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Effects of Oceanic Variations and the West Greenland Fishery on Age at Maturity of Icelandic West Coast Stocks of Atlantic Salmon (*Salmo salar*)[1]

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Investigations were conducted on the effects of oceanic variations (as measured by sea temperatures) and catches by the West Greenland salmon fishery on the sea age composition of Atlantic salmon (*Salmo salar*) stocks from 21 Icelandic west coast rivers. Annual ratios of grilse to two-sea-winter (2SW) salmon were strongly correlated among the 21 rivers. All eight rivers with time series extending back before the expansion of the West Greenland fishery showed lower ratios during the earlier period. Only 2 of the 21 rivers, however, had significantly declining ratios over their time series. In addition, for only one river was West Greenland catch significantly related to the ratios ($P < 0.05$), and for only one river did ratios increase when the expanded West Greenland fishery was active. Overall, the effects of the fishery on stock composition are evidently minimal. The mean April–May temperature when the smolts were to migrate out of rivers was significantly and positively related to subsequent ratios for five of the rivers, which, along with correlations among the ratios, indicated that more rapid growth of smolts in their first summer may have increased the ratios of grilse to 2SW salmon on several rivers.

On a étudié les effets des variations de la température de l'eau de mer et des captures des pêcheurs de saumon de l'ouest du Groenland sur la répartition par phases en eau salée des stocks de saumon de l'Atlantique (*Salmo salar*) dans 21 cours d'eau de la côte ouest d'Islande. Une étroite corrélation a été établie entre les rapports annuels castillons/saumons dibermarins dans les 21 cours d'eau. Dans les huit cours d'eau pour lesquels on disposait d'une série chronologique remontant à une période antérieure à l'intensification de la pêche dans l'ouest du Groenland, les rapports étaient initialement inférieurs. Cependant, d'après les données recueillies au fil des ans, les rapports n'ont diminué de façon significative que dans 2 cours d'eau parmi les 21 examinés au total. En outre, une relation significative entre les captures dans l'ouest du Groenland et les rapports (*P* inférieur à 0,05) n'a été observée que dans l'un des cours d'eau, et les rapports n'ont augmenté que dans une seule rivière lorsqu'il y a eu intensification de la pêche dans l'ouest du Groenland. Dans l'ensemble, les effets des captures sur la composition des stocks sont manifestement minimaux. La température moyenne en avril–mai, au moment où les smolts devaient quitter les cours d'eau, était reliée de façon significative et positive aux rapports ultérieurs dans cinq des cours d'eau, ce qui, de pair avec les corrélations établies entre les rapports, révèle qu'une croissance plus rapide des smolts au cours de leur premier été avait peut-être augmenté les rapports grilses/saumons dibermarins dans plusieurs cours d'eau.

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Recent investigators have sought to identify genetic and environmental factors affecting the age at sexual maturity of Atlantic salmon (*Salmo salar*) (Saunders 1986; see comprehensive reviews by Gardner 1976 and Meerburg 1986). Sea-age at maturity has been shown to have a genetic basis, and differences in mean sea-age *among* stocks have been correlated with large-scale environmental factors (Dahl 1916; Scarnecchia 1983). In addition, the environmental and developmental history of an individual fish has been shown to affect its ultimate sea-age at maturity (Thorpe 1986).

Although it is known that a complex of genetic and environmental factors influences sea-age at maturity, biologists have a poorer understanding of how specific genetic and environmental factors interact and influence age at maturity (Dempson et al. 1986). Investigators have found significant correlations between the number of grilse (i.e. having spent 1 yr at sea) in a stock in 1 yr and the number of two-sea-winter (2WS) salmon the next year (Kristjánsson 1982; Scarnecchia 1984b). There is also some evidence that sea-age at maturity *within* a year-class

[1]Journal Paper No. J-13053 of the Iowa Agriculture and Home Economics Experiment Station, Ames, IA, USA, Project No. 2816.

TABLE 1. Catch (in metric tons) of Atlantic salmon off West Greenland, 1960–85. Catch before 1960 assumed to be 0 for all analyses.

Year	Catch
1960	60
1961	127
1962	244
1963	466
1964	1539
1965	861
1966	1370
1967	1601
1968	1127
1969	2210
1970	2146
1971	2689
1972	2113
1973	2341
1974	1917
1975	2030
1976	1175
1977	1420
1978	984
1979	1395
1980	1194
1981	1246
1982	1077
1983	310
1984	297
1985	851

within a stock either is largely determined genetically or is influenced by environment mainly when the salmon are in freshwater (Chadwick et al. 1986).

However, some investigators of Atlantic and Pacific salmons have concluded that marine factors also influence annual variations in age at maturity. Peterman (1985) found that mean age at maturity varied similarly among Bristol Bay stocks of sockeye salmon (*Oncorhynchus nerka*) for fish of the same smolt class. He concluded that most of the variations in age at maturity probably resulted from conditions during the early marine life of the fish. Martin and Mitchell (1985) found that lower sea temperatures led to higher numbers of grilse relative to multi-sea-winter (MSW) salmon returning to the River Dee, Scotland. In contrast, Dempson et al. (1986) found no evidence of sea temperatures affecting sea-age at maturity of Atlantic salmon in the Restigouche River, Quebec, and other Canadian rivers.

It is not clear if or how oceanic conditions exert an effect on sea-age at maturity of Atlantic salmon. In addition, available data on age composition of salmon from rivers are often biased and confounded by age-selective fishing mortality from mixed-stock fisheries off the west coast of Greenland, in the Norwegian Sea, near the Faroe Islands, as well as from nearshore commercial fisheries.

Inasmuch as Iceland's west coast rivers are geographically close to the location of the West Greenland fishery and the total annual Icelandic harvest of wild salmon is only 200 tonnes (less than 8% of West Greenland catches by weight in the 1970s), it is reasonable to ask if the West Greenland fishery is harvesting large numbers of Icelandic salmon. Because oceanic fisheries off West Greenland harvest potential MSW salmon but not grilse (International Council for the Exploration of the Sea 1986), excessive offshore harvest of potential MSW salmon would be expected to lower mean age at maturity of fish returning to the rivers. Major reductions in age at maturity in these stocks might also be a useful indicator of overharvest (e.g. Paloheimo and Elson 1974) and potential loss of genetic diversity. Such harvests would, in turn, complicate attempts to assess environmental factors affecting sea-age at maturity.

In this paper, we investigate the effects of the West Greenland fishery and between-year variations in oceanic conditions on sea-age of the salmon stocks from 21 Icelandic west coast rivers. We seek to answer if and how age composition of the stocks (expressed as ratios of grilse to 2SW salmon) has changed coincident with fishing off West Greenland. We also investigate how interannual variations in oceanic temperatures affect the grilse to 2SW salmon ratios.

West Greenland Fishery

The West Greenland fishery began more than 200 yr ago, but catches were modest until the early 1960s when catches from a directed gillnet fishery rose rapidly from 60 tonnes in 1960 to more than 1500 tonnes in 1964 (Shearer and Balmain 1967; Pyefinch 1969; International Council for the Exploration of the Sea 1981; Jensen 1988). In 1965, an additional drift gillnet fishery at Greenland was begun by Scandinavians, which resulted in a total annual catch of over 2600 tonnes by 1971. Catches remained about 2000 tonnes per year until 1976, when a quota of 1190 tonnes was established. Catches from 1976 to 1984 were at or near established quotas (i.e. quotas were between 1190 and 1265 tonnes, and catches were between 984 and 1420 tonnes), except for 1983 and 1984 when unusually low oceanic temperatures (Stein and Buch 1985; Reddin and Shearer 1987) resulted in reduced availability of salmon, and catches dropped to 310 and 297 tonnes, respectively. Catches for 1985 were at quota levels of 850 tonnes (Table 1). Estimates of effort are not available (International Council for the Exploration of the Sea 1986). Fish caught are all potential MSW salmon (International Council for the Exploration of the Sea 1986). North American and European stocks of salmon contribute in similar or equal proportions to the fishery in most years (International Council for the Exploration of the Sea 1986; Reddin and Short 1986), and sex ratios are as high as 4.1:1 in favor of females (Pyefinch 1969; Jensen 1988), which tend to mature later and migrate farther than males in most salmon stocks.

