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Oceanic and Riverine Influences on Variations in Yield among Icelandic Stocks of Atlantic Salmon

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Abstract.—Data on yields of Atlantic salmon *Salmo salar* from 59 Icelandic rivers were analyzed with data on streamflows and sea and air temperatures in an attempt to identify why some stocks exhibited more variable yields than others. A group of 24 northern and northeastern rivers, which flowed into seas with wide annual variations in climatic and oceanic conditions (as indicated by coastal sea and air temperatures), exhibited significantly greater variation in Atlantic salmon yields of both grilse and two-sea-winter fish (two winters at sea before first spawning) than the 31 western rivers, which flowed into seas with more stable climatic and oceanic conditions. Yields were the most varied for stocks in the northeast, the region with the greatest annual variation in sea temperatures during spring and summer—the time when smolts migrate to the sea and begin to feed. Rivers with more variable seasonal streamflows also tended to have more variable two-sea-winter Atlantic salmon yields ($P < 0.05$) but not more variable grilse yields ($P > 0.05$). However, variations in streamflows were less useful than variations in sea and air temperatures for explaining variations in yield. We concluded that climatic and oceanic factors exert important influences on the variability in yield and abundance of Icelandic stocks of Atlantic salmon.

In Iceland, anglers, river owners, and managers have noticed that some rivers vary more than 10-fold in their annual yields (catches) of Atlantic salmon *Salmo salar*, whereas others are more stable. One hypothesis is that the causes of observed variations within and among Atlantic salmon stocks are biotic, that is, that they result from density-dependent growth and mortality based on competition for available space and food (Kristjánsson and Tómasson 1981). Such density-dependent growth and mortality, well documented in field studies on salmonids elsewhere (e.g., Chapman 1966; Gee et al. 1978; Buck and Hay 1984), would result in differently shaped stock-recruitment curves with different patterns of oscillations among rivers (Ricker 1954).

Another hypothesis is that causes of the observed variations are physical and climatic and result from variations in streamflow and associated physical habitat conditions in fresh water or from variations in the oceanic conditions encountered by the Atlantic salmon at sea (Scarnecchia 1984). Substantial evidence also has accumulated outside Iceland that streamflows and oceanic conditions influence salmonid abundance and yield (Smoker 1953; Binns and Eiserman 1979; Johnson 1984; Pearcy 1984).

A third hypothesis is that external physical and climatic variations might establish the general level of abundance or yield in a given year. This effect would be more obvious in years of extreme streamflows or climatic and oceanic conditions. However, once this general level is established, the actual stock abundance (or the control of the population in the sense of Nicholson 1933) would be fine-tuned mainly by competition and density-dependent growth and mortality. These hypotheses parallel the more general debate among other ecologists about whether populations vary and are regulated according to biotic factors (Nicholson 1933), climatic factors (Andrewartha and Birch 1954), or a complex (comprehensive) set of factors (Thompson 1929; Huffaker and Messenger 1964; Krebs 1972).

Our objectives were to quantify the variations in yields exhibited by Icelandic stocks of Atlantic salmon and to explain why one stock varies more in yields than another stock. We hypothesized that if physical factors (expressed as streamflows, air temperatures, and sea temperatures) rather than biotic factors (competition, predation, and diseases) exert the dominant influence on the variability of a stock, then those stocks that have the more variable yields of both grilse (one winter at sea before spawning) and two-sea-winter fish (two winters at sea before spawning) should be associated with rivers that have more variable physical attributes, such as more variable seasonal streamflows or flowing into areas of the sea that have more variable climatic and oceanic conditions.

Study Area and Environmental Variations

Rivers.—Rist (1956) classified Icelandic rivers into four types and combinations thereof distinguishable by characteristic seasonal discharge patterns: Dragá (D) or direct runoff; lake or standing-water fed (S); Lindá (L) or spring fed; and Jökulá (J) or glacier fed.

Spring-fed rivers, which originate mostly as gushing springs in younger parts of the Móberg Formation, are characterized by nearly constant flows and headwater temperatures (3–5°C) year-round (Rist 1956). Viable spring-fed Atlantic salmon rivers, such as Álftá, Haffjardará, and Laxá í Adaldal (Figure 1A), typically have non-spring-fed components to them. Laxá í Adaldal also is fed by a large lake, into which springs flow.

Lake-fed rivers comprise some of Iceland's most productive Atlantic salmon rivers (e.g., Úlfarsá, Bugda, and Grímsá). Their streamflows tend to be somewhat more variable than those of spring-fed rivers but much less variable than direct-runoff or glacial rivers.

Direct-runoff rivers typically drain areas with winter snow and usually have high discharges during snowmelt in spring or early summer (e.g., Fnjóská; Figure 1B). Our observations indicate that the more productive direct-runoff rivers commonly have peak discharges no later than late May. Those rivers draining high mountain areas in the north have later flow peaks, and such rivers are still quite cold during the summer growing season. Consequently, Atlantic salmon tend to be few in those rivers.

Glacial rivers have their highest discharges in summer when the glaciers are melting most rapidly (e.g., Blanda; Figure 1C). These rivers sometimes contain Atlantic salmon in sections with glacial flow components, but most fish occur in clear-water tributaries. Glacial rivers are usually highly variable in seasonal discharges.

Most of the larger Icelandic rivers are combinations of these types (Rist 1956), and their hydrographs reflect the various components of their streamflows.

Seas around Iceland.—Major differences in the degree of annual variation in sea conditions exist between the northern coast and the southern and western coasts of Iceland. According to Stefánsson (1960), annual variations in May–June sea temperatures are relatively small west of Iceland, where water from the Atlantic Ocean (salinity >35‰) predominates at all times. Off the north coast, and especially off the northeast coast, however, the influx of Atlantic water varies considerably from year to year, and annual variations in sea temperatures are greater than along the west coast. In warmer years, substantial amounts of warm Atlantic water extend around the northwest peninsula, progress along the north coast in spring and summer, and eventually reach the northeast coast. In most colder years, the East Icelandic and East Greenland currents are more dominant and reduce or eliminate this clockwise flow of Atlantic water around Iceland. More recently Malmberg and Stefánsson (1972) and Malmberg (1984) documented the changes in the East Icelandic Current during 1965–1969, when the current changed from an ice-free arctic current to a polar current that transported drift ice to the area northeast of Iceland. A more detailed summary of some important changes relevant to Atlantic salmon in the sea north and west of Iceland is provided by Scarnecchia (1984). In that paper, the relative stability of sea temperatures for a typical west-coast station is contrasted with the instability of a typical north-coast station.

