river stocks such as the Stuart River. Yet, Stuart River fish traveled over 1000 km

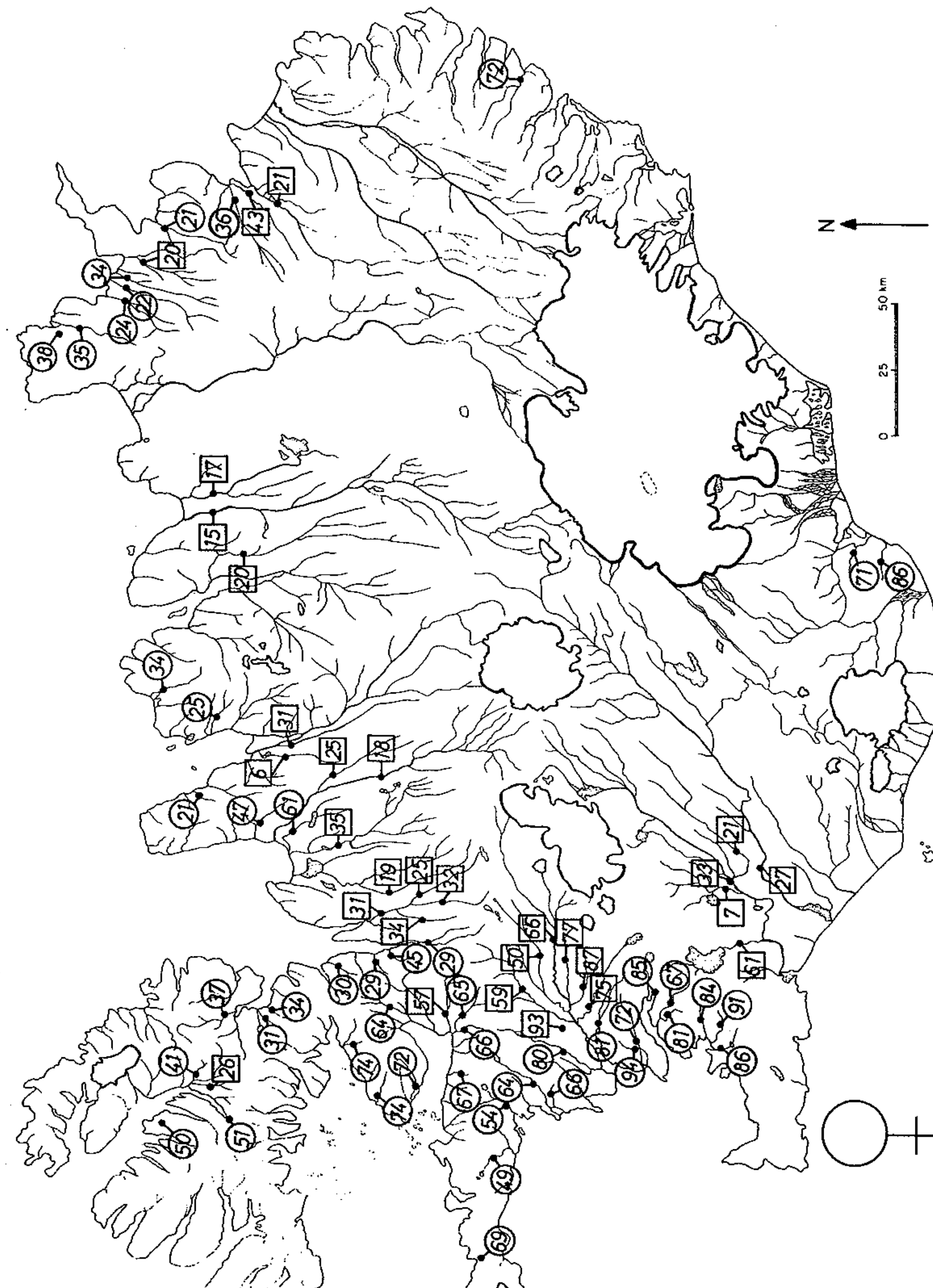

FIG. 2. Percent females that were grilse in the catch of 77 Icelandic rivers; squares: >20 km ascendable length; circles: <20 km ascendable length.

