Climatic and Oceanic Variations Affecting Yield of Icelandic Stocks of Atlantic Salmon (*Salmo salar*)

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Regression analysis was used to investigate the effects of variations in climate, weather, and ocean conditions on yields of Atlantic salmon (*Salmo salar*) to anglers from 15 Icelandic rivers. Catches of grilse from the northern and northeastern group of rivers fluctuated together, as did catches from the southwestern and western group of rivers, but seldom did catches from the two groups of rivers fluctuate together. The dividing point for grouping rivers with similarly fluctuating catches was the northwest peninsula, which separated warm Atlantic water from colder north Icelandic waters of the Iceland Sea. Changes in atmospheric circulation (mid-1950's to mid-1960's) resulted in marked changes in hydrography off north Iceland from 1965 to 1970, which coincided with declines in primary production and standing crops of zooplankton, in reduced abundance and altered distribution of pelagic forage fishes, and in declines in salmon yields from north coast rivers. Few grilse were also caught from most rivers in 1980 after low sea and air temperatures in spring of 1979. Highly significant relationships were found between mean June–July sea temperatures at Hraun on the north coast and yield of grilse the following year from the northern rivers Vatnsdalsá, Víðidalsá, Hrútafjarðará, and Miðfjarðará and its three tributaries. Sea temperatures in April–May and May–June were also closely correlated ($P < 0.01$ and $P < 0.05$) with grilse catches from these rivers. Correlations were similar but less close for two-sea-winter salmon. Fewer statistically significant relations were found between sea temperatures and yields for south coast rivers; sea temperatures were higher there and varied less between years. Inasmuch as low sea temperatures and low river temperatures often occur in the same years, salmon yields may be regulated by several adverse climatic and hydrographic factors acting in combination, resulting in delayed smoltification and reduced growth and survival at sea.

On a utilisé une analyse de régression pour étudier les effets des variations des conditions climatiques, atmosphériques et océaniques sur les rendements de la pêche sportive du saumon de l'Atlantique (*Salmo salar*) dans 15 rivières de l'Islande. Les prises de madeleineaux dans le groupe de rivières du nord et du nord-est variaient de pair, tout comme les prises dans les rivières de l'ouest et du sud-ouest. Les prises entre ces deux groupes de rivières fluctuaient rarement ensemble. La péninsule du nord-ouest, qui sépare les eaux chaudes de l'Atlantique des eaux plus froides du nord de la mer d'Islande, représente le point de division entre les groupes de rivières où les fluctuations sont semblables. Les modifications de la circulation atmosphérique (du milieu de 1950 au milieu de 1960) ont entraîné des changements hydrographiques prononcés au large de la côte nord de l'Islande de 1965 à 1970, changements qui ont coïncidé avec des baisses de la production primaire et des biomasses du zooplancton, une réduction de l'abondance des poissons pélagiques alimentaires et une modification de leur répartition et la chute des rendements de saumon dans les rivières de la côte nord. De plus, un très petit nombre de madeleineaux ont été capturés dans la plupart des rivières en 1980 à la suite des basses températures de l'air et de la mer au printemps 1979. On a trouvé des relations très significatives entre les températures moyennes de la mer à Hraun, sur la côte nord, en juin et juillet, et le rendement des madeleineaux l'année suivante, dans les rivières septentrionales Vatnsdalsá, Víðidalsá, Hrútafjarðará et Miðfjarðará et ses trois tributaires. Les températures de la mer en avril–mai et mai–juin étaient aussi en étroite corrélation ($P < 0,01$ et $P < 0,05$) avec les prises de madeleineaux dans ces rivières. Les corrélations étaient semblables mais moins étroites pour les saumons ayant séjourné deux hivers en mer. On a décelé moins de corrélations statistiquement significatives entre les températures de l'eau et les rendements dans les rivières de la côte sud, où les températures de la mer étaient plus élevées et variaient moins d'une année à l'autre. Dans la mesure où les basses températures de l'eau douce et de l'eau salée surviennent souvent les mêmes années, les rendements de saumon peuvent être régularisés par plusieurs facteurs climatiques et hydrographiques contraires agissant ensemble et entraînant une smoltification tardive ainsi qu'une croissance et une survie diminuées en mer.

Yields of Atlantic salmon (*Salmo salar*) from Icelandic rivers often vary severalfold between years. By understanding and predicting these variations, biologists can reduce economic uncertainty for river owners and

fishermen and suggest prudent harvest rates for maintaining each stock.

Yields of both Atlantic and Pacific salmon from rivers close together within their respective ranges have often fluctuated together: Oregon (McKernan et al. 1950), Sweden (Alm 1954; Lindroth 1957), and Scotland (Thorpe and Mitchell 1981).

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Can. J. Fish. Aquat. Sci., Vol. 41, 1984

917

Salmon yields of neighboring stocks may be similarly affected by variations in large-scale environmental factors such as long-term (>1 yr) climate, short-term (<1 yr) weather, and variations in oceanic factors such as water temperatures, salinities, and currents.

Variations in climate, weather, and ocean conditions have been associated with fluctuations in salmon yield and abundance elsewhere. Vernon (1958) reported that April–August surface seawater temperatures in Georgia Strait, off British Columbia, showed a close inverse correlation ($r = -0.86$) with odd-year catches of Fraser River pink salmon (*Oncorhynchus gorbuscha*) in the following year, from 1935 to 1957. In 1958, an abnormally high percentage of Fraser River sockeye salmon (*O. nerka*) migrated northward through the Queen Charlotte Strait instead of through Juan de Fuca Strait, apparently in response to unusually high sea temperatures and related hydrographic anomalies in the North Pacific (Gilhousen 1960; Royal and Tully 1961). Greater coastal upwelling has been positively correlated with increased yields of coho salmon (*O. kisutch*), both wild (Scarnecchia 1981) and hatchery reared (Gunsolus 1978). Van Hyning (1973) found a significant negative relation between water temperature in June at Amphitrite Point, British Columbia, and subsequent return of fall chinook salmon (*O. tshawytscha*) to the Columbia River for brood years 1938–46. Chadwick (1982) found a positive ($r = 0.57$) but statistically insignificant ($P > 0.05$) relation between marine survival rate of Atlantic salmon smolts from Western Arm Brook, Newfoundland, and May–July sea water temperatures at depths of 1–20 m near St. John's. Despite these findings, the effects of climate, weather, and oceanic conditions on salmon yield are poorly understood. Many investigators doubt that any close causal relation exists between these environmental factors and salmon yields for stocks in individual rivers or groups of rivers. Yet, marine survival rates of salmon often vary substantially between years. Royal and Tully (1961) reported that annual marine survival rates for Fraser River sockeye salmon ranged from 4 to 18%.

In this paper I investigate the effects of variations in climate and weather around Icelandic rivers and the ocean conditions off the rivers on subsequent yields of grilse (one winter at sea) and two-sea-winter Atlantic salmon. I hypothesized that if climate, weather, or ocean conditions significantly affected yield, one stage where these factors would act would be between the presmolt stage and the grilse stage, since the ratio between the yield of grilse in one year and two-sea-winter salmon the next year is rather constant and predictable for most rivers (Kristjánsson 1982). In addition, recognizable statistical relations should exist between weather, climate, and ocean conditions and yield of grilse and two-sea-winter salmon because Icelandic rivers (particularly those on the north coast) are near the northern limit of the Atlantic salmon's distribution. Adverse weather, climate, and ocean conditions in spring and early summer could affect salmon yields by reducing or delaying the smolt migration or by reducing the smolts' growth and survival rates at sea, or both.

The objectives were (1) to investigate the effects of March–July sea surface temperatures on yields of grilse from 15 Icelandic rivers (Fig. 1) 1 yr later and yields of two-sea-winter salmon 2 yr later and (2) to relate these sea temperatures to variations in climate, weather, air temperatures, river temperatures, ocean salinities, changes in currents, and other factors that might cause salmon yields to fluctuate.

Chronology of Recent Climatic, Weather, and Hydrographic Variations around Iceland

Climate, weather, and oceanic conditions vary markedly along Iceland's north coast (Fig. 2) (Stefánsson 1954, 1960). Sudden changes in weather result from alternating intrusions of polar air from the north and warm or transitional air from the Atlantic region (Eythórsson and Sigtryggsson 1971). Either of these intrusions can on average dominate the other over a period of years, resulting in long-term shifts in climate and hydrography.

In the early 1950's, a persistent high pressure system developed over Greenland that on average strengthened through the late 1960's. According to Dickson et al. (1975) the mean pressure at sea level at Greenland rose more than 700 Pa between 1900–39 and 1956–65 and an additional 500 Pa between 1956–65 and 1966–70. Airflow around the high pressure area greatly increased the frequency and duration of northerly winds reaching Iceland, which produced substantial declines in mean air temperature on the north coast by 1965, e.g. a 3–4° decline at Hraun in March (Fig. 3).

Concurrently, the increase in northerlies altered the composition of ocean currents around Iceland (Fig. 2). The East Greenland Current carrying polar water of low salinity (<34.5‰) became more extensive. The East Icelandic Current, which had been an ice-free Arctic current during 1948–63, became an ice-transporting polar current from 1964 to 1971 (Malmberg 1972). Malmberg stated that by 1965, "it was notable how much farther south and west the cold tongue of the East Icelandic Current reached than in previous years." This current became more strongly stratified than in the preceding period because of the cold, low-salinity polar water in the surface layer.

By August 1964 the sea temperatures at 20-m depth were abnormally low, both in the East Icelandic Current and off the northwestern coast of Iceland (Jakobsson 1978). During succeeding years until 1971, northerly winds dominated and the air temperatures (Fig. 3), sea temperatures (Fig. 4), and salinities (Fig. 5) on the north coast were consistently lower throughout spring and early summer than in the previous decade. The low air temperatures and northerly winds apparently resulted in sharply decreased inflow of warm Atlantic water to the north coast (Stefánsson and Gudmundsson 1969) and in the oceanic area between Iceland and Jan Mayen. The formation of sea ice and the wind-driven transport of pack ice close to and against the north coast were also more prevalent in 1965 and 1967–70 than in previous years (Malmberg 1972).

