Effects of the Faroese long-line fishery, other oceanic fisheries and oceanic variations on age at maturity of Icelandic north-coast stocks of Atlantic salmon (Salmo salar)*

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ABSTRACT

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Investigations were conducted on the effects of oceanic variations (as indicated by sea temperatures) and catches of the Faroese, Norwegian Sea and West Greenland salmon fisheries on the sea-age composition of Atlantic salmon ($Salmo\ salar\ L$.) from 22 Icelandic north-coast rivers. Catches of grilse in rivers were strongly correlated among the 22 rivers, as were the ratios of grilse caught to two-sea winter (2SW) salmon caught the next year. Four of the 22 rivers showed increasing ratios over time and three of these rivers, all in the northeast, had significantly higher mean ratios after the expansion of the Faroese fishery than before (P < 0.05). No evidence was found from ratios for the other 18 rivers to suggest that Faroese fishing was significantly depleting those stocks, even though 13 micro-tagged north-coast salmon had been recovered in the fishery in the 1988-89 season. No evidence was found that Norwegian Sea or West Greenland fisheries affected stock composition. The mean April-May sea temperature prior to when the smolts enter the sea was significantly and positively related to ratios in eight of the 22 rivers. This result, along with frequent significant correlations in ratios among rivers, indicated that more rapid growth of smolts in their first summer may have increased grilse to 2SW salmon ratios on several rivers.

INTRODUCTION

The abundance of Atlantic salmon (Salmo salar L.) in Iceland's north-coast rivers has historically fluctuated widely (Kristjánsson, 1982; Scarnecchia, 1984a). In the early 1980s, several-fold declines in the abundance of salmon

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returning to popular angling rivers such as Laxá í Adaldal, Hofsá and Selá occurred simultaneously with the expansion of the non-Icelandic offshore fishery for salmon off the Faroe Islands. Since then, Icelandic river owners, anglers and laymen have expressed growing concern that the expanding Faroese fishery was harvesting significant numbers of Icelandic salmon (e.g. Jóhannesson, 1983). It has been suggested that Icelandic stocks in the northern, and particularly northeastern, districts are most vulnerable to the Faroese fishery because these stocks are closest geographically to the fishery, have high frequencies of multi-sea winter (MSW) salmon (Scarnecchia, 1983) and suffered serious declines in abundance in the early 1980s (Institute of Freshwater Fisheries, Reykjavík, unpublished data, 1988). It has also been speculated that these stocks may long have been harvested in substantial numbers by fisheries in the Norwegian Sea and off the west coast of Greenland.

Kristjánsson (1982) and Scarnecchia (1984b) have presented evidence that the number of two-sea winter (2SW) salmon returning to a river in 1 year can be predicted accurately for most northern stocks from the number of grilse (1 year at sea) returning the previous year. These relations imply that the grilse to salmon ratios do not vary much between years within a stock. Because the available evidence indicates that the Faroese and Norwegian Sea salmon harvest consists primarily of potential MSW salmon, and that the West Greenland harvest is exclusively potential MSW salmon, excessive harvest of north-coast salmon stocks by any of these fisheries should result in an increase in the grilse to MSW salmon ratios for the stocks, both from short-term effects of removal and from long-term selection for earlier maturing fish. (see reviews by Gardner, 1976, and in Meerburg, 1986.)

In addition to the effects of oceanic fishing on grilse to MSW salmon ratios, some investigators have found that marine factors, particularly in the first year at sea, have influenced the mean age at maturity of returning fish and, hence, grilse to MSW ratios. 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 and concluded that most of the variations in age at maturity probably resulted from the early marine period of their life history. However, Dempson et al. (1986) found no evidence that sea temperatures affected sea age at maturity of Atlantic salmon in the Restigouche River, Quebec. Although oceanic conditions, as indicated by sea temperatures, evidently exert a significant influence on the abundance of northern stocks of Icelandic salmon (Scarnecchia, 1984a), the effects of these oceanic variations on grilse to MSW salmon ratios within a smolt class are not known. Thus, if either oceanic fishing or variations in the oceans are affecting these ratios, the ability to accurately predict the yields of MSW salmon from grilse would be hindered. The issues of oceanic fishing, environmental effects on age at maturity and the ability to forecast yields of MSW salmon are related and must be considered together.