Methods

Catch data for Atlantic salmon.—For 59 Atlantic salmon rivers (Figure 2), we based yields on counts of Atlantic salmon caught in carefully controlled recreational rod fisheries. The data are collected routinely by river associations and angling clubs under the overall supervision of the Institute of Freshwater Fisheries in Reykjavík; the data from each source constitute an independent data set. Data used here extended from 1965 to 1985, a period during which catch records were most reliable and Atlantic salmon stocks underwent at least two high and two low periods of yield.

The length of the angling season is limited by law (Salmon, Trout and Char Fishing Act 1970), and

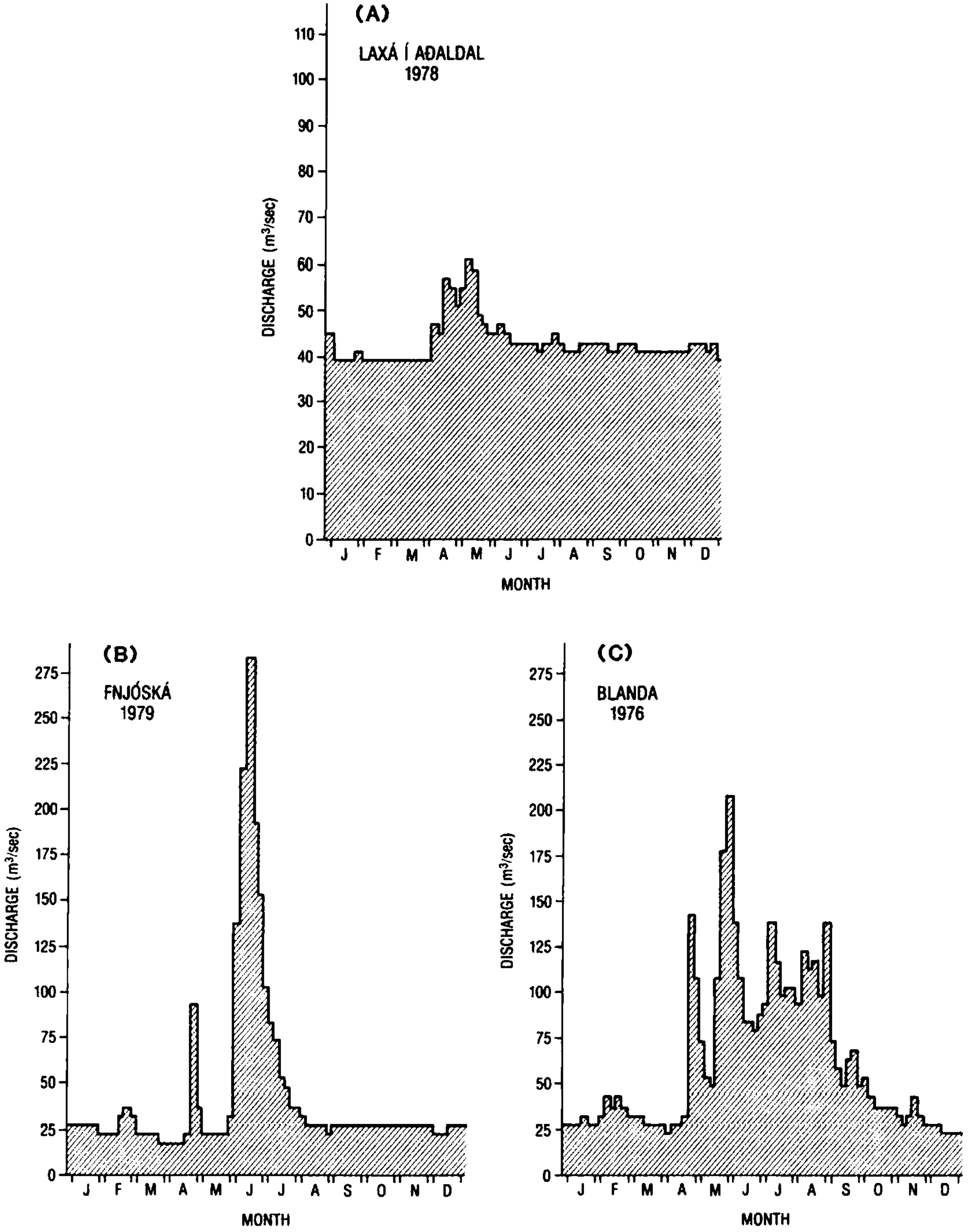

FIGURE 1.—Typical annual hydrographs for (A) spring-fed (Laxá í Aðaldal), (B) direct-runoff (Fnjóská), and (C) glacier-influenced (Blanda) rivers in Iceland.

the number of rods is generally the same from year to year. However, there have been periodic increases in effort on many rivers and, as a result of these increases and more diligent reporting, reported catches have risen (Institute of Freshwater Fisheries, unpublished data). In this paper, we have assumed that catches were indicative of abundance over the years used in the analyses (1965–1985). In some rivers and some years, incompletely reported data, installation of fish ladders, or effort changes known to have increased catch made the data unusable. We omitted all questionable data before any analyses were done, so some time series were less than 21 years long. The resulting data sets undoubtedly still have some deviations from our assumption that yield indicates abundance, but in our opinion, the final data sets were high-quality time series suitable for testing the hypotheses.

Each Atlantic salmon caught by anglers was classified separately by sex as grilse, two-sea-winter fish, or older fish based on weight-frequency distributions (Scarnecchia et al. 1989). Atlantic salmon that had spent more than two winters at sea were excluded from analyses. Scale samples indicated that a few repeat spawners were present. Any such fish classified by weight as a grilse, two-sea-winter, or older Atlantic salmon was included in that group.

For each of the 59 rivers, standard deviations of annual catches of both grilse and two-sea-winter fish were divided by the mean catch to obtain coefficients of variation (Appendix Table A.1; Snedecor and Cochran 1967), which were used as indices of the variability of the abundances and yields of Atlantic salmon from the individual rivers.

Sea temperature data.—Data on sea temperatures at six stations around the Icelandic coast were obtained from the Icelandic National Weather Office and used as indices of general oceanographic conditions around Iceland. For the six stations—Grindavík, Stykkishólmur, Sudureyri, Hraun, Raufarhöfn, and Thorvaldsstadir (Figure 2)—monthly mean sea-surface temperatures were based on several, usually equally spaced, measurements per month. These monthly mean temperatures were averaged separately for each of 4 months, April, May, June, and July, for the years 1957–1985. Those 4 months were chosen because Scarnecchia (1984) found that annual sea temperatures during April–July were related to yields of Atlantic salmon from several north-coast rivers, and the temperatures reflected the broader oceanic and hydrographic conditions around Iceland. Only 28 of the 696 monthly values were missing from the data set, and values were not estimated for these missing points. For each station the standard deviation of sea temperature over this 29-year period was divided by the mean to obtain the coefficient of variation, which was used as an index of variability for sea temperatures (Appendix Table A.1). In the ensuing analyses, the calculated variation in yield for each of the 59 rivers was tested against variation in sea temperature at the station where sea conditions most closely represented conditions off the mouth of that river.