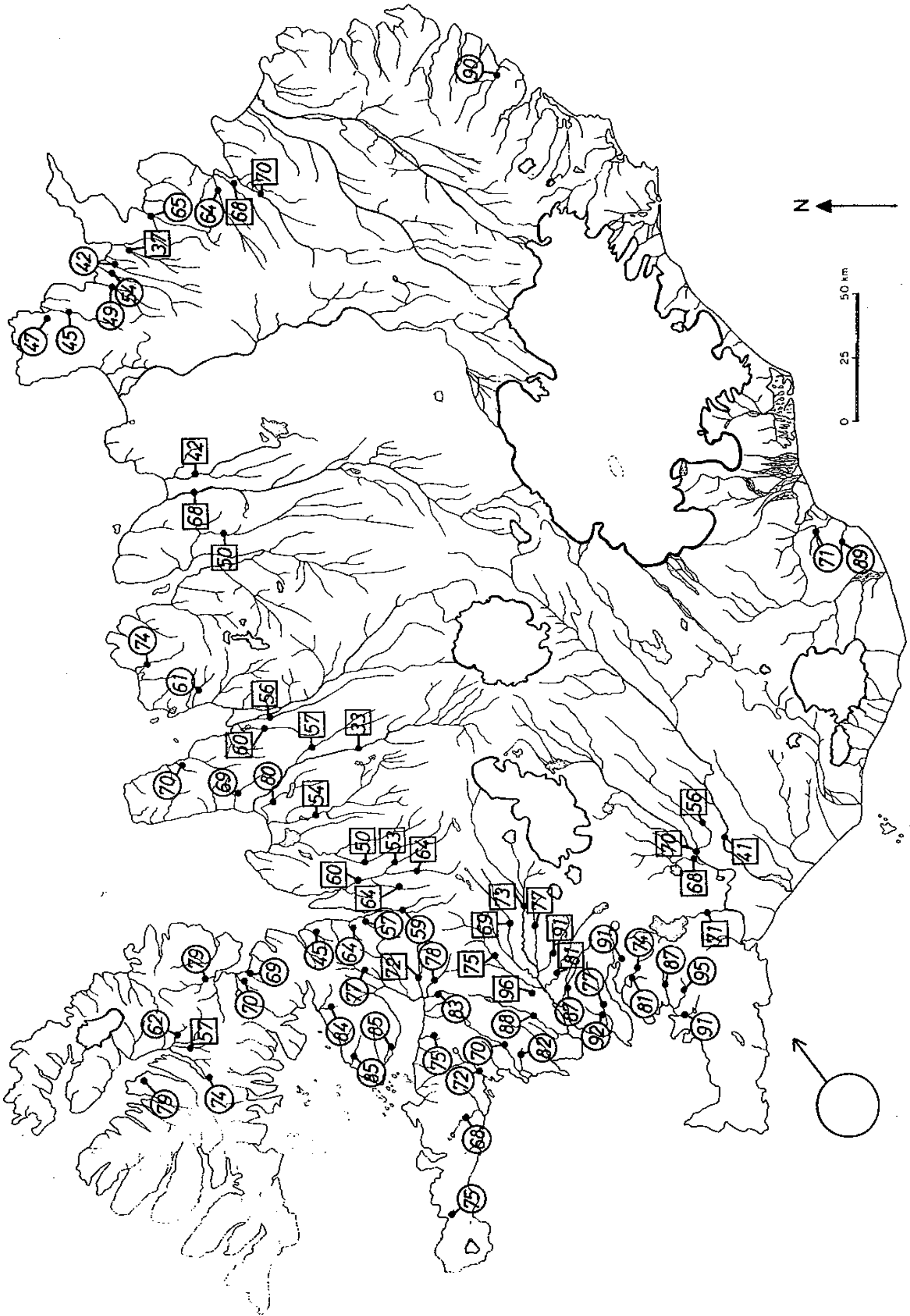

FIG. 3. Percent males that were grilse in the catch of 77 Icelandic rivers; squares: >20 km ascendable length; circles: <20 km ascendable length.