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ICELANDIC SALMON 209

In this paper, we investigate the effects of the Faroese, Norwegian Sea and West Greenland fisheries, as well as between-year variations in oceanic conditions, on sea-age composition of the salmon stocks from 22 Icelandic north coast rivers. We consider if and how the age composition of the salmon stocks has changed coincident with the oceanic fisheries and also how interannual variations in oceanic temperatures affect the grilse to salmon ratios and, thus, our ability to predict MSW yields from grilse yields the previous year.

THE FAROE AND NORWEGIAN SEA FISHERIES

The development and operation of the Faroese fishery have been summarized by Mills and Smart (1982), Shelton (1986) and Jákupsstovu (1988), and only aspects relevant to the Icelandic salmon will be repeated here. The catch of the long-line fishery near the Faroe Islands remained below 60 tonnes before 1978, but rose to 194 tonnes in 1979, 718 tonnes in 1980, and > 1000 tonnes in 1981 (Table 1) as the season became longer and more Faroese and Danish long-liners participated (International Council for the Exploration of the Sea, (ICES), 1982). Catches from calendar years 1982–1985 varied from 960 tonnes in 1982 to 672 tonnes in 1985. Voluntary quotas by the Faroese government have kept the catch in recent years below that of the peak catch of 1981 (Table 1; ICES, 1986b).

Of particular interest in this study is the age composition of the catch. Shearer and Clarke (1983) referenced Struthers (1981) in stating that a mixture of potential grilse and MSW salmon occurred from 1969 to 1979. According to Shelton (1986), "Before the fishery moved to the northern sector of the Faroese EEZ [Exclusive Economic Zone], the catch consisted mainly of potential grilse..., but in 1981, 1982 and 1983 mainly of multi-sea winter fish. For example, in 1981-82 and 1982-83, c [sic] 80% of the catch of virgin fish were 2SW. Samples of catches in 1981-82 and 1982-83 showed 84% and 71% to be female fish. In both seasons, catch rates and the proportion of female fish increased with latitude". Ólafsson (1987) reported that catches by a specific long-line vessel in 1982 were mainly MSW fish and that females constituted 71% of the catch. Shearer and Clarke (1983) suggested that "a significant shift has occurred during the period 1979-1982 away from the 1SW [grilse] component of the stock". In the 1984-85 season, which was under a minimum length limit of 60 cm, the catch was >99% prospective MSW salmon (ICES, 1986b).

Some information is available on the number of undersized fish discarded during fishing operations. In the 1984-85 season, observers determined that the percentage of undersized fish caught on selected vessels ranged from 3 to 31.8% (ICES, 1986b) and varied widely with area and time. The survival of these discards is unknown, but is probably low because of stress and scale loss from handling and prolonged hooking.

TABLE 1

Catch (in metric tonnes) of Atlantic salmon by fisheries off West Greenland, the Faroe Islands and in the Norwegian Sea. All blank entries are assumed to be zero for analyses. Adapted from ICES (1986a,b) and Shelton (1986)

Year	Catch				
	West Greenland	Norwegian Sea	Faroe Islands		
1960	60				
1961	127				
1962	244				
1963	466				
1964	1539				
1965	861				
1966	1370				
1967	1601	77			
1968	1127	403	5		
1969	2210	911	7		
1970	2146	946	12	*	
1971	2689	488	0		- ,.
1972	2113	506	9		
1973	2341	533	28		
1974	1917	373	20		
1975	2030	475	28		
1976	1175	289	40		
1977	1420	192	40		
1978	984	124	51		
1979	1395	118	194		
1980	1194	155	718	•	
1981	1246	213	1027		,
1982	1077	ī	884 ²		٠
1983	310	$(383)^1$	694 ²		
1984	297	0	786 ²	-	
1985	851	0	664 ²	0.1	

¹Non-zero catch, but data unavailable to authors at the time of analyses. Assumed to be zero.