Air temperature data.—Data on mean monthly air temperatures during May and June at 13 coastal stations around Iceland (Figure 2) also were obtained from the Icelandic National Weather Office. These data were based mainly on daily measurements. We used the variation in the monthly means of these temperatures as general indices of climatic variations around Iceland at a time when smolts would be leaving rivers. Most time series extended from 1957 to 1981; the shortest time series was 15 years. The variation in yield for each of the 59 rivers was tested against variation in air temperature at the air temperature station where conditions most closely represented conditions on that river.

Streamflow data.—Indices of seasonal variation in streamflow were based on monthly means and standard deviations of flow data from selected hydrographic stations; these data were obtained from the National Energy Authority (Rist and Sigurdsson 1982). For the 16 Atlantic salmon rivers that had gauging stations located on them, streamflow variations were calculated as the average of the 12 average monthly coefficients of variation (CV). These average monthly CVs were based on a variable number of years, usually 10 or more. Many other rivers with gauges had few or no Atlantic salmon in them but they had flow types (Rist 1956) similar to the rivers for which data were needed. For the 43 rivers whose streamflow variations had to be estimated, each river was identified as a particular hydrologic type (i.e., direct runoff, glacial, lake fed, spring fed, or combinations thereof) and its streamflow variation was estimated as the average of the coefficients of variation for rivers of the same type or type combination for which flow data were available (Appendix Table A.2).

Statistical analyses.—Simple linear and stepwise multiple regressions were used to investigate the relations between variations in Atlantic salmon yields of grilse and two-sea-winter fish (dependent variables) and variations in sea temperatures, air temperatures, and streamflows. Pearson's cor-

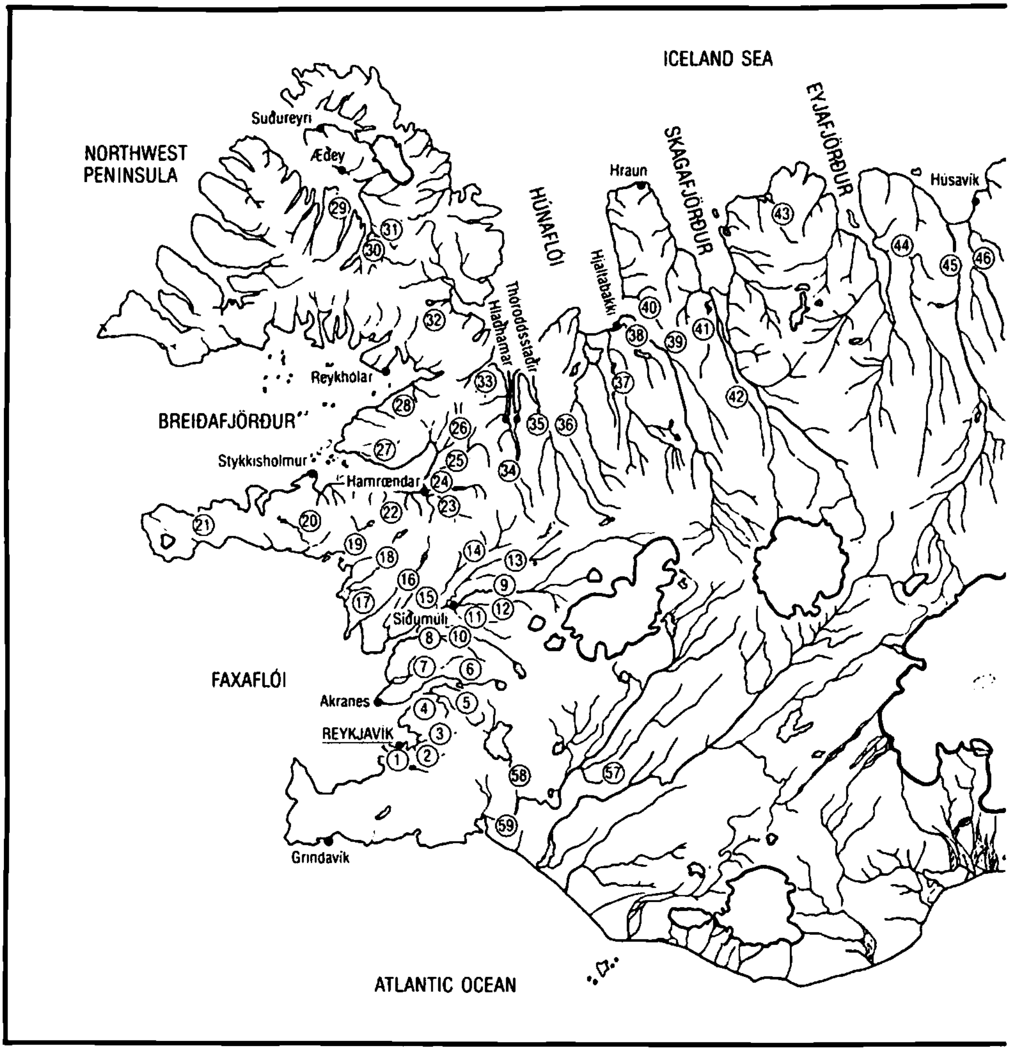

FIGURE 2.—Map of Iceland showing the 59 Atlantic salmon rivers investigated in this study (circled numbers) and the locations of oceanographic, weather, and hydrographic stations and geographic areas mentioned in the text and tables.

relation coefficients also were calculated to assess relations among and between variations in yields, sea and air temperatures, and flows. In addition, as a preliminary analysis of the variation in yields of grilse and two-sea-winter fish among rivers, data on yield variation for the 59 rivers were grouped by region and subjected to a one-way analysis of variance. The intent was to determine if rivers in the western region (rivers 1–28 and 57–59; Figure 2) exhibited yields that were more or less variable than those in the northern region (33–56), and if significant differences in variations in yields were evident among rivers in the southwest (1–20 and 57–59), west-central (21–28), northwest (29–32), north-central (33–46), and northeast (47–56) subregions.