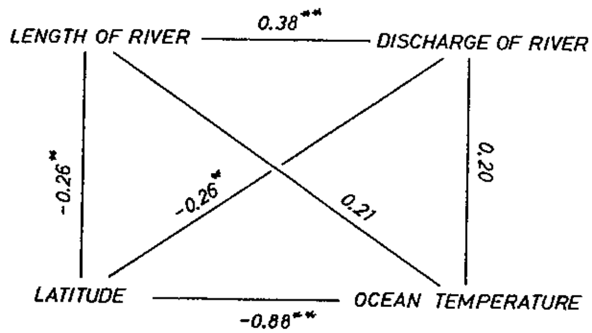

FIG. 4. Correlations between length of river, discharge of river, latitude, and offshore ocean temperature for 77 Icelandic rivers (*$P < 0.05$; **$P < 0.01$).

upstream to spawn, 10 times as far as the Pitt River fish and 10 times the length of the longest ascendable Icelandic river. If large size and late age at maturity were adaptive responses to energy requirements for ascending the river, the upper Fraser stocks should, contrary to observations, have more large, older fish than the lower river stocks. In Iceland, female Atlantic salmon caught in the lower part of Thverá in 1967 and 1968 were 68% grilse, mid-river catches were 69% grilse, and upper river catches in Litla Thverá were 74% grilse (Institute of Freshwater Fisheries, unpublished data). In Scotland, the largest salmon in the River Tweed appear to spawn in the main channel, not in the upper tributaries (D. Mills, letter to author, December 15, 1982). In the River Tana between Norway and Finland, the largest salmon also appear to spawn in the lower main channel (A. Rikstad, letter to author, April 5, 1983). These two observational results cast even more doubt on Schaffer and Elson's hypothesis, despite its intuitive appeal.

Idler and Clemens (1959) and Gilhousen (1980) performed detailed analyses of energy expenditures for Fraser River sockeye and found that males from the Adams River, which migrated 480 km upstream, were maturing at sea and apparently ceased feeding earlier than fish from the Stuart River, which continued feeding until they entered the river. Such differences in maturation schedules indicate the danger of a particular life history trait such as age at maturity can be viewed as an isolated response to one or two environmental factors. Life history traits interact. Age at maturity is best viewed only in the context of the entire life history of the organism (Warren and Liss 1980).

Perhaps age at maturity is not itself the adaptive trait. Rather, perhaps there exist adaptively advantageous stock-specific weights and physiological conditions females and males should attain, and the observed variations in age at maturity are merely indications of how many years it takes fish of each stock to reach this state. How would such an adaptive response explain the lower percentages of grilse in the north than in the south and the decreasing percentages of grilse from Breidafjördur to Vopnafjördur?

Smolts from the northwest may grow faster in the the ocean than those in the northeast because there is more warm Atlantic water in the west and perhaps more accompanying planktonic invertebrates and larval fish. If salmon stocks have

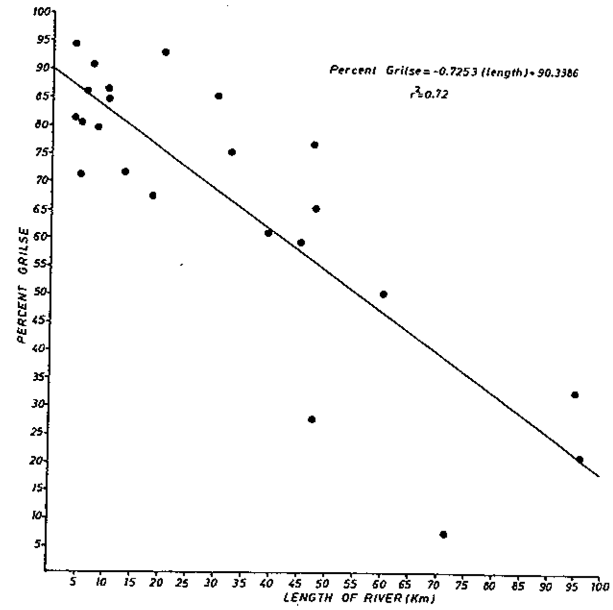

FIG. 5. Relation between length of 23 South Coast salmon rivers and percentage of females in the catch that were grilse.