In winter of 1970–71 the previously dominant high pressure system over Greenland collapsed and the mean pressure at sea level during winter dropped by 960 Pa between 1966–70 and 1971–74 (Dickson et al. 1975). From 1972 to 1974 the flow of Atlantic water into northern Icelandic waters was greater than in any year from 1965 to 1971, but in 1975 there was again drift ice off northern Iceland and in 1976–80 persistent high pressure again began to build over Greenland, increasing 500–600 Pa above 1971–75 values. The percentage of polar water in the East Icelandic Current (as measured at 67–69°N and 11–15°W) again increased (Fig. 5) (Malmberg 1983). Although sea surface temperatures during May–July 1976 and 1977 at Hraun were higher than in 1965–70, by winter 1978–79 and spring 1979, there was more sea ice than in any other year after 1965–70, and the sea surface temperature at Hraun was comparable with temperatures in 1965 and 1967–69 (Fig. 4a).

918

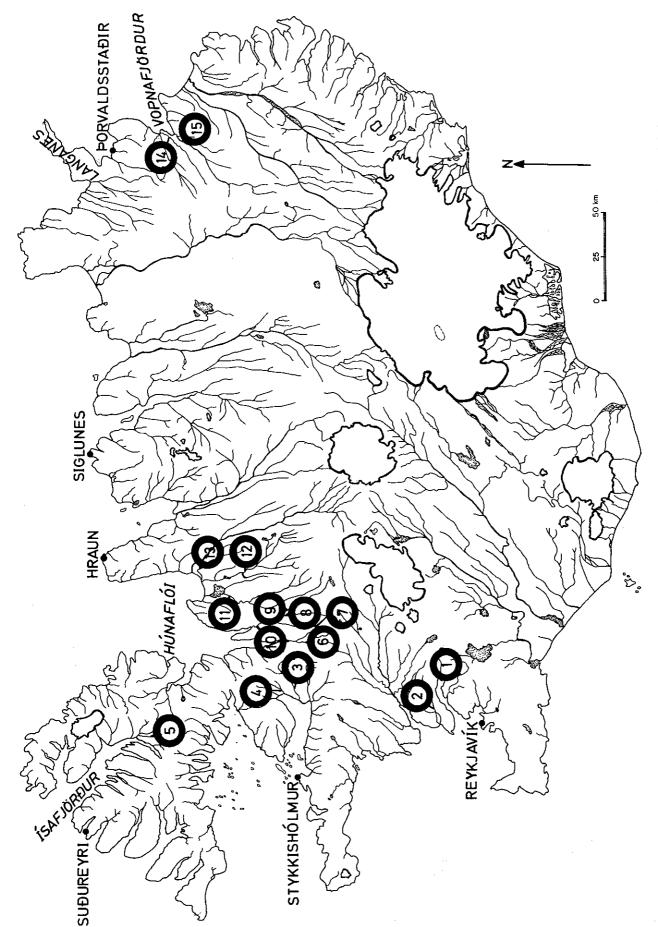*Can. J. Fish. Aquat. Sci., Vol. 41, 1984*

Fig. 1. Locations and rivers of Iceland mentioned in text. 1, Laxá í Kjós; 2, Laxá í Leirársveit; 3, Laxá í Dölum; 4, Fáskrúð; 5, Langadalsá; 6, Hrútafjardará; 7, Vesturá; 8, Núpsá; 9, Austurá; 10, Midfjardará; 11, Viðidalsá; 12, Vatnsdalsá; 13, Laxá á Ásum; 14, Vesturdalsá; 15, Hofsá.

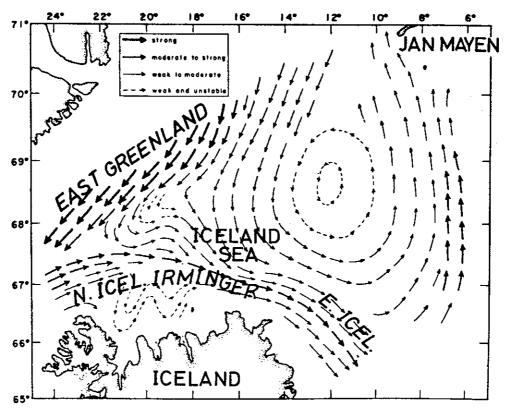*Can. J. Fish. Aquat. Sci., Vol. 41, 1984*

919

FIG. 2. Major currents off the north coast. (Adapted from Stefánsson 1962)

In 1980 there was a strong influx of warm Atlantic water to the north coast from the west, and the East Icelandic Current was dominated by ice-free Arctic water (Vilhjálmsson et al. 1980). In 1981 the upper waters off the north coast were cold but of higher than normal salinity and had an ice-free arctic composition (Malmberg and Svansson 1982; Vilhjálmsson and Magnússon 1981). In August 1982, low-salinity polar water again covered north Icelandic waters (Vilhjálmsson and Magnússon 1982).

It would be misleading to classify each year since the early 1950's as "warm" or "cold" on the basis of combinations of partly but imperfectly linked hydrographic characteristics. In
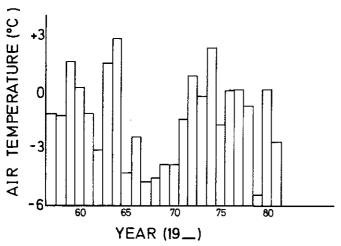
many years there are mixtures of characteristics normally associated with polar or Atlantic influences. For most north coast stations, however, the period from late summer 1964 to 1970 (excluding 1966) and the year 1979 were periods during which sea temperatures in spring and summer were substantially lower than in other years (Fig. 3 and 4) (Stefánsson 1969). In 1981, low sea surface temperatures resulted from Arctic rather than polar waters.

In contrast with the extreme year-to-year variations in ocean temperatures and salinities off the north coast in April–July, temperatures at 20-m depth along the south and west coasts deviated much less from mean values (Stefánsson 1960). The south and west coasts are predominantly influenced by warm, saline Atlantic water, which averages >6°C and >35‰ at 20 m in June (Thomsen 1938; Stefánsson 1962). From 1957 to 1979, the mean temperature and coefficient of variation for average May–June temperatures at Stykkishólmur on the west coast were 6.3°C and 0.17, respectively. At Hraun on the north coast, the mean temperature over this period was lower, at 4.8°C, but the coefficient of variation was higher, at 0.35 (Fig. 4). However, on both the north and west coasts, the sea temperatures were abnormally low in April and May of 1969 and 1979.

Chronology of Variations in Primary Production, Zooplankton Standing Crop, and Pelagic Fish Abundance around Iceland

The variations in climate, weather, and hydrography on the north coast have been correlated with measurable changes in primary production, standing crop of zooplankton, and forage fish abundance and distribution. Thórdardóttir (1977) reported that June primary production at 10-m depth off Siglunes averaged only one-fourth as high in 1965 and 1967–69 as in
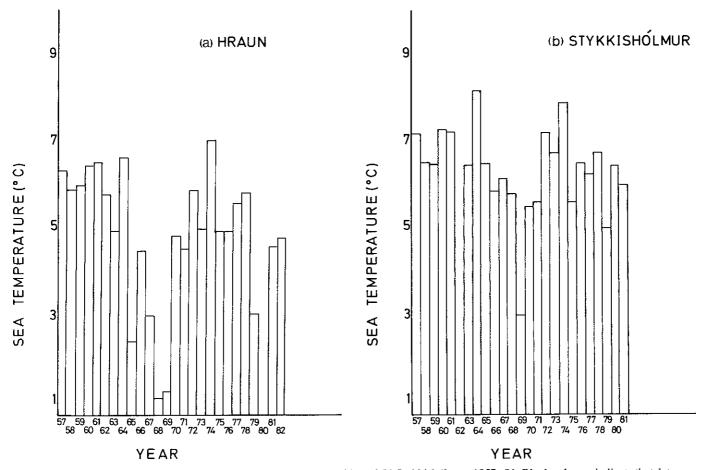

FIG. 3. Mean March air temperature at Hraun, 1957–81. (Source: Icelandic National Weather Service)

920

Can. J. Fish. Aquat. Sci., Vol. 41, 1984

FIG. 4. Mean May–June sea surface temperature at (a) Hraun, 1957–82, and (b) Stykkishólmur, 1957–81. Blank columns indicate that data were unavailable. (Source: Icelandic National Weather Service)
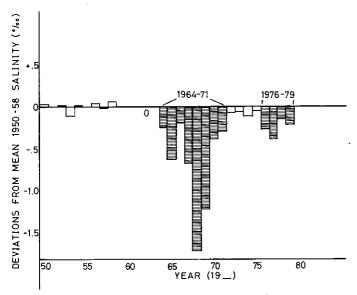

FIG. 5. Salinity at sea surface within latitude 67–69°N and longitude 11–15°W in June 1950–79 expressed as deviations from 1950–58 mean. Years strongly influenced by polar current are shaded. (Data from Malmberg 1983)

1958–64. She concluded that the lower production in 1965 and 1967–69 resulted from the stratified polar water preventing nutrients from reaching the surface layer. After 1971, May–June primary production was alternately high and low but no

series of years with low production was reported (Thórdardóttir 1980).