Results

The 24 northern rivers exhibited significantly greater variation in yields of grilse and two-sea-winter fish than did the 31 western rivers (mean CV, 0.72 versus 0.46 for grilse; 0.68 versus 0.49 for two-sea-winter fish). In the comparisons among the five subregions, the southwest and west-central subregions did not differ from each other for either grilse or two-sea-winter fish ($P > 0.05$), but they did differ from all three northern subregions

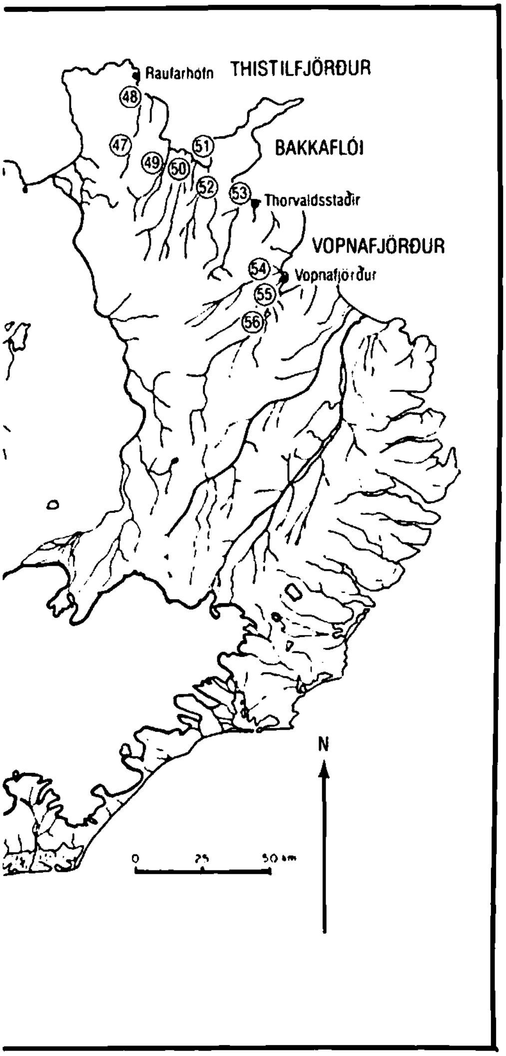

FIGURE 2.—Extended.

for grilse ($P < 0.05$) as well as from the northwest and northeast subregions for two-sea-winter fish ($P < 0.05$; Table 1; Figures 3, 4).

TABLE 1.—Results of least significant difference comparisons to detect significant differences ($P < 0.05$) in mean coefficients of variation in Atlantic salmon yields of grilse and two-sea-winter fish among 59 Icelandic rivers. Rivers were located in five geographic subregions (SW, southwest; WC, west-central; NW, northwest; NC, north-central; and NE, northeast). Yes = difference is significant; no = difference is not significant.

	Subregion			
Subregion	SW	WC	NW	NC
		Grilse		
WC	No			
NW	Yes	Yes		
NC	Yes	Yes	No	
NE	Yes	Yes	No	Yes
		Two-sea-winter fish		
WC	No			
NW	Yes	Yes		
NC	Yes	No	No	
NE	Yes	Yes	No	Yes

All four of the indices of sea temperature variation (April, May, June, and July) and both indices of air temperature variation (May and June) exhibited highly significant positive relations ($P < 0.01$) with variations in yields of both grilse and two-sea-winter fish for the 59 rivers. For grilse, variations in April and May sea temperatures were related most closely to the variations in yields and explained 47 and 42% of the variation in yield, respectively (Table 2). Those rivers with the greatest variations in their yields of grilse were in the north, particularly in the northeast, where variations in April and May sea temperatures were greatest. More specifically, rivers flowing into Faxaflói and Breidafjördur, which have more stable April sea temperatures (mean CV, 0.11 and 0.47, respectively), exhibited more stable grilse catches (Figure 3). Rivers flowing into fjords adjacent to the Iceland Sea (Húnaflói, Skagafjördur, Eyjafjördur, Thistilfjördur, Bakkaflói, and Vopnafjördur), which have progressively more variable sea temperatures from northwest to northeast (Appendix: Table A.1), were also progressively more variable in their grilse yields (Figure 3). Relations for two-sea-winter fish were similar to those for grilse but not as strong (Figure 4). Variations in April sea temperature and May air temperature explained 30 and 25%, respectively, of the variation in the CVs of yields of two-sea-winter fish (Table 2). In general, rivers with highly variable grilse yields also tended to have highly variable yields of two-sea-winter Atlantic salmon ($r = 0.75$, $P < 0.01$).

Rivers with more variable seasonal streamflows were also more likely to have more variable yields of two-sea-winter fish ($r = 0.34$, $P < 0.05$) but were not more likely to have more variable grilse yields ($r = 0.13$, $P > 0.05$; Table 3). Among those northern rivers with the most stable catches of both grilse and two-sea-winter fish were the important salmon rivers Laxá á Ásum, which is fed mainly by a lake, and Laxá í Adaldal, whose source is the spring-fed lake Mývatn. Although other relationships were observed between streamflow variations and yield variations, statistics indicated that streamflows were less useful for explaining variations in yield than sea and air temperatures were.