Although tagged Icelandic salmon have occasionally been caught in the West Greenland fishery (Ísaksson 1980; Jensen 1988), few Icelandic stocks are tagged, and the tags recovered have been so few that it is not known how many Icelandic salmon are being harvested there.

Materials and Methods

Sea-age composition of Icelandic salmon stocks was determined by the use of long-term angling catch records from all 21 west coast rivers having significant percentages of MSW salmon (Fig. 1). Most of these rivers supported rod angling only. Detailed catch records, including number, weight, and sex of individual salmon caught, were available for recreational fisheries. However, significant commercial net fisheries are active in the Hvítá (Borgafjördur) system and in the Ölfusá–Brúará–Hvítá (OBH) system. A small net fishery was also active on Álftá. Data from these fisheries were poor, and the

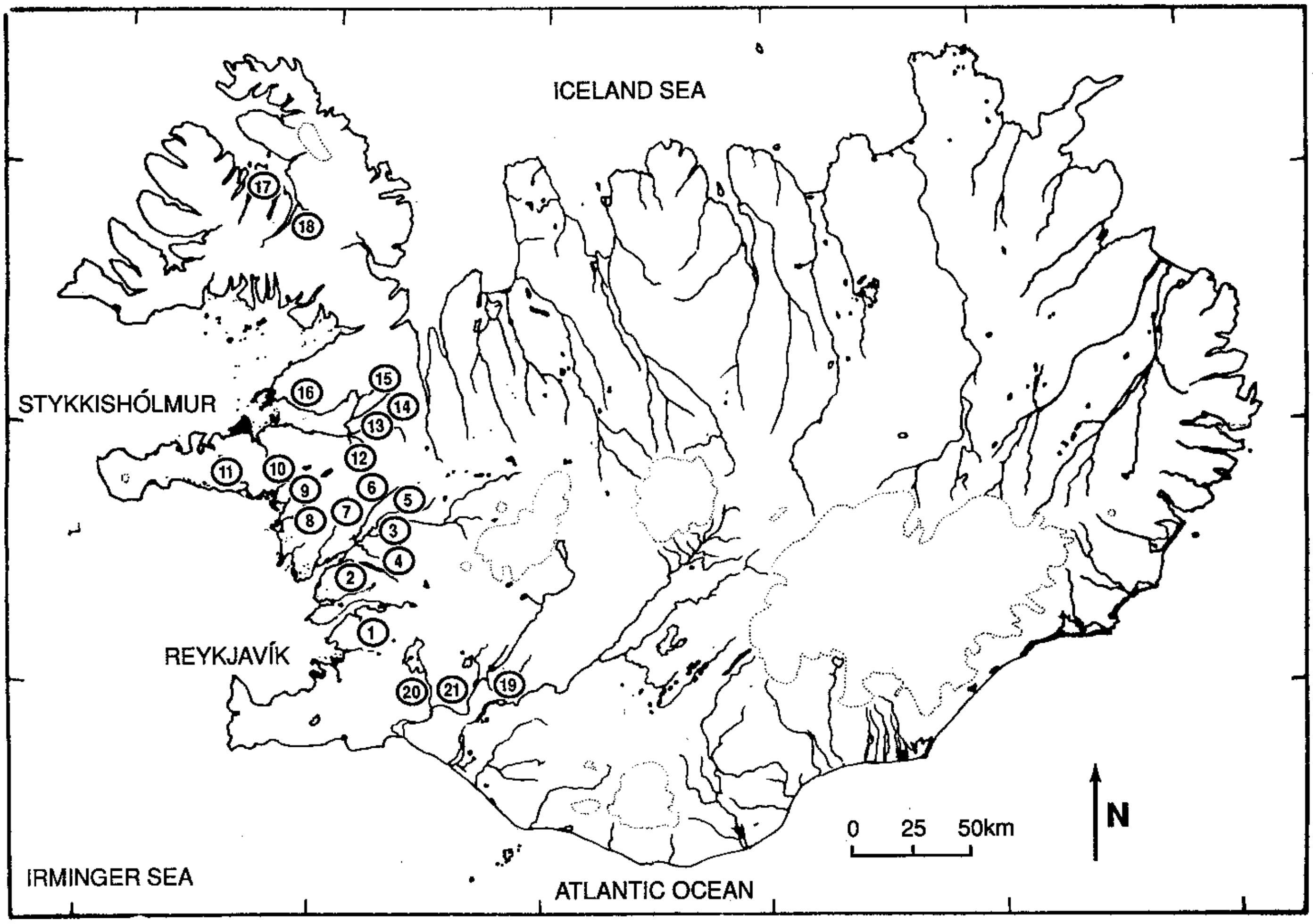

FIG. 1. Locations and rivers of Iceland mentioned in text. 1, Laxá í Kjós; 2, Laxá í Leirársveit; 3, Hvítá (Borgarfjördur); 4, Grímsá/Tunguá; 5, Thverá; 6, Nordurá; 7, Langá; 8, Álftá; 9, Hítará; 10, Haffjardará; 11, Straumfjardará; 12, Midá í Dölum; 13, Haukadalsá; 14, Laxá í Dölum; 15, Fáskrúd; 16, Flekkudalsá; 17, Laugardalsá; 18, Langadalsá; 19, Stóra-Laxá; 20, Sog; 21, Ölfusá–Brúará–Hvitá (combined).

effects of these fisheries on age structure of the salmon stocks are not known.

These net fisheries have been pursued throughout the duration of the useable angling records. It is possible that up to 50% of the returning run may be taken in these fisheries. The net fishery on Hvítá (Borgarfjördur) has a direct effect on subsequent angling catches in Hvítá, and the rivers Grímsá, Thverá, and Nordurá, which drain into Hvítá. Similarly, the net fishery on the Ölfusá-Brúará-Hvítá system has a direct effect on the angling catches in Sog and Stóra-Laxá. Although data are lacking, we assume that harvest emphasizes MSW salmon whenever possible. Results from these rivers should be interpreted with these precautions.

Details of the recreational fishery were provided by Gudjónsson (1978) and Scarnecchia (1983, 1984a). The number of rods per river is strictly regulated, and effort in general remains constant from year to year. The number of rods has, however, gradually increased at variable intervals of several years in most rivers (Scarnecchia 1984a). The effects of this increased effort on catch are not specifically known, although reported catches have risen on most rivers in recent years. In this paper, we assumed that catches were representative of abundance (as had been assumed in Scarnecchia 1983, 1984a, 1984b), at least over periods of adjacent years, and that ratios based on the number of grilse in one year to 2SW salmon the next year could be calculated with minimal bias from year-to-year effort changes. In some rivers, incompletely reported data, known effort changes, or other known biases for a given year made it impossible to compare one year's data with that of the previous or succeeding year. All such years known to us were deleted before any analyses. Data sets ranged from 9 to 39 yr (Table 2).