²Data for the 1982–85 Faroese catch listed in the table are for the 1981–82, 1982–83, 1983–84 and 1984–85 seasons, respectively.

Unlike the West Greenland fishery, then, the Faroese fishery is not exclusively a fishery on MSW salmon. Catches since 1981, however, have clearly been dominated by potential MSW salmon and such salmon evidently are especially dominant in the northern fishing areas (Shearer and Clarke, 1983).

The Norwegian Sea fishery began as a drift-net fishery in the early 1960s, but Danish vessels introduced long-lining in 1966 and the fishery expanded to a peak catch of 946 tonnes in 1970. The fishery closed after the 1983 season under the terms of the North Atlantic Salmon Convention (Shelton, 1986). Studies in 1972 indicated that 80–85% of the catch was MSW salmon and that Norwegian salmon were important contributors to the catch (Table 1).

ICELANDIC SALMON 211

The West Greenland fishery is summarized by Shelton (1986) and is also summarized with reference to Icelandic salmon by Scarnecchia et al. (1989). The catch consists exclusively of MSW salmon (Table 1).

From 1967 to 1988, only four tagged Icelandic salmon were recovered from the Faroese fishery. One of these salmon had been tagged in Selá in north-eastern Iceland, one in Midfjardará in the north central region and two in southwestern Iceland. One additional salmon tagged at Kollafjördur hatchery near Reykjavík was captured in a lake in the Faroe Islands. Since 1982, Iceland has had an active program for microtagging selected north coast stocks, mostly hatchery-reared, but until the 1988–89 season none had been recovered in the Faroese fishery. In the 1988–89 season, however, 13 microtagged, potential MSW Icelandic salmon were recovered in the Faroese fishery: seven from Laxí Adaldal, three from Blanda, two from Midfjardará (one a wild smolt), and one from Hjaltadalsá. All thirteen recoveries of Icelandic salmon were from north coast stocks, even though much more microtagging occurs for west coast stocks than for north coast stocks.

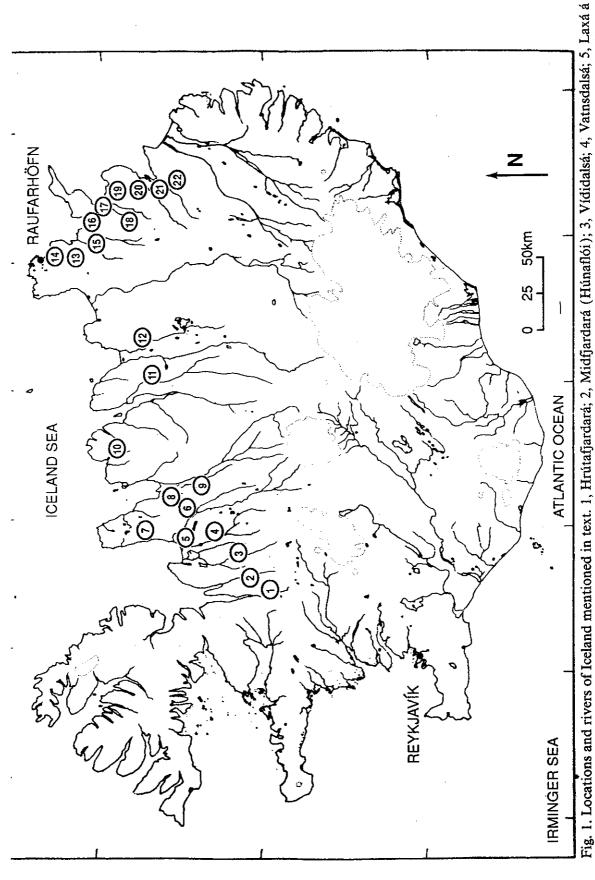
Only one salmon, also tagged at Kollafjördur, was recovered from the Norwegian Sea fishery. As of 1988, twelve tagged salmon have been recovered from the West Greenland fishery; ten of these fish had been released from the west coast and two from the north coast. One additional salmon tagged at Vesturdalsá in northeastern Iceland has been recovered from waters off East Greenland (Ísaksson, 1980; T. Gudjónsson, personal communication, 1989). Inasmuch as overall tagging efforts for north coast stocks have only recently escalated, and recoveries have been few in all fisheries, these recoveries must still be interpreted cautiously. In addition, nearly all of the recoveries have been hatchery-reared fish, sometimes transplanted from natal areas before being released. It is thus poorly understood how many Icelandic salmon, and which stocks, contribute to these fisheries.