Jakobsson (1978) and Ástthórsson and Hallgrímsson (1984) documented the decline during 1964 and 1965 of the dominant north coast copepod *Calanus finmarchicus* at depths of 0–50 m in the Iceland Sea. Jakobsson stated: "It is probable that the greatly reduced primary production has caused a complete collapse of the main stocks of zooplankton in the north coast area. Moreover, this probably already happened in 1965 because in 1966 when the influx of polar water at the north coast was negligible and primary production was rather high off northwest Iceland, there were no signs of high density zooplankton areas." Zooplankton standing crops were low from 1965 to 1970 in Húnaflói, and off Siglunes and Langanes (Fig. 6a–6c), and as of 1983, *C. finmarchicus* had not regained its abundance of the early 1960's (Ástthórsson and Hallgrímsson 1984). Standing crops at these three localities also declined during 1979–81 from a secondary high during the mid-1970's.

Jakobsson (1978) also documented the decline in the mid-1960's of the important north Icelandic fishery for herring (*Clupea harengus*). Whereas some Norwegian and Icelandic spring spawning herring were caught off the north and northwest coasts in June–August 1962 and 1963, virtually none were caught off the north coast in June–September 1964. By 1965, polar water had intruded on former herring areas north and northeast of Iceland, and by 1966 the herring were redistributed northeastward toward Jan Mayen. In 1968, no herring concentrations crossed the cold East Icelandic Current. Jakobsson

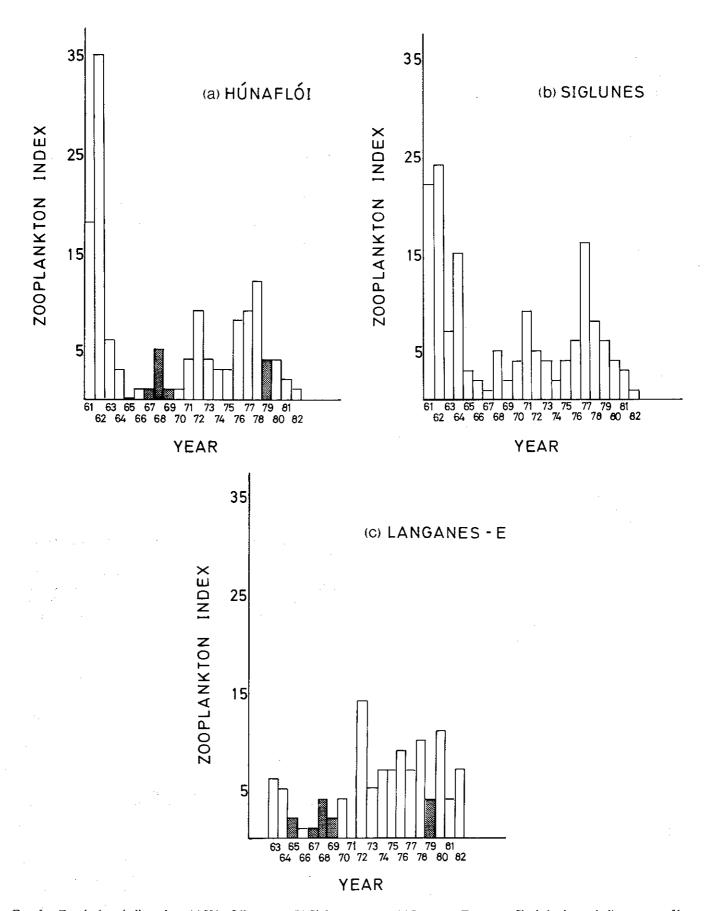*Can. J. Fish. Aquat. Sci., Vol. 41, 1984*

921

FIG. 6.   Zooplankton indices along (a) Húnaflói transect, (b) Siglunes transect, (c) Langanes-E transect. Shaded columns indicate years of lowest May–June sea temperatures at Hraun and Thorvaldsstadir. Blank columns indicate that data were unavailable. (Data from Ástthórsson and Hallgrímsson 1984)

922

Can. J. Fish. Aquat. Sci., Vol. 41, 1984

(1978) concluded that the changing climatic and hydrographic conditions north of Iceland in the mid-1960's were a major cause of the changed migration of the herring and, combined with exploitation, caused the collapse of the fishery.

Although standard annual larval fish surveys were not yet conducted off the north coast in the mid-1960's, Magnússon (1966) found that in June 1964, larval capelin (*Mallotus villosus*) were distributed much as they were in 1960–63, but by July and August the influx of polar water from the northwest resulted in a sudden decrease in their numbers. Since drifting larval fish tend to be more plentiful off the north coast in years with greater influx of Atlantic water around the northwest peninsula, it is likely, but not established, that currents in years such as 1965 and 1967–69 brought fewer larvae to the north coast than in the preceding period. After 1971, 0-group capelin were least abundant off the north coast in 1980 and 1981.

In summary, the changes in hydrography induced by climate off north Iceland have coincided with declines in primary production, declines in standing crops of zooplankton, and altered distributions and declines in abundance of pelagic fish species (Malmberg 1979). Evidence for causal links between these occurrences is largely circumstantial.

Materials and Methods

For 15 rivers (Fig. 1), I estimated annual yield of Atlantic salmon of each smolt class from total counts of salmon caught by anglers. The weight (in 0.5-kg intervals) and sex of each salmon had been recorded at the time of capture. For each year's data, the catch of grilse and two-sea-winter salmon was computed (sexes combined) with the aid of weight–frequency distributions (Scarnecchia 1983). Three-sea-winter and older salmon were scarce on most of the rivers and were not considered. Catch from Midfjardará was the sum of catches from its tributaries Vesturá, Núpsá, and Austurá plus lower river fish from all three stocks. There is no significant fishery for salmon in the ocean by Icelanders (Ísaksson 1980), and my analysis indicated that slight or no changes in age composition had occurred in most stocks since detailed catch data were recorded. The angling seasons, which generally run from mid-June to mid-September, are of the same duration each year for a given river. Nominal daily fishing effort, which is

TABLE 1. Angling effort (number of rods per day) for 15 rivers in 1958 and 1976, when surveys were compiled. Data provided by Einar Hannesson, Veidi-málastofnunin. ND = no data available.

River	1958	1976
Laxá í Kjós	7–8	11
Laxá í Leirársveit	3	7
Laxá í Dölum	5	6
Fáskrúd	3	2
Langadalsá	ND	4
Hrútafjardará	2	3
Vesturá, Núpsá Austurá, and lower Midfjardará combined	7	9
Vídidalsá	6	8
Vatnsdalsá	2	4
Laxá á Asum	2	2
Vesturdalsá	3	2–3
Hofsá	ND	7

TABLE 2. Years of data used in correlations of catches of Atlantic salmon between rivers and between sea temperatures and catches.

River	Correlations between rivers	Correlations between sea temperatures and catch
Laxá í Kjós	1955–81	1970–80
Laxá í Leirársveit	1961–81	1970–80
Laxá í Dölum	1946–81	1958–81
Fáskrúd	1949–81	1958–81
Langadalsá	1961–81	1961–81
Hrútafjardará	1958–81	1958–81
Vesturá	1957–81	1958–81
Núpsá	1957–81	1958–81
Austurá	1957–81	1958–81
Midfjardará	1957–81	1958–81
Vídidalsá	1960–81	1960–81
Vatnsdalsá	1962–81	1962–81
Laxá á Ásum	1957–81	1958–81
Vesturdalsá	1956–81	1958–81
Hofsá	1960–81	1960–81

regulated by the government and enforced by river owners, was nearly constant on 12 of the 15 rivers (Table 1). However, effective fishing effort on all these rivers may have increased after 1976 because the rising cost of permits may have induced more aggressive angling. For Laxá í Kjós, Laxá í Leirársveit, and Vatnsdalsá, nominal as well as effective angling effort increased (Table 1). Because I lacked information on how effective effort on a returning smolt class varied with such factors as number of competing rods, cost of permits, and absolute and relative abundance of returning salmon from adjacent smolt classes, it was assumed for this analysis that the catch statistics reflected actual abundance regardless of changes in nominal and effective effort. I also assumed that the contribution of hatchery-reared salmon to the catches was insignificant compared with that of wild fish. Even with these assumptions, the catch data from these rivers appeared to be at least as accurate as any other long-term Atlantic salmon angling statistics worldwide.

Data on sea surface temperatures used in regression analyses with catch were monthly mean surface values at five coastal stations around Iceland compiled by the Icelandic National Weather Service. For four of the stations, Stykkishólmur, Sudereyri, Hraun, and Thorvaldsstadir, monthly means were based on 6–15 usually equally spaced daily measurements per month. For these stations, I used data from April through July from 1957 to 1980 (Table 2). For the fifth station, Reykjavík Harbor (Fig. 1), I calculated monthly means from March 1 to June 30, 1969 to 1979, from 10-d means of daily measurements. For computing average temperature over 2-mo periods, 10-d averages were summed and divided by 6.

Catches in the various rivers were evaluated in relation to sea temperatures at different stations: catches in Laxá í Kjós and Laxá í Leirársveit, sea temperatures at Reykjavík Harbor; Hofsá and Vesturdalsá, Thorvaldsstadir; Laxá í Dölum and Fáskrúd, Stykkishólmur; Langadalsá, Sudureyri; and Hrútafjardará, Vídidalsá, Vatnsdalsá, Laxá á Ásum, and Midfjardará and its three tributaries (Vesturá, Núpsá, and Austurá), Hraun.