For the 21 rivers, we determined the number of years salmon had spent at sea by analyzing weight frequencies of rod-caught salmon separately by sex and calculating the number of fish of each age separately for each river and year. Each salmon was classified as a grilse (1SW), 2SW fish, or 3SW fish. Available scale samples indicated that MSW salmon included repeat spawners. Our analysis considered only grilse and 2SW salmon and included any repeat spawners which would have fallen into the appropriate weight frequency categories. We did not consider 3SW fish nor repeat spawners that fell into this weight category. Such fish were uncommon in the rivers. Because catches on all rivers were low, sexes were combined in our analyses to increase our sample sizes. Ratios of grilse in year x to 2SW salmon in year $x + 1$ (henceforth called ratios) were calculated and used in subsequent analyses.

The total West Greenland catch was used as a variable and the relationship investigated between the Greenland catch in year x and the grilse (year x) to 2SW (year $x + 1$) salmon ratios for the 21 rivers.

Sea Temperatures

Data on sea temperatures used were monthly mean surface values at Stykkishólmur, a long-standing and well-documented

TABLE 2. Years of data used in all analyses reported in this paper.

River	Years investigated
Laxá í Kjós	1949–50
	1953–56
	1959–82
Laxá í Leirársveit	1955–83
Hvítá (Borgarf)	1967–79
	1982–84
Grímsá/Tunguá	1972–84
Thverá	1956–73
	1976–82
Nordurá	1949–78
	1981–84
Langá	1965–84
Álftá	1965–84
Hítará	1961–62
	1965–84
Haffjardará	1969–84
Straumfjardará	1965–84
Midá í Dölum	1970–78
	1981–84
Haukadalsá	1948–60
	1963–84
Laxá í Dölum	1946–84
Fáskrúd	1949–84
Flekkudalsá	1961–82
Laugardalsá	1954–84
Langadalsá	1961–74
	1978–84
Stóra-Laxá	1974–78
	1981–84
Sog	1975–84
Ölfusá-Brúará-Hvítá	1964–84

station on Iceland's west coast. Monthly means were based on several, usually equally spaced measurements per month obtained through the Icelandic National Weather Office. Three different combinations of temperatures were analyzed against ratios. The first temperature variable (T1) was the sum of monthly mean temperatures from May to December (year $x - 1$), corresponding to the time when the smolts would enter the sea and begin rapid growth until their first winter at sea. The second variable (T2) was the sum of mean monthly temperatures from May (year x) to April (year $x + 1$), corresponding to the time from when the grilse would be returning to rivers to when the 2SW salmon would be returning. The third variable (T3) was the mean April–May (year $x - 1$) temperature, which was used to indicate sea conditions in spring and early summer, just before or during the time smolts would be entering the sea. This variable was selected because Peterman (1985) concluded that this period may be critical in influencing sea-age at maturity of Bristol Bay sockeye salmon and because Scarnecchia (1984a) and others have concluded that the time soon after smolts enter the sea is important in determining year-class strength.

Of all 485 possible available monthly mean temperatures from January 1945 to May 1985, only 4 values were missing. These four monthly values were estimated from the average of the 10 monthly means from surrounding years, 5 before and 5 after.

Statistical Analyses

Pearson correlation coefficients were calculated for comparing grilse catches as well as ratios among rivers. Linear, mul-

TABLE 3. Correlations among grilse catches for 21 Icelandic west coast rivers. Italicized data, $P < 0.01$; *$P < 0.05$.

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U
Laxá í Kjós	A	—																				
Laxá í Leirársveit	B	*0.77*	—																			
Hvítá	C	0.10	0.54*	—																		
Grímsá	D	0.60*	*0.83*	0.57*	—																	
Thverá	E	*0.59*	*0.57*	0.62*	0.58*	—																
Nordurá	F	*0.76*	*0.76*	0.52*	*0.78*	*0.73*	—															
Langá	G	0.52*	*0.82*	*0.71*	*0.80*	*0.74*	*0.73*	—														
Álftá	H	−0.10	0.04	0.31	0.23	0.36	0.15	0.39	—													
Hítará	I	*0.75*	*0.73*	0.30	*0.74*	0.51*	*0.59*	*0.63*	−0.03	—												
Haffjardará	J	0.55*	*0.62*	0.43	*0.70*	0.51	*0.84*	*0.70*	−0.17	*0.62*	—											
Straumfjardará	K	0.55*	*0.73*	0.36	*0.78*	0.27	*0.59*	*0.61*	−0.04	*0.85*	*0.65*	—										
Midá í Dölum	L	0.45	0.29	0.00	0.32	0.12	0.53*	0.22	−0.09	0.47	0.23	0.54*	—									
Haukadalsá	M	*0.79*	*0.73*	0.18	0.43	0.47	*0.73*	*0.59*	−0.01	0.51*	*0.61*	*0.58*	0.45	—								
Laxá í Dölum	N	*0.45*	*0.63*	0.27	0.32	0.27	*0.59*	0.28	−0.16	0.03	0.54*	0.25	0.14	*0.61*	—							
Fáskrúd	O	0.42*	*0.50*	0.50*	*0.73*	0.30	*0.58*	0.47*	−0.28	0.32	*0.76*	0.53*	0.44	*0.51*	*0.66*	—						
Flekkudalsá	P	*0.63*	*0.60*	0.31	0.49	*0.71*	*0.73*	*0.68*	−0.01	*0.71*	0.61*	0.48*	0.39	*0.53*	0.17	0.40	—					
Laugardalsá	Q	*0.52*	*0.64*	*0.61*	0.50	*0.74*	*0.57*	*0.79*	0.37	*0.60*	*0.62*	*0.56*	0.14	*0.56*	0.30	0.32	*0.63*	—				
Langadalsá	R	*0.59*	*0.55*	0.44	0.60*	0.52*	*0.67*	*0.74*	−0.06	*0.55*	*0.81*	*0.61*	0.45	*0.67*	0.39	*0.71*	*0.71*	*0.67*	—			
Stóra-Laxá	S	0.42	−0.08	−0.07	0.25	0.36	0.34	0.07	0.31	0.10	0.26	−0.15	0.29	0.10	0.12	−0.00	0.43	−0.02	0.16	—		
Sog	T	*0.77*	*0.90*	0.46	*0.74*	0.67*	0.56	*0.88*	0.28	*0.91*	0.72*	*0.82*	0.12	0.56	−0.30	0.36	0.72*	*0.74*	0.73	−0.01	—	
OBH	U	0.38	0.25	0.41	0.62*	*0.66*	0.44*	0.49*	0.42	0.53*	0.43	0.35	0.07	0.22	0.01	0.08	0.48*	0.43*	0.26	0.67*	0.64*	—

TABLE 4. Correlations among ratios for 21 Icelandic west coast rivers. Italicized data, $P < 0.01$; *$P < 0.05$.