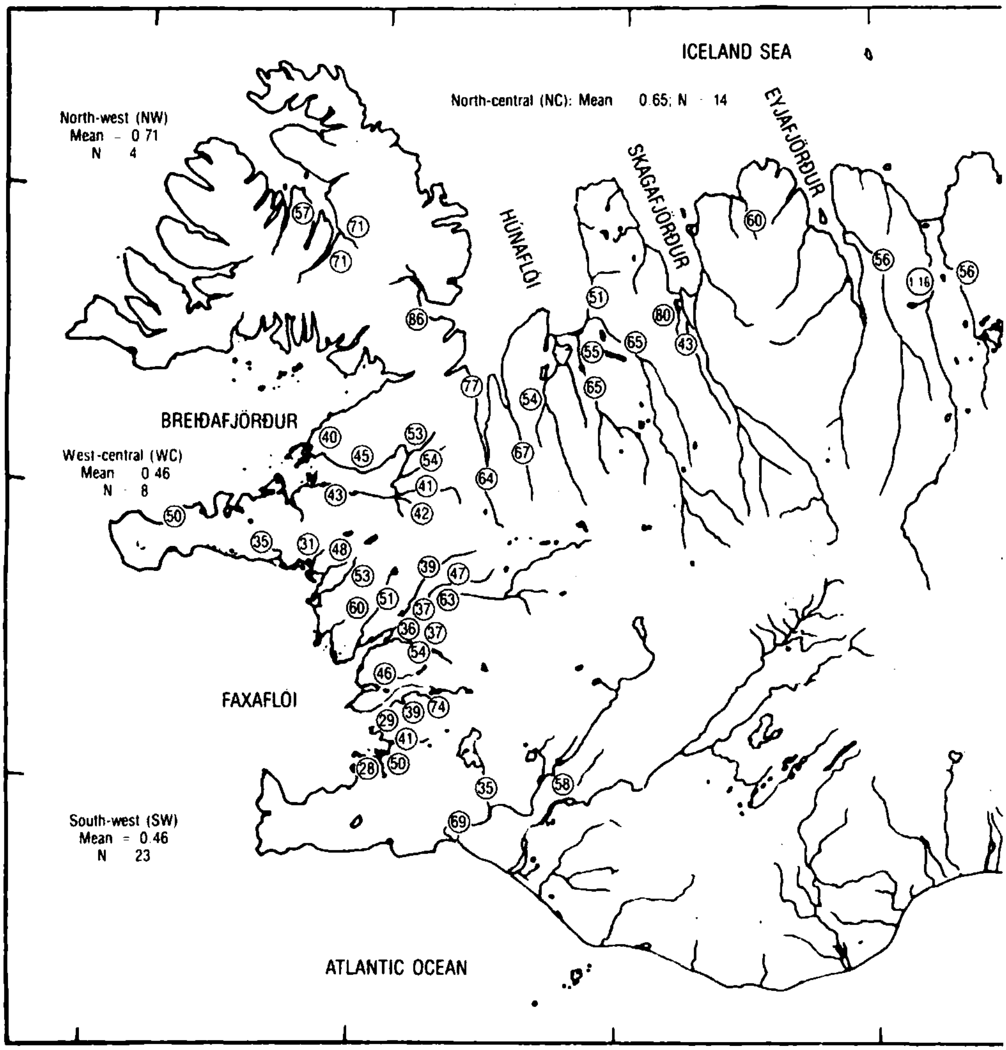

FIGURE 3.—Mean coefficients of variation (CV, 100 × SD/mean; circled numbers) of yields of Atlantic salmon grilse from 59 Icelandic rivers, 1965–1985. Overall mean CV for each subregion and number of rivers in the subregion are given around the perimeter of the map. (River names and characteristics are given in Figure 2 and Appendix Table A.1.)

In the stepwise model, April sea temperature and streamflow were the only two variables that significantly ($P < 0.05$) explained the observed variations in yield of two-sea-winter Atlantic salmon (Table 4). Inasmuch as the indices of variation for the four sea temperatures and two air temperatures were highly interrelated (Table 3), the other sea and air temperature variables were ineffective in explaining additional variations in yield once April sea temperature had entered the model. For grilse, once April sea temperature was included in the model, no other variables were important (Table 4).

Discussion

These results support the hypothesis that climatic and oceanic aspects of the environment exert an important influence on the variability in abundance of Atlantic salmon stocks in Iceland. West coast stocks tend to be more stable in their yield of both grilse and two-sea-winter Atlantic salmon than stocks on the north coast. The west coast stocks inhabit rivers flowing into less thermal-variable seas that are consistently influenced by Atlantic Ocean water (Stefánsson 1960). Yields from north-coast stocks (rivers 29–56; Figure 2) tend to fluctuate widely. These northern stocks

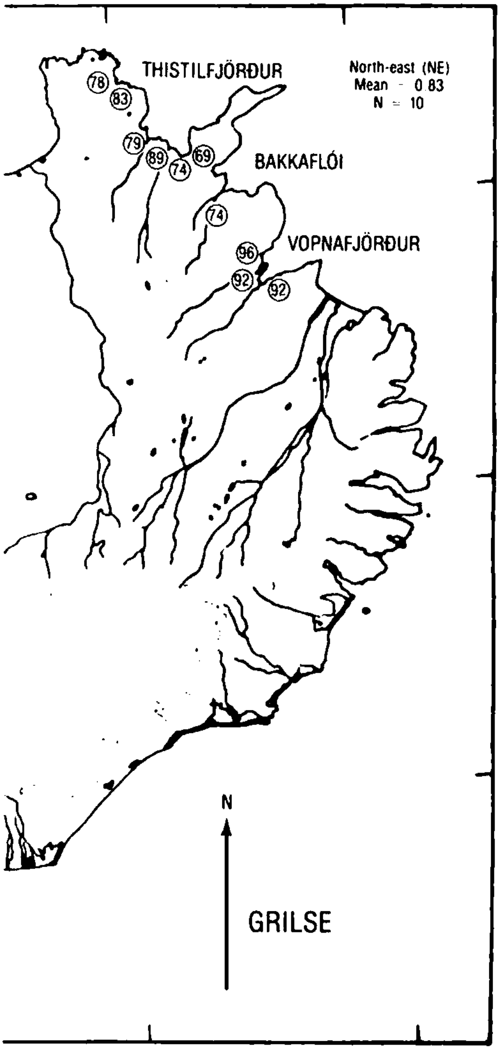

FIGURE 3.—Extended.

TABLE 2.—Linear relations and coefficients of determination (r^2) between environmental variables and variations in yields of Atlantic salmon grilse and two-sea-winter (2-SW) fish for 59 Icelandic rivers. Variables are coefficients of variation (CV) of yields of grilse and two-sea-winter fish (salmon); other variables are air or sea-water temperatures or streamflows in the months indicated. Asterisks indicate significant values at $P < 0.01$**.

Equation	r^2
Grilse versus air or sea temperature, or streamflow	
Grilse CV = 0.3918 + 0.4200(Sea Apr CV)	0.47**
Grilse CV = 0.3838 + 0.7419(Sea May CV)	0.42**
Grilse CV = 0.3548 + 1.4012(Sea Jun CV)	0.30**
Grilse CV = 0.2065 + 3.7629(Sea Jul CV)	0.38**
Grilse CV = 0.2479 + 0.8475(Air May CV)	0.41**
Grilse CV = 0.1664 + 3.2631(Air Jun CV)	0.30**
Grilse CV = 0.4863 + 0.0019(Flow)	0.02
2-SW fish versus air or water temperature, or streamflow	
Salmon CV = 0.4373 + 0.3209(Sea Apr CV)	0.30**
Salmon CV = 0.4426 + 0.5243(Sea May CV)	0.23**
Salmon CV = 0.4345 + 0.9148(Sea Jun CV)	0.14**
Salmon CV = 0.3266 + 2.5674(Sea Jul CV)	0.19**
Salmon CV = 0.3354 + 0.6272(Air May CV)	0.25**
Salmon CV = 0.2734 + 2.4280(Air Jun CV)	0.18**
Salmon CV = 0.3410 + 0.0046(Flow)	0.11**
2-SW fish versus grilse	
Salmon CV = 0.1241 + 0.7878(Grilse CV)	0.56**

inhabit rivers flowing into more thermal-variable seas that are influenced to variable degrees by Atlantic, arctic, and polar currents (Stefánsson 1960; Malmberg 1984, 1986). The rivers in the northeast exhibit particularly variable Atlantic salmon yields (Figures 3, 4), and it is along the northeast coast that oceanic conditions, as indicated by sea temperatures (Appendix Table A.1), are the most variable.