Relations between sea surface temperatures and both untransformed catches and their natural logarithms (Shepherd et al. 1982) were investigated by linear and multiple regression analyses (Snedecor and Cochran 1967). Pearson correlation
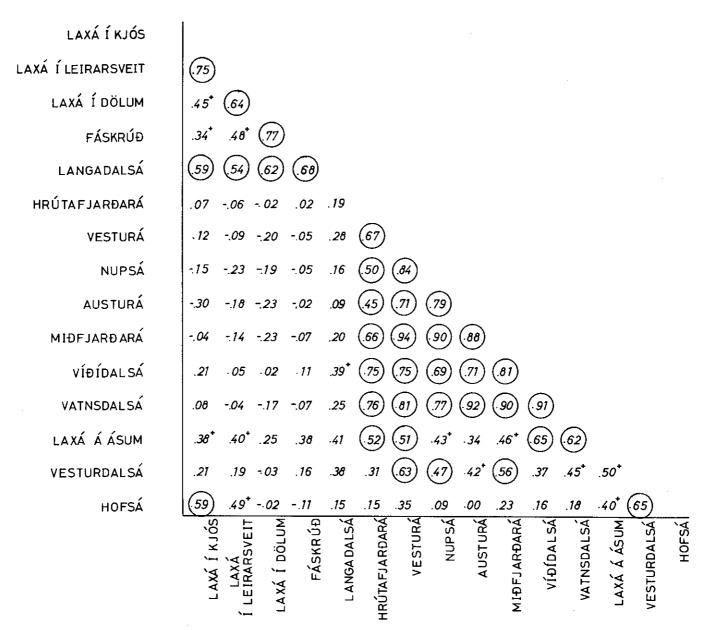
Can. J. Fish. Aquat. Sci., Vol. 41, 1984

923

	LAXÁ Í KJÓS	LAXÁ Í LEIRARSVEIT	LAXÁ Í DÖLUM	FÁSKRÚÐ	LANGADALSÁ	HRÚTAFJARÐARÁ	VESTURÁ	NUPSÁ	AUSTURÁ	MIÐFJARÐARÁ	VÍÐIDALSÁ	VATNSDALSÁ	LAXÁ Á ÁSUM	VESTURDALSÁ
LAXÁ Í LEIRARSVEIT	(.75)													
LAXÁ Í DÖLUM	.45*	(.64)												
FÁSKRÚÐ	.34*	.48*	(.77)											
LANGADALSÁ	(.59)	(.54)	(.62)	(.68)										
HRÚTAFJARÐARÁ	.07	-.06	-.02	.02	.19									
VESTURÁ	.12	-.09	-.20	-.05	.28	(.67)								
NUPSÁ	-.15	-.23	-.19	-.05	.16	(.50)	(.84)							
AUSTURÁ	-.30	-.18	-.23	-.02	.09	(.45)	(.71)	(.79)						
MIÐFJARÐARÁ	-.04	-.14	-.23	-.07	.20	(.66)	(.94)	(.90)	(.88)					
VÍÐIDALSÁ	.21	.05	.02	.11	.39*	(.75)	(.75)	(.69)	(.71)	(.81)				
VATNSDALSÁ	.08	-.04	-.17	-.07	.25	(.76)	(.81)	(.77)	(.92)	(.90)	(.91)			
LAXÁ Á ÁSUM	.38*	.40*	.25	.38	.41	(.52)	(.51)	.43*	.34	.46*	(.65)	(.62)		
VESTURDALSÁ	.21	.19	-.03	.16	.38	.31	(.63)	(.47)	-.42*	(.56)	.37	.45*	.50*	
HOFSÁ	(.59)	.49*	-.02	-.11	.15	.15	.35	.09	.00	.23	.16	.18	.40*	(.65)

FIG. 7. Correlation coefficients between grilse catches from 15 Icelandic rivers. Encircled, $P < 0.01$; superscript plus sign, $P < 0.05$.

coefficients were computed for comparisons of grilse catches between rivers. For selected regressions of temperature against log catch, two regression model assumptions were tested. Homoscedasticity was tested with Kendall's (1955) Tau statistic, and normality of residuals was tested with the Kolmogorov–Smirnov one-sample goodness-of-fit statistic (Pearson and Hartley 1976). Predictive regression equations were developed and other statistics calculated with the aid of the *Statistical Package for the Social Sciences* (Nie et al. 1975; Hull and Nie 1981).

Results

Correlations between Yields of Grilse from Individual Rivers

Catches of grilse from southwest and west coast rivers (Laxá í Kjós through Langadalsá) fluctuated together as a group, and catches from the north and northeastern rivers (Hrútafjarðará through Hofsá) fluctuated together (Fig. 7). However, catches from north and northeast rivers seldom fluctuated in synchrony with those from southwest and west coast rivers; usually, they showed no correlations between catches. Yields from Hrútafjarðará, which flows into Húnaflói, and Langadalsá, which flows into Ísafjördur, were not significantly correlated with each other. Furthermore, catches from Laxá í Dölum and Fáskrúd were not significantly correlated with those from northern or northeastern rivers. The dividing point for grouping rivers with similarly fluctuating catches was the northwest peninsula, which separates the warm Atlantic influenced water from the colder north Icelandic waters of the Iceland Sea (Fig. 2 and 7). Catches from the north coast rivers Midfjardará, Vídidalsá, and Vatnsdalsá were especially closely correlated with each other ($r \geqslant 0.80$, df $\geqslant 20$). The northeastern rivers Hofsá and Vesturdalsá correlated significantly with several north coast rivers ($0.40 \leqslant r \leqslant 0.65$, df $\geqslant 19$) but generally less strongly than the north coast rivers correlated among themselves. Hofsá was the only river in the north–northeast group for which grilse catch was closely correlated ($P < 0.01$) with the catch in a western or

924

TABLE 3. Coefficients of variation for grilse catches from 15 Icelandic rivers.

River	Years of catch	Coefficient
Laxá í Kjós	1955–81	0.30
Laxá í Leirársveit	1961–81	0.47
Laxá í Dölum	1946–81	0.56
Fáskrúd	1949–81	0.51
Langadalsá	1961–81	0.56
Hrútafjardará	1958–81	0.54
Vesturá	1957–81	0.53
Núpsá	1957–81	0.54
Austurá	1957–81	0.71
Midfjardará	1957–81	0.55
Vídidalsá	1960–81	0.46
Vatnsdalsá	1962–81	0.64
Laxá á Ásum	1957–81	0.51
Vesturdalsá	1956–81	0.74
Hofsá	1960–81	0.78

FIG. 9. Catches of two-sea-winter salmon from Hrútafjardará. Shaded columns indicate years of lowest May–June sea temperatures 2 yr earlier.

southwestern river. There were isolated instances of significant ($P < 0.05$) correlations between grilse catch on north–northeast and south–southwest rivers, but correlation coefficients were low ($r \leqslant 0.40$).

Coefficients of variation (standard deviations of catch divided by the mean catch) indicated that the two southwestern rivers Laxá í Leirársveit and Laxá í Kjós and the northern river Vídidalsa had the most stable annual grilse catches, whereas catches from the two northeastern rivers Hofsá and Vesturdalsá were the most variable (Table 3).

Sea Temperatures and Salmon Yields

All 11 rivers in the north–northeast group showed a characteristic decline from former and subsequent yields of grilse during 1965–70 and 1980 (Fig. 8–15). The exact year of low catches varied between rivers, e.g. grilse catch was high in Hrútafjardará in 1965 (Fig. 8) and in Vesturdalsá in 1970 (Fig.
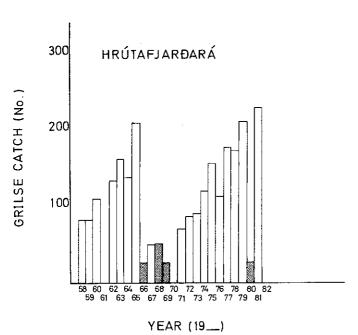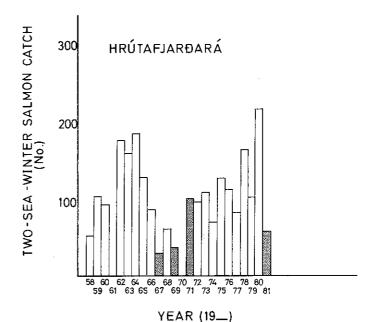
15), but in general, catches were low in most rivers in 1965 and 1970. From 1966 to 1969, the average catches as percent of average catches during 1960–64 were 16% in Laxá á Ásum, 29% in Midfjardará, 28% in Hrútafjardará, and 49% in Vídidalsá. On several rivers, low catches of grilse in one year were followed by low catches of two-sea-winter salmon the next year. For example, catches of grilse on Midfjardará were especially low in 1966, 1969, and 1980 (Fig. 10) and catches of two-sea-winter salmon were low in 1967, 1970, and 1981 (Fig. 11). These three smolt classes were migrating from Midfjardará during three of the five years since 1957 of lowest mean April–May, May–June, and June–July sea temperatures (Fig. 10 and 11). The average mean May–June temperature at Hraun
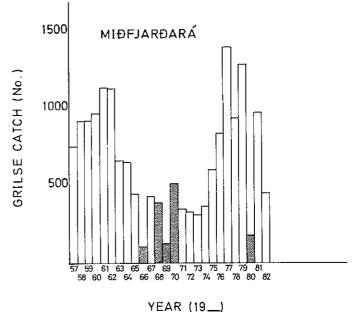

FIG. 8. Catches of grilse from Hrútafjardará. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.

FIG. 10. Catches of grilse from Midfjardará. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.
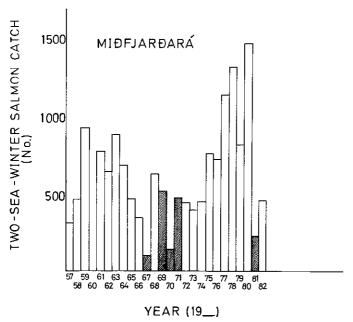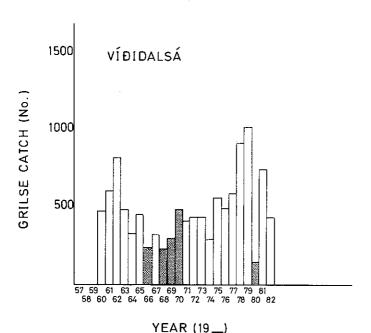
Can. J. Fish. Aquat. Sci., Vol. 41, 1984

925

FIG. 11. Catches of two-sea-winter salmon from Midfjardará. Shaded columns indicate years of lowest May–June sea temperatures 2 yr earlier.