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U
Laxá í Kjós	A	—																				
Laxá í Leirársveit	B	*0.57*	—																			
Hvítá	C	0.26	0.41	—																		
Grímsá	D	*0.86*	*0.89*	0.45	—																	
Thverá	E	0.47*	0.44*	0.39	0.71*	—																
Nordurá	F	0.47*	0.28	0.41	0.54	*0.89*	—															
Langá	G	0.20	*0.64*	0.47	*0.74*	0.46	0.56*	—														
Álftá	H	0.28	0.45	0.47	0.66*	0.61*	0.43	0.51*	—													
Hítará	I	0.49*	*0.74*	*0.63*	*0.87*	*0.63*	0.43	0.56*	0.52*	—												
Haffjardará	J	0.03	0.35	0.36	0.46	0.39	0.55*	0.47	0.14	0.56*	—											
Straumfjardará	K	*0.71*	*0.70*	0.44	*0.81*	*0.83*	*0.78*	0.52*	*0.58*	*0.68*	0.48	—										
Midá í Dölum	L	0.47	0.50	0.29	0.25	0.43	0.39	0.01	0.08	0.20	0.17	0.48*	—									
Haukadalsá	M	*0.77*	0.27	0.51*	*0.78*	0.36	0.43*	0.31	0.33	*0.71*	0.41	*0.66*	−0.00	—								
Laxá í Dölum	N	*0.48*	0.19	0.18	0.17	0.45*	*0.46*	0.11	0.55*	0.18	0.09	*0.58*	0.50	*0.49*	—							
Fáskrúd	O	*0.68*	0.37*	0.49	0.48	*0.55*	*0.52*	−0.04	0.35	*0.55*	0.13	*0.64*	0.54	*0.57*	*0.60*	—						
Flekkudalsá	P	0.31	*0.63*	0.46	*0.75*	*0.66*	*0.69*	*0.65*	0.35	*0.77*	0.43	0.52*	0.28	0.43	0.08	0.38	—					
Laugardalsá	Q	0.39*	*0.53*	0.43	*0.73*	0.21	0.12	0.34	0.51*	*0.60*	0.10	*0.62*	0.60*	0.30	0.35	*0.47*	0.33	—				
Langadalsá	R	−0.04	−0.21	−0.17	−0.15	0.17	−0.00	−0.22	−0.04	−0.15	−0.35	−0.20	0.15	−0.07	0.06	−0.05	0.31	−0.05	—			
Stóra-Laxá	S	0.52	0.71*	0.66	0.59*	0.86	0.72*	*0.81*	0.77*	0.63	0.58	0.56	0.20	0.48	0.10	0.07	0.84*	0.18	−0.03	—		
Sog	T	−0.34	−0.01	0.42	−0.04	0.08	0.37	0.13	0.13	0.08	0.27	0.06	0.17	−0.02	0.23	−0.16	−0.33	0.34	−0.82*	0.02	—	
OBH	U	0.43	*0.63*	0.33	0.66*	0.51*	0.53*	*0.63*	*0.58*	*0.70*	0.35	*0.60*	0.15	0.38	0.36	0.40	0.51*	0.37	−0.27	*0.89*	0.20	—

tiple, and stepwise regressions were used to identify if and how sea temperatures or West Greenland catch related to ratios from rivers. A $P < 0.20$ value was the criterion for entry into the stepwise model. Because both sea temperatures and salmon catch time series tend to be autocorrelated, residuals of linear relationships between variables entering the stepwise models were analyzed with a Durbin–Watson statistic for possible problems with autocorrelation that might produce misleading results (Dempson et al. 1986). Homogeneity of variance and normality of residuals, two other regression assumptions, were also evaluated in the stepwise models.

Results

Correlations between Grilse Catches and between Ratios

Annual grilse catches were strongly and positively correlated among the 21 rivers. Of the 210 correlations of grilse between pairs of rivers, 82 were positive and highly significant ($P < 0.01$), 33 were positive and significant ($P < 0.05$), and none were negative and significant at either 0.01 or 0.05 (Table 3). Correlations among ratios were less strong but similar. Of these 210 correlations, 50 were positive and highly significant ($P < 0.01$), 33 were positive and significant ($P < 0.05$), and 1 was negative and significant ($P < 0.05$; Table 4). For correlations between grilse and for those between ratios, the closer relationships were found for those rivers with some of the larger catches and more reliable catch records. For example, the Rivers Álftá, Hvítá (Borgafjördur), and Midá í Dölum showed poor relationships and have low catches and less complete records than most of the other rivers. Nearly all rivers had certain years (e.g. 1978) with unusually high ratios, even though all fishing, data collection, and data analyses were conducted independently for each river.

Trends in Grilse to Salmon Ratios over Time

Based on regression analyses, only two rivers, Laxá í Leirársveit and Langadalsá, had significantly increasing ratios over their time series (indicating fewer 2SW salmon relative to grilse; Table 5). Eighteen of the 21 rivers had coefficients of determination less than 0.09, which indicated that no long-term trends existed in the ratios. Several rivers, however, did have a series of particularly low ratios in the late 1940s and 1950s, before the expanded Greenland fishery (e.g. Fáskrúd, Laxá í Dölum, Thverá, and others; Fig. 2a–2e). Low ratios were also found for these and other rivers sporadically throughout the years that the West Greenland fishery was active.

Ratios before and during the West Greenland Fishery

Because the intense harvest of salmon off West Greenland began in the early 1960s and time series for Icelandic salmon catches are of moderate duration, ratios for years before the fishery began could be calculated for only eight rivers with the longest time series (Table 6). These rivers produced between 4 and 14 ratios before the West Greenland fishery began and 21 to 25 ratios during the fishery. All eight rivers had lower mean ratios before the fishery began than during the fishery. Results were highly significant (t-test; $P < 0.01$) for Laxá í Leirársveit, which also showed a highly significant increasing ratio with time. Three of the rivers (Laxá í Kjós, Thverá, and Nordurá) showed significantly higher ratios during the fishery than before it ($P < 0.05$; Table 6). Three other rivers (Haukadalsá, Fás-

TABLE 5. Coefficients of determination for relations of ratios versus year and for stepwise analyses of ratios (dependent variable) versus West Greenland catch and three sea temperature variables (T1, T2, and T3). Variables entered stepwise models at $P < 0.20$. *$P < 0.05$; **$P < 0.01$.

River	Ratio vs. year	Ratio vs. year, 1960 onward	Variables entering stepwise model	Significance of equation ($P < 0.05$)	Percentage of variation in ratios explained	Individual variables with significance of $P < 0.05$
Laxá í Kjós	0.02	0.08	T3(+)	Yes	17	T3(+)
Laxá í Leirársveit	0.14*	0.00	Green(+)	Yes	22	Green(+)
Hvítá	0.01	0.01	None	No	—	None
Grímsá	0.06	0.06	T1(+)	Yes	44	T1(+)
Thverá	0.00	0.02	Green(+), T2(+), T3(+)	Yes	32	None
Nordurá	0.02	0.08	T2(+), Green(+)	No	15	None
Langá	0.01	0.01	None	No	—	None
Álftá	0.00	0.00	T3(+)	No	20	None
Hítará	0.00	0.00	None	No	—	None
Haffjardará	0.05	0.05	T3(−)	Yes	35	T3(−)
Straumfjardará	0.17	0.17	T3(+)	No	12	None
Midá í Dölum	0.03	0.03	T2(−), Green(+)	No	47	None
Haukadalsá	0.02	0.10	T3(+)	Yes	15	T3(+)
Laxá í Dölum	0.02	0.07	T3(+), T2(−)	Yes	31	T3(+)
Fáskrúd	0.00	0.12	T3(+), Green(+)	Yes	43	T3(+), Green(+)
Flekkudalsá	0.02	0.02	None	No	—	None
Laugardalsá	0.00	0.00	T3(+)	Yes	15	T3(+)
Langadalsá	0.41**	0.41**	Green(−), T1(−)	No	12	None
Stóra-Laxá	0.03	0.03	None	No	—	None
Sog	0.00	0.00	None	No	—	None
OBH	0.07	0.07	T3(+)	No	12	None

krúd, and Laxá í Dölum) showed significantly higher ratios at $P < 0.10$. Nevertheless, despite this increase in mean ratios with the onset of significant fishing off West Greenland, there was no progressive increase in ratios as the fishery continued through the 1960s, 1970s, and 1980s. Only 1 of the 21 rivers, Langadalsá, showed significantly ($P < 0.05$) increasing ratios from 1960 forward, i.e. once the fishery had expanded (Table 5). In addition, there was no significant relationship between ratios and West Greenland catch for 20 of the 21 rivers ($P < 0.05$; Table 5).