Nickelson and Lichatowich (1984), in an attempt to explain why catches of coho salmon *Oncorhynchus kisutch* in Oregon were more variable than those in Washington, British Columbia, and Alaska, suggested that "one reason for the greater variation for Oregon landings may be Oregon's location near the southern edge of the [coho salmon's] distribution. The environment is likely to be sub-optimum more often near the edge of coho distribution than it is near the center of coho distribution, thus resulting in a more variable population." We believe that this explanation for coho salmon in Oregon also applies to Atlantic salmon in Iceland. The northern stocks are nearer the northern edge of the species' distribution than the southern stocks. It is also the northern stocks that must cope with the extreme variations in conditions in the Iceland Sea. The oceanic effect exerting a major influence on yield variation is the relative dominance of oceanic currents in a given year. Scarnecchia (1984) reported that colder, less saline waters off north Iceland from 1965 to 1970 coincided with declines in primary production (Thórdardóttir 1977), standing crops of zooplankton (Ástthórsson et al. 1983), Atlantic herring *Clupea harengus harengus* (Jakobsson 1980), numbers and weights of Atlantic cod *Gadus morhua* and capelin *Mallotus villosus* (Malmberg 1986), and Atlantic salmon yields. This effect through the food chain is one possible mechanism that could explain the observed variations in Atlantic salmon yield and abundance. The other mechanism that potentially reduced yields, that of reduced or delayed smolt migrations in colder years (Scarnecchia 1984), cannot be ruled out.

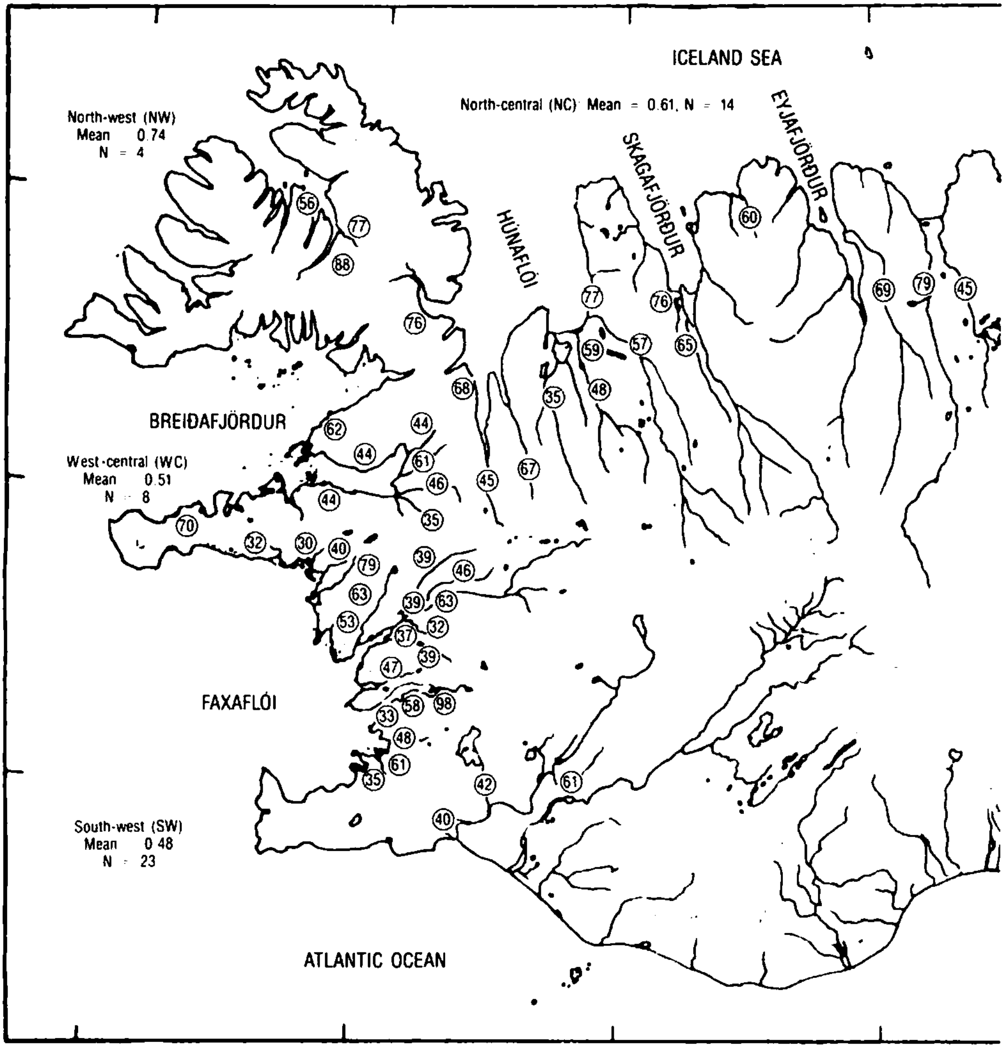

FIGURE 4.—Mean coefficients of variation (CV, 100 × SD/mean; circled numbers) of yields of two-sea-winter Atlantic salmon from 59 Icelandic rivers, 1965–1985. Overall mean CV for each subregion and number of rivers in the subregion are given around the perimeter of the map. (River names and characteristics are given in Figure 2 and Appendix Table A.1.)

The observed significance of streamflow variations in explaining the variable yields of two-sea-winter fish (Table 4) is consistent with the results of Binns and Eiserman (1979) and others whose data have indicated that rivers with more stable flows provided a more stable rearing environment for salmonids. At least two factors, however, may have produced the lack of a significant relation between variations in grilse yields and flows and the only weakly significant relation between variations in yields of two-sea-winter fish and flows. First, the actual streamflow data were unavailable for most of the rivers, so indices of streamflow variation were developed by using mean values for rivers of the same type. To test the relation between variations in streamflows and yield more accurately, more comprehensive flow data are needed for more salmon rivers in Iceland.

Secondly, not only streamflow variation but also thermal and habitat conditions in the rivers affect the habitat quality and also may affect yield variations. For example, some spring-fed rivers with stable flows may have stream temperatures at the lower margin of acceptability for Atlantic salmon growth and survival. In such cases, the stream may be quite unstable as a rearing habitat, and a

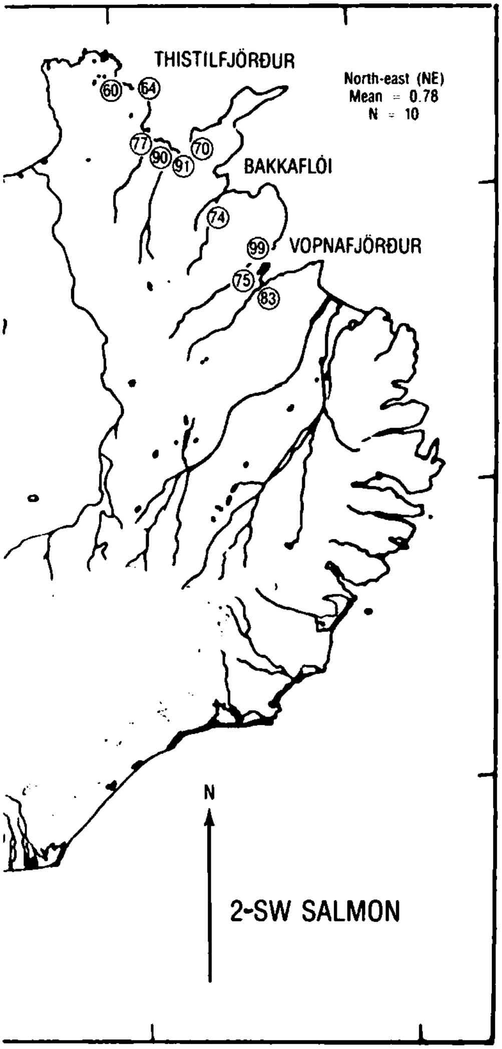

FIGURE 4.—Extended.