FIG. 13. Catches of grilse from Vatnsdalsá. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.

during 1965–69 was only 2.4°C, whereas it was 6.0°C during 1960–64. The mean in 1979 was 3.0°C, 3° lower than the mean for 1960–64.

In contrast, grilse catches in Fáskrúd and Laxá í Dölum did not decline during 1965–70 except in 1969 (Fig. 16 and 17). Average yields from Fáskrúd and Laxá í Dölum during 1966–69 averaged 75 and 104%, respectively, of catches during 1960–64. And notably, the mean May–June temperatures at Stykkishólmur, near the rivers, averaged 5.4°C in 1965–69 and 7.2°C in 1960–64, a much smaller absolute and relative difference than was found for north coast stations.

Catches of grilse from southwestern and western rivers (Fig. 16–20), as on the north coast, were lower in 1980 than in

previous years. Mean March–June temperatures at Reykjavík Harbor for the period 1969–79 were lowest in 1979, and catches of grilse from Laxá í Leirársveit declined 49 and 61%, respectively, from average catches in the previous three years (Fig. 18 and 19). Catches of two-sea-winter salmon were subsequently also low in 1981. May–June temperature at Stykkishólmur in 1979 was the second lowest recorded from 1957 to 1981, 0.5° lower than the 1965–69 average and 2.3° lower than the 1960–64 average (Fig. 4b).

Regression Analyses for Sea Temperatures and Salmon Yields

Correlation coefficients for every simple linear regression performed, whether significant or not, are summarized in

FIG. 12. Catches of grilse from Vídidalsá. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.

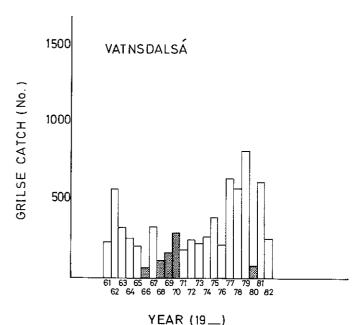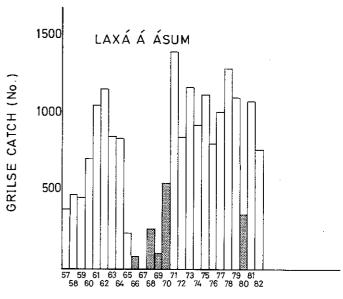FIG. 14. Catches of grilse from Laxá á Ásum. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.
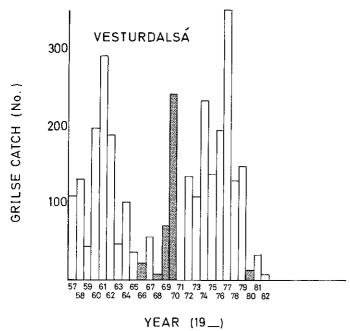
926

FIG. 15. Catches of grilse from Vesturdalsá. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.

Tables 4–6. I found highly significant relations between average June–July sea temperature at Hraun and grilse catches the following year from Vatnsdalsá, Vídidalsá, Hrútafjardará, and Midfjardará and its tributaries (Table 4; Fig. 21). Sea temperatures in April–May and May–June were also significantly correlated ($P < 0.05$ and $P < 0.01$) with grilse catches on northern rivers. For example, catches of grilse from Midfjardará, Austurá, and Hrútafjardará showed highly significant correlations with mean May–June and mean April–May temperatures in the previous year (Table 4). In contrast, no statistically significant relations were found for any combination of April–July temperatures and catch from Fáskrúd, Laxá í Dölum, or Langadalsá, nor were significnt relations apparent between sea temperatures and subsequent catches of grilse from Hofsá or Vesturdalsá, although the latter correlations had positive slopes (Table 4).

For Laxá í Leirársveit, I found significant positive relations between May, June, and average May–June sea temperatures at Reykjavík Harbor and catches of grilse the following year from 1969 to 1979 (Table 6). However, these and other positively sloped relations on this river and Laxá í Kjós (Fig. 22) were mainly attributable to poor catches of fish from the 1979 smolt class, which had entered abnormally cold seas.

In 90% (94 of 105) of the cases, sea temperature correlated more closely with logarithms of grilse catch than with the untransformed catches previously described. For north coast rivers, I found highly significant ($P < 0.01$) relations between many combinations of April–July sea temperatures at Hraun and grilse catches in the following year (Table 4), e.g. July temperature versus log catch from Vatnsdalsá (Fig. 23), May–June temperature versus log catch from Hrútafjardará (Fig. 24), June–July temperature versus log catch from Vídidalsá (Fig. 25), and May–June temperature versus log catch from Austurá (Fig. 26). I also found significant positive correlations between April–May temperatures and subsequent grilse catch from Vesturdalsá. As with untransformed catches, no significant relations were found between sea temperatures and catches from Laxá í Dölum, Fáskrúd, or Langadalsá. The

significant relations between sea temperatures and log catches from Laxá í Leirársveit (Fig. 27) and Laxá í Kjós, although improved statistically (Table 6), still resulted mainly from low catches of grilse in 1980. If the 1980 catches are omitted, there was little relation between temperature and catch.

For two-sea-winter salmon, I found highly significant ($P < 0.01$) and significant ($P < 0.05$) relations between combinations of April–May, May–June, and June–July sea temperatures at Hraun and catches from Midfjardará, Austurá, Vesturá, Núpsá, and Hrútafjardará (Table 5). I also found one highly significant and four significant inverse relations between sea temperature over periods from April to July and catches on western rivers (two for Laxá í Dölum, one for Fáskrúd, and one for Langadalsá). These relations had opposite slopes to all other significant relations found. No significant relations between sea temperatures and two-sea-winter salmon catches were found for Vídidalsá, Laxá á Ásum, Hofsá, Vesturdalsá, Laxá í Leirársveit, or Laxá í Kjós (Tables 5 and 6).

In only 62% (65 of 105) of the cases were the correlations of sea temperature with catches of two-sea-winter salmon improved by transforming the catches to natural logarithms. As with untransformed catches, the log two-sea-winter salmon catches in general correlated less closely with sea temperatures than did grilse catches (Table 5). Highly significant relations were found between April–May, May–June, and June–July temperatures and log catches from Hrútafjardará as well as from Midfjardará (Fig. 28) and its three tributaries.

As a result of strong correlations between monthly temperatures at a station, once the most significant monthly temperature entered the stepwise regression models, other monthly mean temperature variables were usually unable to subsequently enter the models at the $P < 0.05$ level. This result held for untransformed catches on 14 of 15 rivers. Although it would have been possible to increase statistically the explanatory power of temperature by adding insignificant variables, I did not pursue this approach.

According to analysis of residuals for 33 of the most significant relations between sea temperature and log transformed catches, nine of these relations had a significant Kendall's tau value at the $P < 0.05$ level. Seven of the cases showed higher absolute values of residuals with increasing values of x; the other two cases showed lower values with increasing values of x. Of the 33 sets of residuals, none was significantly different from normal (Kolmogorov–Smirnov test, $P < 0.05$). Overall, the data conformed well with these two assumptions of regression models.

Discussion

The northwest Icelandic peninsula, which has primarily colder, less saline waters of the Iceland Sea to the east and warmer, more saline Atlantic waters to the south (Stefánsson 1960), separates the similarly fluctuating catches of the north coast rivers from those of the southwest and west coasts (Fig. 1 and 7). Scarnecchia (1983) found that the sea-age of returning salmon in various stocks was also different east and south of the peninsula; female salmon on the north coast, east of the peninsula, tended to return after two winters at sea, but females from west and southwest coast stocks tended to return as grilse. Apparently the abrupt hydrographic and climatic gradient off northwest Iceland influences both the age composition and the abundance of salmon stocks.
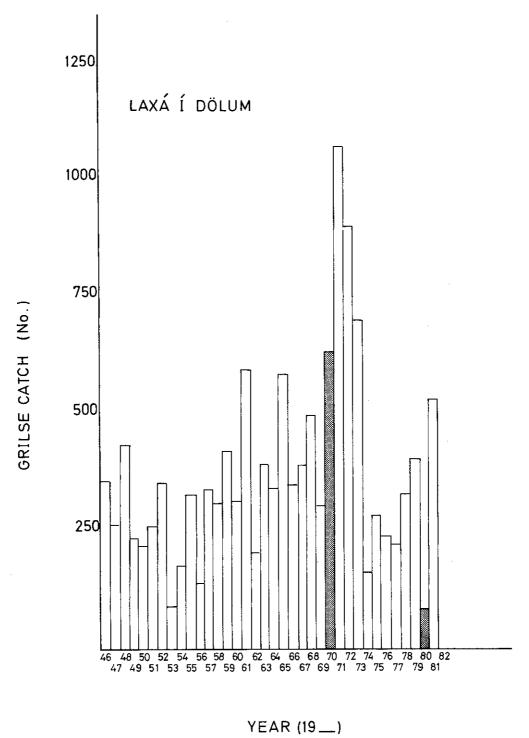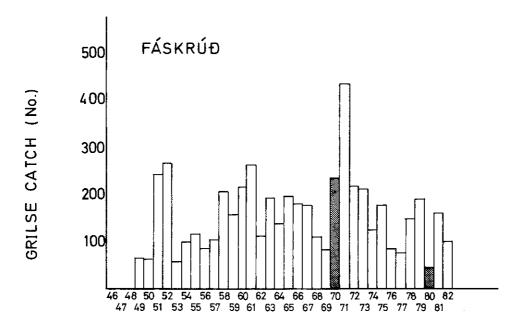
Although I found many statistically significant relations

Can. J. Fish. Aquat. Sci., Vol. 41, 1984

927

FIG. 16.   Catches of grilse from Laxá í Dölum. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.

between sea temperature and salmon catch (Tables 4–6), many of these relations resulted from the close correlation of catches between rivers within a region. Thus, a significant relation between sea temperature and grilse catch in Midfjardará almost certainly implied significant relations for Hrútafjardará and Vídidalsá, as well. The large number of significant results should be interpreted with this warning in mind.