Influence of Sea Temperatures and West Greenland Catches on Ratios

The mean April–May temperature (T3) was significantly ($P < 0.05$) positively related to ratios for five of the rivers: Laxá í Kjós, Haukadalsá, Laxá í Dölum, Fáskrúd, and Laugardalsá (Table 5; Fig. 3a–3c). For one river, Haffjardará, the mean April–May temperature entered negatively. For Grímsá, the total May–December sea temperature (T1) entered positively and significantly ($P < 0.05$).

For only one river, Laxá í Leirársveit, was the West Greenland catch significantly related to the ratios (Fig. 4). The relationship was positive, as hypothesized, and held for one of the two rivers that had shown increasing ratios over time (Table 5). In addition, the West Greenland catch entered the model significantly ($P < 0.05$) for Fáskrúd once the mean April–May sea temperature (T3) had entered the model (Table 5). These significant results for Greenland catch occurred with a frequency similar to that expected by chance.

Thirteen of the 21 rivers had no variables enter the stepwise models at the 0.05 level (Table 5). At lower levels of significance ($P < 0.10$ or $P < 0.20$), other variables entered the stepwise models (Table 5). Final stepwise equations for 9 of the 21 rivers were significant ($P < 0.05$). In three cases, the combinations of variables entering the stepwise models explained 43, 44, and 47% of the variations in the ratios, but most equations explained far less than half of the variations in the ratios (Table 5). Residuals of all the stepwise models listed in Table 5 were analyzed to check regression assumptions and to assess if autocorrelation problems existed. Of the 16 rivers that had variables enter stepwise models, 1 (Laxá í Kjós) had autocorrelated residuals ($P < 0.05$). Two rivers (Fáskrúd and Laxá í Dölum) had heteroscedastic residuals that might have called for a method to stabilize variance. The frequency of these problems was similar to that expected by chance.

Discussion

The effects of harvesting MSW salmon on age composition of Atlantic salmon stocks are manifested in at least three ways, each associated with increasingly intensive harvest. In Case 1, there is a shift toward younger fish spawning that results from direct, selective annual removal of MSW fish. This shift may be short term and need not drastically change the genetic composition of the next generation of spawners if the remaining MSW salmon are still numerous and are more effective at spawning and leaving offspring than are grilse.

In Case 2, greater depletion of MSW salmon results in a long-term intergenerational genetic change in the stock. In this case, higher frequencies of grilse spawn and leave offspring, which results in higher frequencies of grilse in succeeding generations.

In Case 3, harvest rates of MSW salmon may be so high that, in addition to genetic changes in the spawning stock, stream habitat for their offspring as parr may be underutilized. The reduced number of parr, which are already likely to be offspring of grilse, grow rapidly, which further increases their tendency to mature precociously as parr (for males) or as grilse rather than as MSW salmon. Case 3 is an indirect life history response by the stock to reduced optimal age at maturity as a result of higher harvest rates on adults and lower densities of parr in streams (Gibson 1978; Montgomery 1983; Caswell et al. 1987).

In the Icelandic stocks, we see possible evidence of Case 1, but no evidence of Case 2 or 3. The lack of significant declines

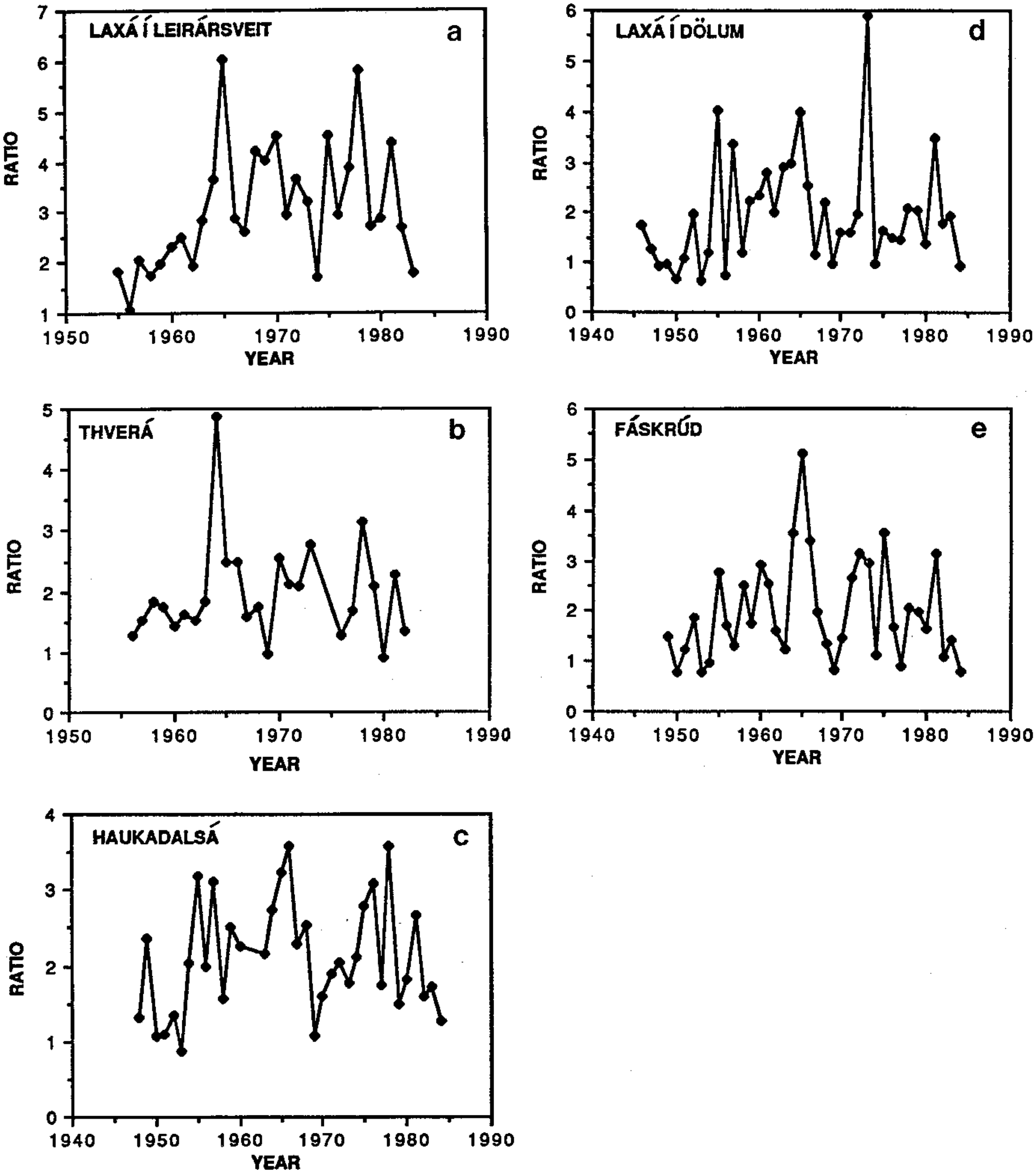

FIG. 2. Ratios of grilse (year x) to 2SW salmon (year $x + 1$) for (a) Laxá í Leirársveit, Ratio $= -0.65755 + 0.0540$(Year), (b) Thverá, Ratio $= 1.7507 + 0.00310$(Year), (c) Haukadalsá, Ratio $= 3.0745 - 0.0139$(Year), (d) Laxá í Dölum, Ratio $= 0.96615 + 0.01519$(Year), and (e) Fáskrúd, Ratio $= 1.5447 + 0.0065$(Year).