TABLE 4.—Variables that explained significant variation in coefficients of variation (CV) of Atlantic salmon yields of grilse and two-sea-winter fish in stepwise analyses for 59 Icelandic rivers. Asterisks denote significant values at $P < 0.05$* and $P < 0.01$**. The criterion for entry into the stepwise model was $P < 0.05$.

Variable entered	Percent of variation explained
CV for grilse	
CV for April sea temperature	47**
Total variation explained	47**
CV for two-sea-winter fish	
CV for April sea temperature	30**
CV for streamflow	5*
Total variation explained	35**

productive or unproductive year may depend on the degree of warming of the water. Stocks in such streams may have less stable yields than in other spring-fed rivers that might warm more rapidly and to higher temperatures in spring and early summer. These observations merely underscore the established idea that several factors determine the suitability of habitats for salmonids (Binns and Eiserman 1979). If more comprehensive streamflow data and other habitat information were available, more of the yield variations among Atlantic salmon stocks probably would be explained.

In an earlier paper, Scarnecchia (1984) suggested that perhaps it is not a question of whether climate and ocean conditions or density-dependent growth and smolt production regulate annual abundance of Atlantic salmon in Icelandic rivers. Instead, climatic and hydrographic factors, oceanic productivity, and density of spawners, parr, and smolts all may interact to produce long-term fluctuations in abundance and yield. We have shown that the extent of fluctuations in yields among Icelandic rivers is related to the extent of climatic (i.e., air temperature) and oceanic (i.e., sea tem-

TABLE 3.—Correlations between coefficients of variation (CV) for environmental variables and for Atlantic salmon yields of grilse and two-sea-winter fish (2-SW fish) for 59 Icelandic rivers. Other variables are CVs of air or seawater temperatures or streamflow in the months indicated. Asterisks denote significant values at $P < 0.01$**.

	Variable							
Variable	A	B	C	D	E	F	G	H
Grilse (A)								
Salmon (B)	0.75**							
Flow (C)	0.13	0.34**						
Air May (D)	0.64**	0.50**	0.24					
Air Jun (E)	0.55**	0.43**	0.24	0.93**				
Sea Apr (F)	0.68**	0.55**	0.21	0.92**	0.86**			
Sea May (G)	0.65**	0.48**	0.12	0.90**	0.88**	0.96**		
Sea Jun (H)	0.55**	0.37**	0.07	0.81**	0.84**	0.88**	0.97**	
Sea Jul (I)	0.61**	0.44**	0.07	0.88**	0.86**	0.89**	0.96**	0.94**

perature) variations associated with a stock. For Icelandic stocks of Atlantic salmon, especially those on the north coast, we suggest that these climatic variations, manifested most visibly in hydrographic conditions at sea, most commonly establish the outer boundaries of variation likely to be observed. Within these outer bounds, yield variations resulting from variations in streamflow and other physical conditions may be manifested. As long as flow variations are not severe (e.g., from catastrophic flooding or drought), variations in yields resulting from flow variations probably will lie inside the range of effects caused by oceanic factors. Within the range of variations caused by the physical effects, variations from biotic effects (i.e., competition and resultant density-dependent growth and mortality) may occur. More research is needed on the importance of biotic effects on the population size of Atlantic salmon in Icelandic rivers. If investigators search for evidence of the effects of density-dependent growth and mortality on adult Atlantic salmon yields, we suggest that they would most likely detect it in western Icelandic rivers with stable streamflows, and they would least likely detect it in northern rivers with highly variable streamflows. The latter streams, as seen in this paper and in Scarnecchia (1984), most likely would exhibit yields strongly influenced by climatic and oceanic variations.

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Appendix: Coefficients of Variation in Yield and Environmental Factors

TABLE A.1.—River type (Rist 1956) and coefficients of variation (SD/mean) in yields of grilse and two-sea-winter Atlantic salmon, streamflows, and air and sea temperatures for 59 Icelandic rivers. Specific information on stations used for air and sea temperatures and streamflows is available from the authors. River types: D = direct runoff, J = glacier fed, L = spring fed, and S = lake or standing-water fed.

River			Coefficient of variation								
						Air temperature		Sea temperature			
Number[a]	Name	Type	Grilse	Two-sea-winter fish	Flow[b]	May	Jun	Apr	May	Jun	Jul
Southwest subregion											
1	Ellidaár	L+S+D	0.28	0.35	47	0.21	0.08	0.11	0.10	0.09	0.07
2	Úlfarsá	S+D+L	0.50	0.61	52	0.21	0.08	0.11	0.10	0.09	0.07
3	Leirvogsá	D+L	0.41	0.48	60	0.21	0.08	0.11	0.10	0.09	0.07
4	Laxá i Kjós	D+S	0.29	0.33	49	0.21	0.08	0.11	0.10	0.09	0.07
5	Bugda	D+S	0.39	0.58	49	0.21	0.08	0.11	0.10	0.09	0.07
6	Brynjudalsá	D	0.74	0.98	61	0.21	0.08	0.11	0.10	0.09	0.07
7	Laxá i Leirársveit	D+S	0.46	0.47	49	0.21	0.08	0.11	0.10	0.09	0.07
8	Andakilsá	D+S	0.54	0.39	60	0.30	0.11	0.11	0.10	0.09	0.07
9	Hvitá	D+L+J	0.36	0.37	20	0.30	0.11	0.11	0.10	0.09	0.07
10	Grímsa–Tunguá	S+L+D	0.37	0.32	29	0.30	0.11	0.11	0.10	0.09	0.07
11	Flókadalsá	D	0.37	0.39	61	0.30	0.11	0.11	0.10	0.09	0.07
12	Reykjadalsá	D+L	0.63	0.63	60	0.30	0.11	0.11	0.10	0.09	0.07
13	Thverá	D	0.47	0.46	61	0.30	0.11	0.11	0.10	0.09	0.07
14	Nordurá	D	0.39	0.39	61	0.30	0.11	0.11	0.10	0.09	0.07
15	Gljúfurá	D	0.60	0.63	61	0.30	0.11	0.11	0.10	0.09	0.07
16	Langá	D+S	0.51	0.53	49	0.30	0.11	0.11	0.10	0.09	0.07
17	Álftá	L+D	0.53	0.79	40	0.30	0.11	0.11	0.10	0.09	0.07
18	Hitará	S+D	0.48	0.40	65	0.30	0.11	0.11	0.10	0.09	0.07
19	Haffjardará	L+D+S	0.31	0.30	43	0.30	0.11	0.11	0.10	0.09	0.07
20	Straumfjardará	D+S	0.35	0.32	57	0.30	0.11	0.11	0.10	0.09	0.07
West-central subregion											
21	Fródá	D+L	0.50	0.70	60	0.33	0.12	0.47	0.23	0.15	0.08
22	Laxá i Skógarströnd	D	0.43	0.44	61	0.33	0.12	0.47	0.23	0.15	0.08
23	Midá i Dölum	D	0.42	0.35	61	0.33	0.12	0.47	0.23	0.15	0.08
24	Haukadalsá	D+S	0.41	0.46	63	0.33	0.12	0.47	0.23	0.15	0.08
25	Laxá i Dölum	D	0.54	0.61	61	0.33	0.12	0.47	0.23	0.15	0.08
26	Fáskrúd	D	0.53	0.44	61	0.33	0.12	0.47	0.23	0.15	0.08
27	Flekkudalsá	D	0.45	0.44	61	0.33	0.12	0.47	0.23	0.15	0.08
28	Hvolsá–Stadarhólsá	D	0.40	0.62	61	0.36	0.12	0.47	0.23	0.15	0.08