evolved adaptively advantageous weights (and resultant fecundities) at which to mature under their unique environmental conditions and mortality rates, they may reach this weight (and resultant fecundity) after 1 yr at sea more often in the northwest than in the northeast, and more often in the south and west than in the northeast and northwest. This result would explain the strong correlations between sea temperature and percentages of grilse. It may also be advantageous for a smolt in the north to delay seaward migration until later in the season, when higher oceanic water temperatures and better feeding conditions may permit faster growth and better survival.

Smolts from northern stocks may emigrate later than those of southern stocks not only because of ocean conditions but because of slower warming of northern rivers and resulting later smoltification. In general, relative coastal air temperatures in spring and summer decrease from southwest to northeast around Iceland, parallel to sea temperatures (unpublished data, Icelandic Meteorological Office).

There have been few studies of smolts in Iceland, but most smolts from Ellidaár (No. 1) migrate into warm Atlantic water (8°C at 25 m) in late May and early June (Poe 1975). Preliminary results from some northern rivers show that salmon parr are silvery as late as September (S. Einarsson, personal communication). If salmon in the north and south spawn at about the same time, northern stocks would have fewer productive spring and summer months in the sea for active growth than southern stocks from when they left the river until they spawned. Because growth in weight and fecundity increase faster than linearly (Pope et al. 1961), there would still be strong selection within a year's growing season for reaching a large size (especially for courtship in males) and a large fecundity (especially for females). More large salmon that had reached this adaptively advantageous weight would mature (Alm 1959), but smaller fish would tend to remain in the sea. Fewer salmon in the northeast would attain this weight than in the northwest, and far fewer than in the south.

Similarly, perhaps the long, large rivers in the south have smolts which emigrate from the lower river in summer or autumn as well as in spring. Such a migration would explain the delayed maturity in these rivers. Although early warming of rivers may produce faster growth and earlier smoltification, in the end, the timing of the smolt migration must be a physiological response to short-term environmental conditions (e.g. weather, immediate food supply) superimposed upon an adaptive response to long-term environmental conditions (e.g. climate, food production cycles).

Although length, discharge, latitude, and ocean temperatures have been clearly correlated with age at maturity in Icelandic salmon, much more information is needed on smolt size, timing of smolt migrations, migration and feeding areas at sea, and maturation schedules both at sea and in the rivers before we clearly understand how these four factors affect age at sexual maturity.

Also according to Schaffer's (1974) model, high mortality during the second year at sea should favor fish returning as grilse, whereas high growth rates during the second year at sea should favor fish returning as multi-sea-winter salmon. If natural mortality during the second year at sea is less in the north than in the south, for a given fecundity, more fish would delay maturation in the north than in the south. Unfortunately, there is as yet no information on mortality rates of Icelandic salmon stocks.

I was better able to explain variations in percent of female grilse than male grilse because male parr mature in many rivers. In a river with many such parr, there would appear to be a higher proportion of multi-sea-winter salmon than actually exists. As no mature female parr have been found in Iceland, the percentages of grilse are more reliable for females than for males.

A higher percentage of male grilse than female grilse is found in nearly all rivers because it is probably less important for a male than for a female to have a high fecundity. Even mature male parr have abundant sperm and compete with large males during spawning (Jones and King 1949). Apparently male salmonids have more flexibility in their responses to age at maturity because of their lower reproductive investment (lower weight of sperm; Jonsson 1977).

Within a region, salmon from long, large, Icelandic rivers probably will show greater genetic tendencies toward late maturity than salmon from short, small rivers, as Ísaksson (1982) found for salmon in Dalsá. It is unclear if the differences in age at maturity between northern and southern stocks inhabiting short, small rivers have a strong genetic basis or if individual fish will readily alter their age at maturity physiologically under new environmental conditions imposed by fish breeders. Well-controlled breeding and rearing experiments should clarify in which cases genetic or environmental influences are dominant.

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