in ratios for all but 2 of the 21 rivers (Table 5) contrasted with results from the analyses of variance for pre- versus post-Greenland fishery ratios, where eight of eight rivers had higher ratios after the fishery had expanded in 1960. Although the ratios were higher for the eight rivers after the fishery began than before (as would be expected in Case 1), there was no progressive shift in age structure associated with the continuation, expansion, and later contraction of the fishery in the succeeding 25 yr. As indicated in Table 5, only 1 of the 21 rivers showed significantly increasing ratios from 1960 to 1985. If Case 2 or 3 had been occurring in the stocks, widespread significant increases in ratios would have been expected. It may be argued that since the West Greenland fishery harvested more potential MSW salmon in the middle portion of the time series than at

TABLE 6. Comparison of ratios before and after expansion of Greenland fishery. Number of years of data are in parentheses.

River	Before Greenland	During Greenland	Comparison of means Prob > T
Laxá í Kjós	2.11 (7)	2.97 (23)	0.05
Laxá í Leirársveit	1.73 (5)	3.35 (24)	0.01
Thverá	1.60 (4)	2.03 (21)	0.05
Nordurá	1.67 (11)	2.31 (23)	0.05
Haukadalsá	1.87 (12)	2.22 (23)	0.10
Laxá í Dölum	1.57 (14)	2.17 (23)	0.10
Fáskrúd	1.56 (11)	2.16 (25)	0.10
Laugardalsá	2.17 (6)	2.39 (25)	>0.10

either end, progressively higher ratios would not be expected. However, Greenland catch was poorly related to changes in ratios (Table 5), so the observed changes in ratios after 1960 must have been caused by other factors. These factors may be ecological or a result of subtle changes in harvesting patterns or data reporting in the riverine fisheries. But the changes evidently are not related to differences in mean April–May sea temperature, inasmuch as the temperatures before 1960 and after 1960 each averaged 3.5°C.

The long-term stability in ratios for all but 2 of the 21 rivers is in marked contrast with results from Atlantic salmon stocks in areas where significant oceanic and coastal fisheries are harvesting potential MSW salmon (e.g. Paloheimo and Elson 1974; Bielak and Power 1986). Ricker (1981) reported similar declines in mean sea-age of Pacific salmon. In Iceland, there is no directed oceanic or coastal fishery, and in-river rod fisheries harvest low to moderate numbers of returning salmon (total harvest rates most often 25–50%; Gudjónsson 1988). Rod fishing is undoubtedly less selective toward MSW salmon than large-meshed gill nets would be. Thus, even with harvest off West Greenland, numbers and genetic makeup of spawners and densities of parr in rivers are high enough to maintain historical percentages of MSW salmon. Case 2 and Case 3 effects from reduced frequencies of MSW salmon and reduced parr densities would be minimized. Perhaps the prudent harvests of Icelandic anglers have kept densities of spawners and parr up (as well as maintained different genotypes among the spawners and parr)

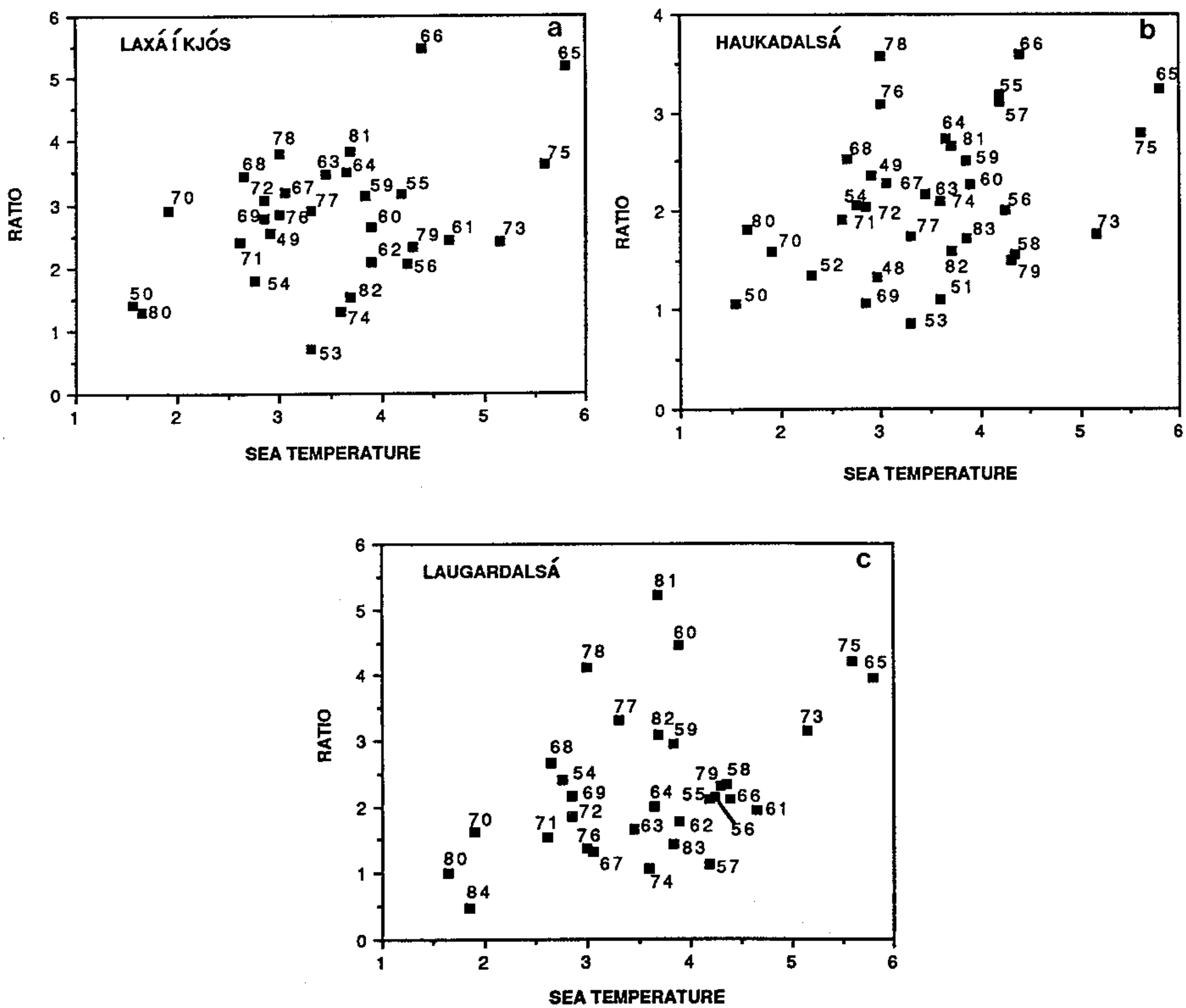

FIG. 3. Ratios versus mean April–May sea temperatures (year $x - 1$) for (a) Laxá í Kjós, Ratio = 1.2752 + 0.4264(Temp), (b) Haukadalsá, Ratio = 1.1008 + 0.2938(Temp), and (c) Laugardalsá, Ratio = 0.76428 + 0.44805(Temp).