TABLE A.1.—Continued.

River			Coefficient of variation								
Number[a]	Name	Type	Grilse	Two-sea-winter fish	Flow[b]	Air temperature May	Air temperature Jun	Sea temperature Apr	Sea temperature May	Sea temperature Jun	Sea temperature Jul
Northwest subregion											
29	Laugardalsá	D+S	0.57	0.56	49	0.35	0.12	0.47	0.16	0.09	0.07
30	Langadalsá	D	0.71	0.88	61	0.35	0.12	0.47	0.16	0.09	0.07
31	Hvannadalsá	D	0.71	0.77	61	0.35	0.12	0.47	0.16	0.09	0.07
32	Vídidalsá í Stgrf	D	0.86	0.76	61	0.50	0.16	0.70	0.46	0.26	0.13
North-central subregion											
33	Víkurá	D	0.77	0.68	61	0.50	0.16	0.70	0.46	0.26	0.13
34	Hrútafjardará–Síká	D	0.64	0.45	61	0.50	0.16	0.70	0.46	0.26	0.13
35	Midfjardará	D	0.67	0.67	61	0.60	0.16	0.70	0.46	0.26	0.13
36	Vídidalsá–Fitjaá	D+S	0.54	0.35	49	0.60	0.16	0.70	0.46	0.26	0.13
37	Vatnsdalsá	D+L+S	0.65	0.48	31	0.60	0.16	0.70	0.46	0.26	0.13
38	Laxá á Ásum	S+D	0.55	0.59	58	0.40	0.13	0.70	0.46	0.26	0.13
39	Blanda–Svartá	D+J	0.65	0.57	39	0.40	0.13	0.70	0.46	0.26	0.13
40	Laxá-ytri	D	0.51	0.77	61	0.51	0.18	0.70	0.46	0.26	0.13
41	Saemundará	D	0.80	0.76	61	0.51	0.18	0.70	0.46	0.26	0.13
42	Húseyjarkvísl	D+L	0.43	0.65	60	0.51	0.18	0.70	0.46	0.26	0.13
43	Fljótaá	S+D	0.60	0.60	49	0.51	0.18	0.70	0.46	0.26	0.13
44	Fnjóská	D	0.56	0.69	61	0.51	0.18	0.70	0.46	0.26	0.13
45	Skjálfandafljót	D+L+J	1.16	0.79	28	0.38	0.14	0.70	0.46	0.26	0.13
46	Laxá í Adaldal	L+S	0.56	0.45	10	0.38	0.14	0.70	0.46	0.26	0.13
Northeast subregion											
47	Ormarsá	D+L	0.83	0.64	60	0.63	0.17	0.88	0.44	0.21	0.15
48	Deildará	D+S	0.78	0.60	49	0.63	0.17	0.88	0.44	0.21	0.15
49	Svalbardsá	D	0.79	0.77	61	0.63	0.17	0.88	0.44	0.21	0.15
50	Sandá	D+L	0.89	0.90	60	0.63	0.17	0.88	0.44	0.21	0.15
51	Hölkná	D	0.74	0.91	61	0.63	0.17	0.88	0.44	0.21	0.15
52	Hafralónsá	D	0.69	0.70	61	0.63	0.17	0.88	0.44	0.21	0.15
53	Midfjard–Bakk	D	0.74	0.74	61	0.58	0.16	0.92	0.48	0.22	0.12
54	Selá	D+L	0.96	0.99	60	0.62	0.16	0.92	0.48	0.22	0.12
55	Vesturdalsá	D	0.92	0.75	61	0.62	0.16	0.92	0.48	0.22	0.12
56	Hofsá	D	0.92	0.83	61	0.62	0.16	0.92	0.48	0.22	0.12
Southwest subregion											
57	Stóra-Laxá	D	0.58	0.61	61	0.21	0.08	0.11	0.10	0.09	0.07
58	Sogid	L+S	0.35	0.42	13	0.21	0.08	0.11	0.10	0.09	0.07
59	Ölfusa–Hvítá	D+J+S+L	0.69	0.40	21	0.21	0.08	0.11	0.10	0.09	0.07

[a] See Figure 2. [b] 100 × CV.

TABLE A.2.—Mean coefficients of variation (CV; 100 × SD/mean) for different types of Icelandic rivers (Rist 1956; Rist and Sigurdsson 1982) with gauging stations on them. These data, obtained from some rivers that had Atlantic salmon and some that did not were used as estimates of streamflow variations for similar types of rivers that had Atlantic salmon but did not have gauging stations. River type: D = direct runoff; L = spring fed; S = lake or standing-water fed; and J = glacier fed.

River type	N	Mean CV	SD	River type	N	Mean CV	SD
D	16	61	10.8	S+D	4	65	16.0
L	8	22	20.3	L+D+S	1	43	
D+L	2	60	2.1	S+D+L	3	43	7.8
L+D	4	40	22.8	D+L+J	1	28	
L+S	5	19	15.9	D+L+S	2	46	21.2
D+S	4	49	15.0	D+J+L	1	29	
D+J	9	38	13.6	D+J+S+L	1	39	