There is strong evidence that the declines in catch from north coast rivers from 1965 to 1970 indicated decreased abundance

in those years. First, as previously mentioned, low catches of grilse in one year usually resulted in low catches of two-sea-winter salmon the following year (compare Fig. 8 and 9 with 10 and 11). Also, although sea temperatures in March–July tended to be low in these years, air temperature in July and August, the two main months when the rivers are fished, were not unusually low. Despite a strong linear correlation between June–July air temperature and sea temperature at Hraun (Table 7), average July air temperature at Hraun from 1965 to 1969 was only 0.1°

928

FIG. 17.   Catches of grilse from Fáskrúd. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.

lower than the mean from 1960 to 1964 and was even 0.2° higher than the mean from 1970 to 1974. Years with abnormally low sea temperatures in March–July resulted mainly from low air temperatures 1–3 mo earlier than the corresponding sea temperatures (Stefánsson and Gudmundsson 1969). Exceptionally low July and August temperatures would perhaps have decreased nominal or effective fishing effort, but no such low temperatures occurred.

A positive rather than a negative relation between sea temperature and catch is expected in Iceland because Atlantic salmon are near the northern limit of their distribution and because years with low sea temperatures tend to coincide with years of reduced primary and secondary production (Fig. 4 and 6). Vernon (1958) found a negative relation between sea temperature and pink salmon catches in the Fraser River, which is near the southern end of the distribution of that species. Furthermore, off the west coast of North America, low sea temperatures frequently coincide with higher upwelling and
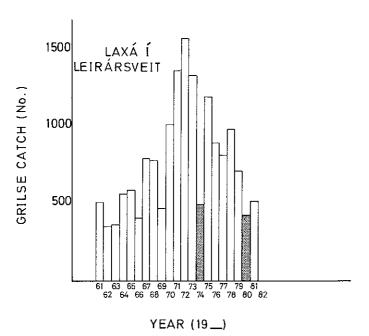

FIG. 18.   Catches of grilse from Laxá í Leirársveit. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.
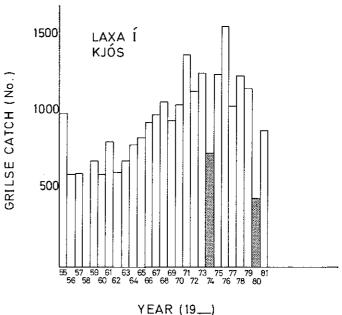

FIG. 19.   Catches of grilse from Laxá í Kjós. Shaded columns indicate years of lowest May–June sea temperatures 1 yr earlier.

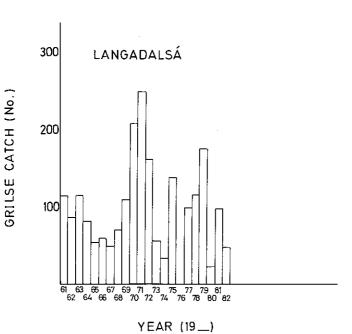Can. J. Fish. Aquat. Sci., Vol. 41, 1984
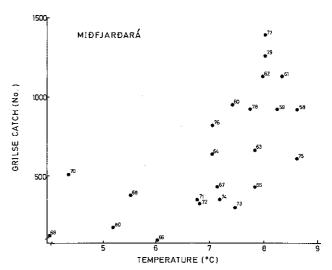
929

FIG. 20. Catches of grilse from Langadalsá.

FIG. 21. Grilse catch from Midfjardará, 1958–80, versus mean June–July sea surface temperature at Hraun in the previous year. Catch = 192.698 (temperature) − 716.768; $r = 0.66$, $P < 0.01$.

TABLE 4. Correlation coefficients for linear regressions of monthly and combined monthly sea surface temperatures and catch of grilse the following year for Icelandic rivers. Coefficients with log transformed catches are italicized.   *$P < 0.05$;   **$P < 0.01$.

River	Residual df	April	May	June	July	April–May	May–June	June–July
Laxá í Dölum	21	0.10	−0.06	−0.22	−0.21	0.08	−0.17	−0.24
		0.24	*0.10*	*−0.18*	*0.00*	*0.24*	*−0.04*	*−0.13*
Fáskrúd	21	0.19	0.13	−0.19	−0.04	0.19	−0.03	−0.15
		0.36	*0.30*	*−0.13*	*0.13*	*0.39*	*0.11*	*−0.04*
Langadalsá	18	−0.22	0.02	0.20	0.04	−0.12	0.12	0.13
		−0.13	*0.12*	*0.27*	*0.21*	*0.02*	*0.22*	*0.26*
Hrútafjardará	19	0.61**	0.73**	0.63**	0.61**	0.70**	0.71**	0.69**
		*0.70***	*0.83***	*0.75***	*0.66***	*0.81***	*0.83***	*0.79***
Vesturá	21	0.41*	0.57**	0.44*	0.67**	0.52*	0.52*	0.58**
		*0.48***	*0.64***	*0.53***	*0.65***	*0.59***	*0.61***	*0.63***
Núpsá	21	0.42*	0.52*	0.43*	0.62**	0.49*	0.49*	0.55**
		*0.46***	*0.56***	*0.52***	*0.61***	*0.53***	*0.56***	*0.61***
Austurá	21	0.49*	0.61**	0.51*	0.65**	0.58**	0.58**	0.62**
		*0.60***	*0.72***	*0.68***	*0.66***	*0.68***	*0.72***	*0.73***
Midfjardará	21	0.48*	0.61**	0.51*	0.73**	0.57**	0.58**	0.66**
		*0.56***	*0.69***	*0.62***	*0.69***	*0.65***	*0.68***	*0.71***
Vídidalsá	19	0.40	0.59**	0.46*	0.64**	0.52*	0.54*	0.58**
		*0.48***	*0.67***	*0.49***	*0.71***	*0.61***	*0.60***	*0.64***
Vatnsdalsá	17	0.36	0.53*	0.43	0.70**	0.47*	0.49*	0.59**
		*0.48***	*0.63***	*0.48***	*0.71***	*0.59***	*0.57***	*0.63***
Laxá á Ásum	20	0.34	0.56**	0.54**	0.42	0.48*	0.57**	0.54**
		0.41	*0.61***	*0.61***	*0.43***	*0.54***	*0.62***	*0.58***
Vesturdalsá	20	0.34	0.34	0.17	0.13	0.35	0.28	0.17
		*0.49***	*0.48***	*0.28*	*0.29*	*0.50***	*0.41*	*0.31*
Hofsá	19	0.32	0.34	0.13	0.18	0.34	0.27	0.17
		0.43	*0.42*	*0.25*	*0.27*	*0.43*	*0.37*	*0.29*

930

Can. J. Fish. Aquat. Sci., Vol. 41, 1984

TABLE 5. Correlation coefficients for linear regressions of monthly and combined monthly sea surface temperatures and catch of two-sea-winter salmon 2 yr later for 15 Icelandic rivers. Coefficients with log transformed catches are italicized. *$P < 0.05$; **$P < 0.01$.

River	Residual df	April	May	June	July	April–May	May–June	June–July
Laxá í Dölum	21	−0.31	−0.46*	−0.40	−0.26	−0.39	−0.51*	−0.39
		−0.24	*−0.43*	*−0.38*	*−0.15*	*−0.34*	*−0.48**	*−0.33*
Fáskrúd	21	−0.35	−0.18	−0.60**	−0.19	−0.26	−0.38	−0.50*
		−0.25	*−0.04*	*−0.49**	*−0.03*	*−0.12*	*−0.24*	*−0.36*
Langadalsá	18	−0.47*	−0.21	0.04	−0.05	−0.38	−0.10	−0.01
		−0.31	*−0.08*	*0.13*	*0.12*	*−0.22*	*0.03*	*0.14*
Hrútafjardará	19	0.43	0.56**	0.40	0.57**	0.52*	0.50*	0.53*
		*0.49**	*0.62***	*0.47**	*0.55***	*0.58***	*0.57***	*0.56***
Vesturá	21	0.44*	0.58**	0.46*	0.59**	0.54**	0.54**	0.56**
		*0.50**	*0.65***	*0.57***	*0.56***	*0.60***	*0.63***	*0.62***
Núpsá	21	0.37	0.52*	0.41	0.50*	0.47*	0.48*	0.49*
		*0.42**	*0.60***	*0.50**	*0.55***	*0.54***	*0.57***	*0.57***
Austurá	21	0.40	0.47*	0.44*	0.64**	0.46*	0.47*	0.57**
		*0.46**	*0.56***	*0.54***	*0.60***	*0.53***	*0.57***	*0.62***
Midfjardará	21	0.38	0.51*	0.44*	0.64**	0.47*	0.49*	0.57**
		*0.49**	*0.63***	*0.58***	*0.61***	*0.59***	*0.63***	*0.65***
Vídidalsá	19	0.03	0.20	0.28	0.24	0.14	0.24	0.29
		0.04	*0.22*	*0.30*	*0.23*	*0.15*	*0.26*	*0.30*
Vatnsdalsá	17	0.07	0.26	0.19	0.46*	0.19	0.23	0.33
		0.02	*0.23*	*0.16*	*0.36*	*0.15*	*0.20*	*0.27*
Laxá á Ásum	20	0.01	0.17	0.21	0.16	0.10	0.20	0.21
		0.01	*0.24*	*0.28*	*0.23*	*0.15*	*0.27*	*0.28*
Vesturdalsá	20	0.32	0.41	0.19	0.27	0.38	0.34	0.26
		*0.48**	*0.56***	*0.30*	*0.41*	*0.54***	*0.48**	*0.39*
Hofsá	19	0.34	0.34	0.14	0.24	0.35	0.27	0.21
		*0.48**	*0.47**	*0.24*	*0.36*	*0.49**	*0.40*	*0.33*

TABLE 6. Correlation coefficients for linear regressions of monthly sea surface temperatures and catch of grilse the following year and two-sea-winter salmon 2 yr later for Laxá í Kjós and Laxá í Leirársveit. Coefficients with log transformed catches are italicized. *$P < 0.05$; **$P < 0.01$.