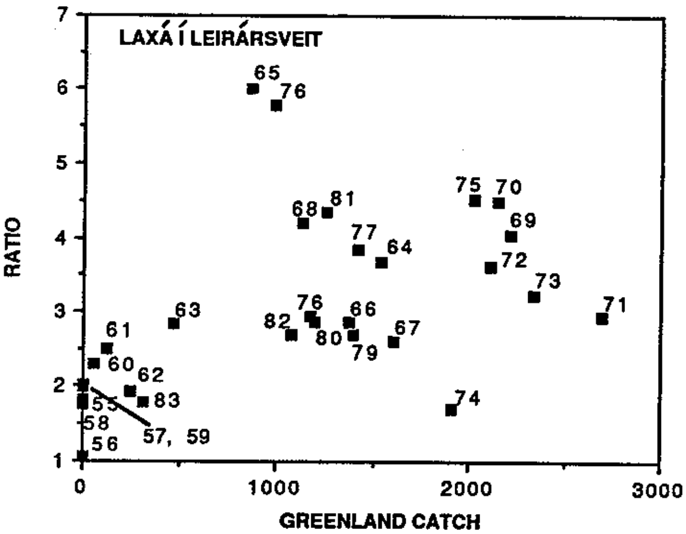

FIG. 4. Greenland catch in year x versus ratio for Laxá í Leirársveit. Ratio = 2.3177 + 0.00069(Catch).

and helped to maintain stock composition. Instead of declines in MSW salmon like those seen in many regions, anglers in Iceland can still catch the more desirable MSW salmon rather than just grilse.

In the absence of more detailed genetic data, the observed stability in sea-age composition serves as phenotypic evidence that serious total (oceanic plus riverine) overharvest of Icelandic salmon is not widespread. Excessive harvest from a combination of West Greenland or riverine fisheries over generations would have been expected to shift age composition toward more grilse. Declines in mean age at maturity from historical (i.e. lower harvest) frequencies should be used in other areas as an ersatz tool of genetic analysis to alert biologists to identify overharvest and possible loss of genetic diversity. Age structure relative to historical composition should be one of several indicators of sufficient genetic diversity and of a ''safe biological limit'' for Atlantic salmon that the International Council for the Exploration of the Sea's (1986) Working Group on North Atlantic Salmon has attempted to define.

However, close monitoring of certain rivers with increasing ratios (e.g. Laxá í Leirársveit and Langadalsá) is warranted. Even though the West Greenland fishery is not harvesting high percentages of potential MSW Icelandic salmon, nonsignificant relationship between West Greenland catch and ratios for a given stock does not imply that salmon of that stock are not being caught off West Greenland. In addition to the actual observed recoveries of tagged Icelandic salmon there, the variations in ratios produced by low harvest rates are often small relative to observed natural variations in the ratios resulting from differential annual riverine catch or abundance estimates. Because of noise in the ratios, they may be ineffective at detecting low or moderate harvest rates off West Greenland.

For example, if we assume constant natural mortality between the grilse and 2SW stages and a constant riverine fishery and consider a stock with a natural constant 1:1 grilse to salmon ratio, it would take a 50% harvest rate in the West Greenland fishery on the potential 2SW salmon eventually returning to the river for the ratio to rise to 2:1 (Fig. 5). Many Icelandic stocks exhibit substantial variation in ratios, e.g. Thverá, whose ratios vary from 0.90 to 3.13 (mean = 1.96; n = 25). Assuming that the observed mean pre-Greenland ratio for Thverá (1.6, n = 4) represented the natural situation, then a post-Greenland ratio of 2.4 might correspond to a harvest rate of 33% on 2SW salmon, and a ratio of 3.2 might correspond to a harvest rate of 50% (Fig. 5). Since 1960, Thverá has had 5 yr with ratios 2.4 or higher and no years with a ratio as high as 3.2. It is therefore unlikely that 2SW fish from Thverá are harvested at rates as high as 33–50%. Given the inherent annual variation in the ratios, however, a harvest rate below 33% is difficult to detect (Fig. 5). The observed annual variability in the ratios thus limits their applicability for indicating subtle effects of environmental factors. Some of this annual variability undoubtedly is noise — an artifact of the data collection and analysis procedures (e.g. classification into ages by weight-frequencies or variable annual effort).

If variations in environmental conditions as well as the substantial inherent variation in the catch data can be averaged over time and if only Case 1 effects (direct removal) are acting, it is possible to estimate what the average harvest rates off West Greenland would be to result in the observed changes in ratios before and after 1960. Expected harvest rates for the seven rivers with sufficient data and significantly higher mean ratios after 1960 varied from 16% of the MSW salmon that would have eventually been caught from Haukadalsá to 48% of the MSW salmon that would have been caught from Laxá í Leirársveit. Hypothetical mean harvest rates for the other five rivers were 29% for Laxá í Kjós (Fig. 6), 21% for Thverá, 28% for Nordurá, 27% for Laxá í Dölum, and 28% for Fáskrúd.

The close correlation between annual grilse catches in these rivers indicates to us that a widespread environmental factor (or factors) is strongly affecting the abundance of Icelandic salmon (Scarnecchia 1984a). Similarly, the significant correlations of ratios among rivers indicates that some large-scale environmental factor is responsible, even if this influence is small compared with the known close grilse-to-salmon relationship within stocks (Scarnecchia 1984b). Strong correlations between ratios do not imply an oceanic effect on age at maturity per se. The same correlations may result simply from similar conditions in freshwater during the presmolt period or from straying of salmon among groups of rivers. Our results do agree, however, with those of Peterman (1985), who found that mean age at maturity of Bristol Bay stocks of sockeye salmon of the same smolt class tended to vary in the same direction. Peterman (1985) also concluded that late ocean life probably was not a major source of variation in age at maturity. Our results also support that conclusion; in none of our 21 rivers was age at maturity significantly correlated with sea temperatures between the times of return of grilse and 2SW salmon to the rivers. If age at maturity is affected by oceanic variations, it evidently occurs during the time from when smolts leave the river to when grilse return.

If age at maturity of an individual fish can be influenced by oceanic conditions early in marine life, we would expect to see a relationship between sea temperatures early in marine life and ratios of that smolt class. Six of the 21 rivers showed a significant, positive relationship between pre-grilse sea temperatures (T1 or T3) and ratios. Although, at first inspection, this frequency is higher than would be likely to occur by chance, the correlation between ratios makes these results not strictly independent of each other. Our variable results among rivers underscore the importance of using several rivers in this sort of analysis. We thus have only suggestive evidence that oceanic conditions, as reflected in sea temperatures, affect the ratios. Such a relationship would occur if the warmer sea was indicative of better conditions for feeding, growth, and survival of

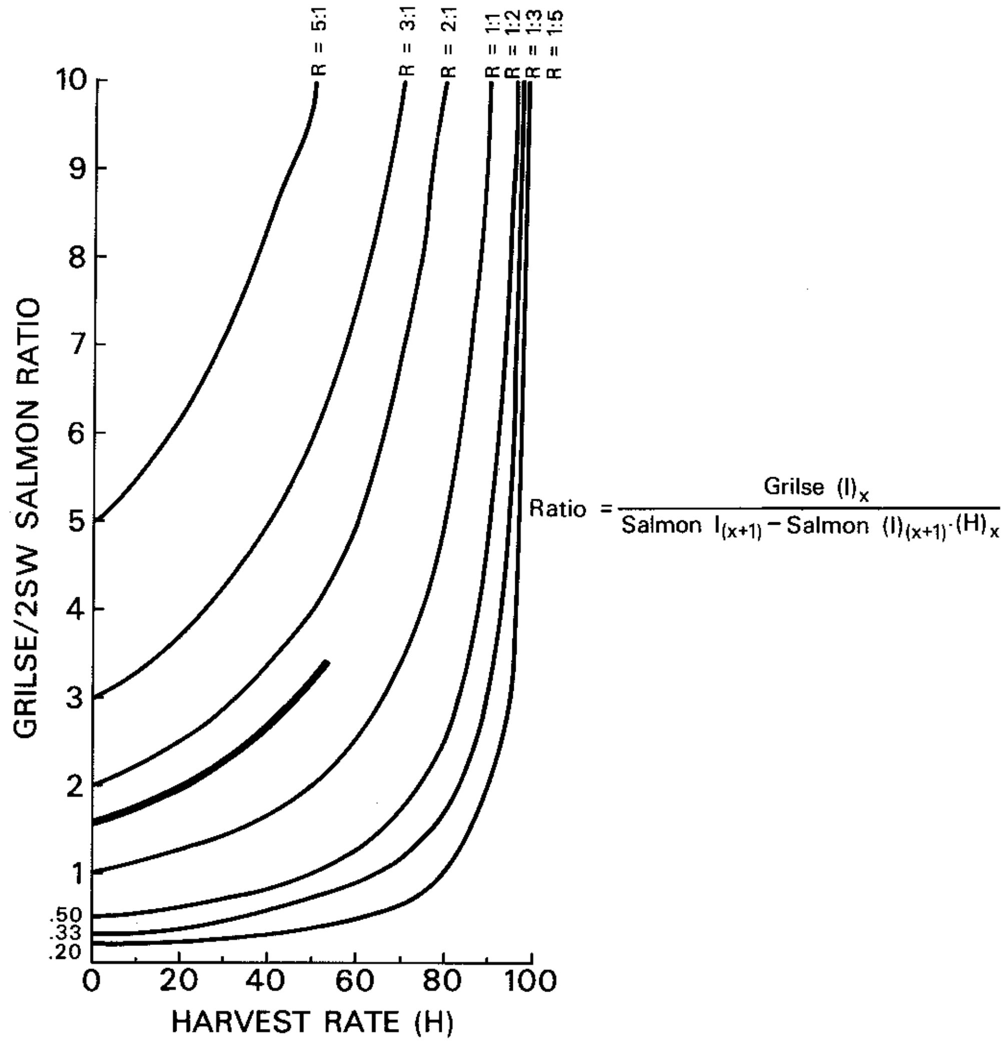

FIG. 5. Relationship between ratios and harvest rates for stocks with several different age compositions. Heavy, abbreviated curve is for Thverá assuming that the observed mean ratios before the Greenland fishery represented baseline ratio for the stock. See text for example.

smolts (Scarnecchia 1984a). If the smolts grew faster in their first year, relatively more of them might make a physiological decision (Thorpe 1986) to mature as grilse. In years of poorer growth, relatively fewer would mature as grilse, and relatively more MSW salmon would result.

Evidence of this process can be most easily seen from pen-rearing data for salmon (summarized by Dempson et al. 1986), where individual fish can be followed to maturation. Catch data and scale data, with the inherent biases of size-specific growth and mortality, merely confuse the issue. Dempson et al. (1986) cited numerous studies (e.g. Simpson and Thorpe 1976; Naevdal 1983; Gjerde 1984) indicating that marine growth in early-maturing fish was greater in the first year than in non-maturing fish, which is consistent with the positive relationship between sea temperature and ratios.

Dempson et al. (1986) questioned whether available evidence from wild salmon supported the findings of pen-rearing experiments. We believe, however, that reported results for wild fish do not contradict the results of pen-rearing experiments. Studying the relationship between growth rate and subsequent maturity *before the maturation occurs*, as in pen-rearing, is not comparable with studying the relationship based on scale samples from adult fish, i.e. *after the maturation occurs*. Assuming that the faster growing pen-reared fish do make a physiological decision to mature earlier, their growth slows relative to nonmaturing ones once they actually begin to mature, as energy is diverted into sex products. Thus, for wild fish, the initially faster growing individuals may in fact be smaller at time of first oceanic annulus formation, which would account for the smaller first-year growth increment in grilse than in MSW salmon in much of Gardner's (1976) scale data, as well as in the recalculated scale data of Dempson et al. (1986). The end products of the maturation process (scales of returning adult fish) may thus indicate that growth during the first year at sea was slower for fish destined to return as grilse, when the opposite was true.

Because we have not found evidence of excessive widespread harvest of Icelandic west coast salmon stocks by the West Greenland fishery, perhaps many MSW salmon from western Icelandic stocks feed in other areas and do not migrate to West Greenland. Mathisen and Gudjónsson (1978) suggested that most grilse from southwestern rivers might feed in the Irminger Sea but hypothesized that the 2SW salmon migrate either to West Greenland or toward the Faroe Islands. Perhaps many of the 2SW salmon have a localized migration pattern as well and remain in the Irminger Sea or off East Greenland (Ísaksson 1986). More tagging and recovery studies are needed to answer this question. Such studies are also needed to obtain direct evi-

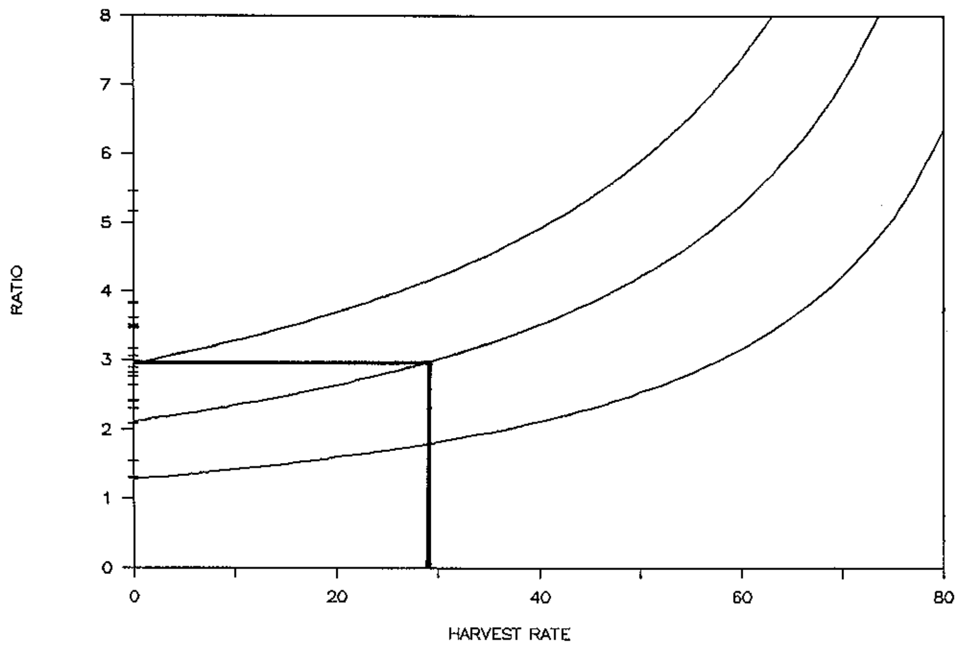

FIG. 6. Mean hypothetical harvest rate of 29% for would-be 2SW salmon off West Greenland for Laxá í Kjós. Annual ratios comprising the mean for the river are marked on the y-axis. Lower and upper curves are 95% confidence limits. Harvest rates mentioned in the text for the four other rivers were calculated analogously.

dence concerning harvest of Icelandic salmon off West Greenland.

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