Age of salmon	Residual df	March	April	May	June	March–April	April–May	May–June
Grilse								
Laxá í Kjós	9	0.50	0.41	0.57	0.47	0.50	0.52	0.54
		0.54	*0.49*	*0.66**	*0.57*	*0.56*	*0.61**	*0.64**
Laxá í Leirársveit	9	0.32	0.42	0.67*	0.67*	0.40	0.58	0.69*
		0.39	*0.48*	*0.74***	*0.74***	*0.47*	*0.65**	*0.75***
Two-sea-winter salmon								
Laxá í Kjós	9	0.10	−0.10	−0.28	−0.49	0.00	−0.20	−0.36
		0.11	*−0.07*	*−0.25*	*−0.47*	*0.03*	*−0.17*	*−0.34*
Laxá í Leirársveit	9	−0.12	−0.08	0.08	−0.11	−0.11	0.00	0.01
		0.01	*0.07*	*0.17*	*−0.02*	*0.04*	*0.13*	*0.10*

higher primary and secondary production (Smith 1968). Populations near the edge of their distributions are more likely than those centrally distributed to be regulated by extreme environmental conditions as opposed to internal dynamics. A dome-shaped or flat-topped response curve may exist for many environmental factors, which would reduce the effectiveness of linear regression models for detecting environmental effects in centrally distributed populations (Shepherd et al. 1982). In Iceland, the effects of climate on variation in salmon catches appear more clearly on the north coast rivers where the greatest extremes and variations in sea temperatures occur (Fig. 4a). Off the south coast, where temperatures are higher and less variable (Stefánsson 1960), only extreme conditions, such as occurred in 1979, appear to affect salmon yields. For intermedi-
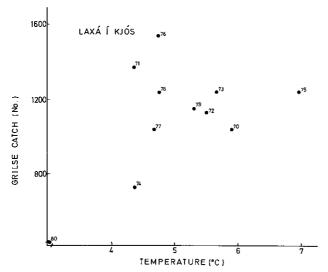
FIG. 22. Grilse catch from Laxá í Kjós, 1970–80, versus mean April–May sea surface temperature at Reykjavík Harbor in the previous year. Catch = 156.332 (temperature) + 326.059; $r = 0.52$, $P < 0.05$.
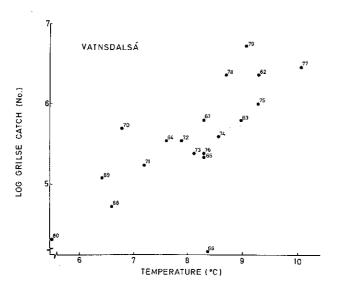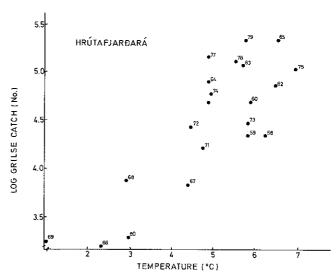

FIG. 24. Log grilse catch from Hrútafjardará, 1958–80, versus mean May–June sea surface temperature at Hraun in the previous year. Log catch = 0.3622 (temperature) + 2.7253; $r = 0.83$, $P < 0.01$.

ate levels of environmental factors, annual smolt production or other factors are mainly responsible for determining annual yield.

On Iceland's north coast, low air temperatures are significantly correlated with immediate sea temperatures and those 1–3 mo later (Table 7) (Stefánsson and Gudmundsson 1969). These cold air temperatures are also correlated with lower river temperatures in spring. The correlation is close for direct-runoff rivers such as Austurá but less close for lake-fed river systems such as Vatnsdalsá and Laxá á Ásum (Institute of Freshwater Fisheries, Reykjavík, unpubl. data). Thus, in years such as 1965, 1967–69, and 1979, temperatures were low not only in the sea but in most of the rivers as well. Consequently, I do not know why lower sea temperatures and concurrent low air and river temperatures result in small grilse and salmon catches 1 and 2 yr later, respectively. No thorough field studies have been performed, but I believe two main mechanisms may act in combination.

First, smolt migration may be reduced or delayed in years with low river and sea temperatures in spring. In Sweden, the smolts migrated from the Ricklean River when the water temperature rose to approximately 10°C (Österdahl 1969), although neither Österdahl nor Solomon (1982) found direct causal connections between river temperatures and smolt migration. Colder springs may delay smolt migrations, perhaps until summer, autumn, or longer, resulting in additional mortality. Several consecutive short summers could reduce growth of juvenile salmon and reduce output of smolts, but these suggestions clearly need to be tested on an Icelandic river with natural smolts.

Second, perhaps the feeding opportunities for outmigrating smolts at sea are poorer in years with low sea temperatures, such as in 1965–70 and 1979, than in years when temperatures are higher. The below-normal primary productivity and zooplankton standing crops during 1965, 1967–69, and 1979 and the disappearance of stocks of herring from the north coast during

FIG. 23. Log grilse catch from Vatnsdalsá, 1962–80, versus mean July sea surface temperature at Hraun in the previous year. Log catch = 0.4185 (temperature) + 2.1691; $r = 0.71$, $P < 0.01$.
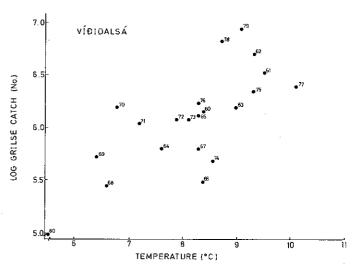

FIG. 25. Log grilse catch from Vídidalsá, 1960–80, versus mean July sea surface temperature at Hraun in the previous year. Log catch = 0.2966 (temperature) + 3.6512; $r = 0.71$, $P < 0.01$.

932

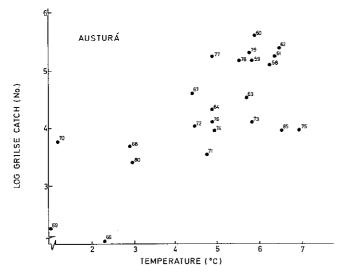Can. J. Fish. Aquat. Sci., Vol. 41, 1984

FIG. 26. Log grilse catch from Austurá, 1958–80, versus May–June sea surface temperature at Hraun in the previous year. Log catch = 0.4113 (temperature) + 2.3682; $r = 0.72$, $P < 0.01$.

1965–70 coincided with reduced salmon yields. Available evidence indicates that Atlantic salmon inhabit the first few metres of the water column at sea (Stasko et al. 1973), and during the aforementioned years, low primary and secondary production resulted partly from the presence of stratified polar water near the surface. During cold years, the salmon may grow more slowly and remain susceptible to high mortality from predation for a long time. Or perhaps oceanic migration patterns are significantly altered in years with much polar water and the accompanying changes in currents. These hypotheses are speculative and must be tested. No information is available on the oceanic feeding grounds of salmon from the northern stocks (Ísaksson 1980), so it is unclear whether smolts leave the north coast for southern waters or stay much or all of their life within the Iceland Sea or other northern waters.

In only one case for grilse (none for two-sea-winter salmon) was as much as two-thirds (67%) of the variation in yields
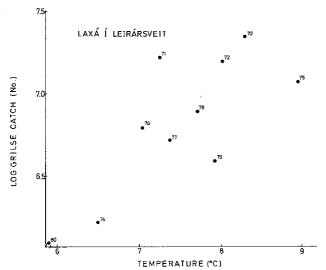

FIG. 27. Log grilse catch from Laxá í Leirársveit 1970–80, versus mean May–June sea surface temperature at Reykjavík harbor in the previous year. Log catch = 0.3526 (temperature) + 4.1440; $r = 0.75$; $P < 0.01$.
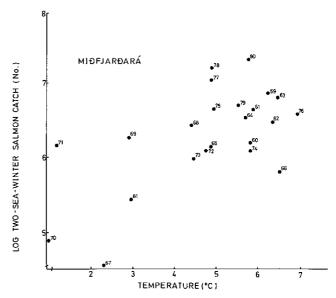

FIG. 28. Log two-sea-winter salmon catch from Midfjardará, 1959–81, versus mean May–June sea surface temperature at Hraun 2 yr earlier. Log catch = 0.2485 (temperature) + 5.1050; $r = 0.63$, $P < 0.01$.

explained by sea temperatures. Clearly, other factors influence yield. One factor is the variation in the number of smolts leaving the rivers each year. In Newfoundland, Chadwick (1982) reported that the largest smolt migration in Western Arm Brook over a 10-yr period was 2.7 times the smallest migration. Icelandic rivers may show this much annual variation in numbers of smolts.

Yields of salmon from several northern rivers (e.g. Midfjardará, Hrútafjardará, and Vesturdalsá) show oscillations that could be interpreted as density-dependent cycles. Many stock-recruitment curves deflected from equilibrium by external factors generate regular cycles of abundance with a period of twice the mean generation time (Ricker 1954). Grilse catches in Vesturdalsá, for example, peak at about 12-yr intervals, which is twice the mean generation time for this river (Institute of Freshwater Fisheries, unpubl. data). My findings do not explicitly invalidate the possibility of such density-dependent cycles. Yet, declines in salmon yields in northern rivers have corresponded to marked declines in sea temperatures, air temperatures, salinities, primary production, zooplankton standing crops, and standing crops of forage fishes. The statistically significant correlations between sea temperatures and salmon yields suggest that climatic factors are important in regulating salmon yields in Icelandic rivers, and especially in the northern rivers. I also found one highly significant ($P < 0.01$) and several significant ($P < 0.05$) relations between grilse catches on north and south coast rivers, yet the average smolt age is 4–6 yr in

TABLE 7. Correlation coefficients between sea temperature and air temperature at Hraun from 1957 to 1980. All significant at $P < 0.01$.

Air temperature	Sea temperature		
	April–May	May–June	June–July
April–May	0.82	0.76	0.71
May–June		0.87	0.84
June–July			0.90

Can. J. Fish. Aquat. Sci., Vol. 41, 1984

933

Hofsá but only 3–4 yr in Laxá í Kjós (Institute of Freshwater Fisheries, unpubl. data). I conclude that climate, weather, and oceanic conditions regulate abundance of salmon in the rivers over and above density-dependent factors, at least in years of extreme environmental variations. Density-dependent smolt production may occur within the outer bounds set by these environmental variations (Kristjánsson and Tómasson 1981). This mechanism is best investigated by collecting long-term data on smolt migrations and escapements to go with the catch data and relating these data to densities of spawners, presmolts, and smolts in particular streams.

Perhaps the question in Iceland's rivers is not whether climate and ocean conditions, rather than density-dependent growth and smolt production, regulate abundance in all years, or vice versa, but rather, how climatic and hydrographic factors, oceanic productivity, and densities of spawners, parr, and smolts interact to produce short-term and long-term fluctuations in abundance and yield.

Acknowledgments

References

ALM, G. 1954. Laxfisket och laxbestandet i Östersjöområdet under senare är (The salmon catch and the salmon stock in the Baltic during recent years). Sven. Vattenkraftfören. Publ. 444(5): 41–100.

ÁSTTHÓRSSON, Ó. S., AND I. HALLGRÍMSSON. 1984. Variations in zooplankton densities in Icelandic waters in spring during the years 1961–1982. Rit Fiskideildar. (In press)

CHADWICK, E. M. P. 1982. Dynamics of an Atlantic salmon stock (*Salmo salar*) in a small Newfoundland river. Ph.D. thesis, Memorial University of Newfoundland, St. John's, Nfld. 267 p.

DICKSON, R. R., H. H. LAMB, S.-A. MALMBERG, AND J. M. COLEBROOK. 1975. Climatic reversal in the northern North Atlantic. Nature (Lond.) 256: 479–482.

EYTHÓRSSON, J., AND H. SIGTRYGGSSON. 1971. The climate and weather of Iceland. The zoology of Iceland. VI. Part 3. Ejnar Munksgaard, Copenhagen and Reykjavík. 62 p.

GILHOUSEN, P. 1960. Migratory behaviour of adult Fraser River sockeye. Int. Pac. Salmon Fish. Comm. Prog. Rep. 78 p.

GUNSOLUS, R. T. 1978. The status of Oregon coho and recommendations for managing the production, harvest and escapements of wild and hatchery-reared stocks. Oregon Dept. Fish Wildl. Rep. 59 p.

HULL, C. H., AND N. H. NIE. 1981. SPSS update manual. McGraw-Hill, New York, NY. 402 p.

ÍSAKSSON, Á. 1980. Salmon ranching in Iceland, p. 131–156. *In* J. Thorpe [ed.] Salmon ranching. Academic Press, London.

JAKOBSSON, J. 1978. The North Icelandic herring fishery and environmental conditions, 1960–68. ICES Symposium on the Biological Basis of Pelagic Fish Stock Management. No. 30: 101 p.

KENDALL, M. G. 1955. Rank correlation methods. 3rd ed. Charles Griffin and Co., Ltd., London.

KRISTJÁNSSON, J. 1982. Athugun á veidiskýrslum úr nokkrum laxveidiám NA- og A- lands 1969–1981. Ægir 75(3): 121–126.

KRISTJÁNSSON, J., AND T. TÓMASSON. 1981. Sveiflur í laxgöngum og hugsanlegar orsakir theirra. Freyr 77(11): 417–422.

LINDROTH, A. 1957. Baltic salmon fluctuations: a reply. Inst. Freshw. Res. Drottningholm 38: 109–130.

MAGNÚSSON, J. 1966. On capelin larvae (*Mallotus villosus* O. F. Müller) in Icelandic waters during the years 1960 to 1964. Rit Fiskideildar 4(4): 36 p.

MALMBERG, S.-A. 1972. Annual and seasonal variations in the East-Icelandic Current between Iceland and Jan Mayen, p. 42–54. Sea Ice Conference Proceedings, Reykjavík.

  1979. Ástand sjávar og fiskstofna vid Ísland. III. Ástand sjávar og lodnu. Ægir 72(11): 642–649.

  1983. Hydrographic conditions in Icelandic waters in May–June 1979 and 1980. Ann. Biol. 37: 47–56.

MALMBERG, S.-A., AND A. SVANSSON. 1982. Variations in the physical marine environment in relation to climate. ICES CM 1982/GEN:4. Mini-symposium, hydrographic committee. 31 p.

MCKERNAN, D. L., D. R. JOHNSON, AND J. I. HODGES. 1950. Some factors influencing the trends of salmon populations in Oregon. Trans. No. Am. Wildl. Conf. 15: 427–449.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences. McGraw-Hill, New York, NY. 675 p.

ÖSTERDAHL, L. 1969. The smolt run of a small Swedish river, p. 205–215. *In* T. G. Northcote [ed.] Symposium on Salmon and Trout in Streams. H. R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver, B.C.

PEARSON, E. S., AND H. O. HARTLEY. 1976. Biometrika tables for statisticians. Biometrika Trust, London.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

ROYAL, L. A., AND J. P. TULLY. 1961. Relationship of variable oceanographic factors to migration and survival of Fraser River salmon. Calif. Coop. Oceanic Fish. Invest. 8: 65–68.

SCARNECCHIA, D. L. 1981. Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. Can. J. Fish. Aquat. Sci. 38: 471–475.

  1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 40: 1456–1468.

SHEPHERD, J. G., J. G. POPE, AND R. D. COUSENS. 1982. Variations in fish stocks and hypotheses concerning their links with climate. ICES CM 1982/Gen:6. 22 p.

SMITH, R. L. 1968. Upwelling. Oceanogr. Mar. Biol. Annu. Rev. 6: 11–46.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods. The Iowa State University Press, Ames, IA. 593 p.

SOLOMON, D. J. 1982. Smolt migration in Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.), p. 196–203. *In* E. L. Brannon and E. O. Salo [ed.] Proceedings of the Salmon and Trout Migratory Behavior Symposium. School of Fisheries, University of Washington, Seattle, WA.

STASKO, A. B., A. M. SUTTERLIN, S. A. ROMMEL, JR., AND P. F. ELSON. 1973. Migration–orientation of Atlantic salmon (*Salmo salar* L.) Int. Atl. Salmon Found. Symp. Spec. Publ. 4(1): 119–137.

STEFÁNSSON, U. 1954. Temperature variations in the North Icelandic coastal area. Rit. Fiskideildar 2(2): 27 p.

  1960. Temperature at 20 meters in Icelandic waters in May–June, 1950–1959. Rit Fiskideildar 2(8): 18 p.

  1962. North Icelandic waters. Rit Fiskideildar 3: 269 p.

  1969. Temperature variations in the North Icelandic coastal area during recent decades. Jökull 19: 18–28.

STEFÁNSSON, U., AND G. GUDMUNDSSON. 1969. Hydrographic conditions off the northeast coast of Iceland in relation to meteorological factors. Tellus 21(2): 245–258.

THOMSEN, H. 1938. Hydrography of Icelandic waters. The zoology of Iceland. VI. Part 4. Levin and Munksgaard, Copenhagen and Reykjavík. 36 p.

THÓRDARDÓTTIR, T. 1977. Primary production in North Icelandic waters in relation to recent climatic changes, p. 655–665. *In* M. J. Dunbar [ed.] Polar oceans. Proceedings of the Conference held at McGill University, Montreal, Que.

  1980. Bretingar á frumframleidni í hafinu nordan Íslands, 1970–1979. Sjávarfrettir 8(3): 18–25.

THORPE, J. E., AND K. A. MITCHELL. 1981. Stocks of Atlantic salmon (*Salmo salar*) in Britain and Ireland: discreteness and current management. Can. J. Fish. Aquat. Sci. 38: 1576–1590.

VAN HYNING, J. M. 1973. Factors affecting the abundance of fall chinook salmon in the Columbia River. Fish. Comm. Oregon Res. Rep. 4(1): 87 p.

934

Can. J. Fish. Aquat. Sci., Vol. 41, 1984

VERNON, E. H. 1958. An examination of factors affecting the abundance of pink salmon in the Fraser River. Int. Pac. Salmon Fish. Comm. Prog. Rep. 49 p.

VILHJÁLMSSON, H., AND J. V. MAGNÚSSON. 1981. Report on the 0-group fish survey in Icelandic and East Greenland waters, 1981. ICES CM 1981/H:41: 11 p.

1982. Report on the 0-group fish survey in Icelandic and East Greenland waters, August 1982. ICES CM 1982/H:63: 26 p.

VILHJÁLMSSON, H., J. V. MAGNÚSSON, AND E. FRIDGEIRSSON. 1980. Report on the 0-group fish survey in Icelandic and East Greenland waters. ICES CM 1980/H:64: 11 p.

Can. J. Fish. Aquat. Sci., Vol. 41, 1984

935