METHODS

Salmon catches

Icelandic salmon data consisted of long-term angling catch records from all 22 north-coast rivers having sufficient catches of grilse and MSW salmon to justify the analyses (Fig. 1). The rivers support angling with rods. Gudjónsson (1978) and Scarnecchia (1983) described the details of the recreational fishery. The number of rods per river per season is strictly regulated and nominal effort has generally remained constant from year to year. However, the number of rods has gradually increased at variable intervals of several years in most rivers (Table 2). In this paper, we assumed that catches were representative of abundance, at least over periods of adjacent years, and that ratios of grilse in 1 year to MSW salmon the next year could be calculated with

212



Ásum; 6, Blanda-Svartá; 7, Laxá-Ytri; 8, Saemundará; 9, Húseyjarkvísl; 10, Fljótaá; 11, Fnjóská; 12, Laxá í Adaldal; 13, Ormarsá; 14, Deildará; 15, Svalbardsá; 16, Sandá; 17, Hölkná; 18, Hafralónsá; 19, Midfjardará (Bakkaflóa); 20, Selá, 21, Vesturdalsá; 22, Hofsá.

Years of data used in all analyses reported in this paper, and angling effort (number of rods per day) for 21 rivers in 1958, 1976 and 1982 when surveys were compiled. Data provided by Einar Hannesson, Veidimálastofnunin. ND=no data available

River	Years investigated	Effort (1958)	Effort (1976)	Effort (1982)
Hrútafjardará	1958–59 1962–68 1971–81	2	3	3
Midfjardará	1956–84	7	9	10
Vídidalsá	1961-75 1978-84	6	8	8
Vatnsdalsá	1961–84	2	4	6
Laxá á Ásum	1961–65 1968–84	2	2	2
Blanda/Svartá	1964–77 1980–84	ND	8	8
Laxá-Ytri	1956–82	ND	1	ND
Saemundará	1967–68 1971–81	ND	2	ND
Húseyjarkvísl	1970–84	ND	2	ND
Fljótaá	1964 1969–84	ND	3	ND
Fnjóská	1969–84	ND	6	6
Laxá í Adaldal	1949-76 1979-84	14	18	18
Ormarsá	1974–76 1979–84	ND	4	ND
Deildará	1970–76 1979–84	ND	2	ND
Svalbardsá	1969-76 1979-84	ND	2	ND
Sandá	1964-76 1979 1982-84	3	2	ND

TABLE 2 (continued)

River	Years investigated	Effort (1958)	Effort (1976)	Effort (1982)
Hölkná	1971–76 1979–84	ND	2	ND
Hafralónsá	1971–76 1979–80	ND	6	ND
Midfjardará (B)	1970–76 1979–84	ND	2	ND
Selá	1956–66 1969–75 1979–84	ND	2–3	2–3
Vesturdalsá	1956–69 1972–76 1979–84	3	2–3	2–3
Hofsá	1961–76 1979–84	ND	7	7

minimal bias from year-to-year effort changes. In several 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 analyses were begun. Data sets ranged in length from 9 to 34 years (Table 2).

We determined the number of years salmon had spent at sea by analyzing the 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 or 3SW fish. Available scale samples indicated that the catch included a few repeat spawners. These fish were classified as 1SW, 2SW or 3SW according to the same criteria used for virgin spawners. The analysis did not consider 3SW fish, which were uncommon in most of the rivers. Because catches from all the rivers were low (often < 500 fish), data from both sexes were combined to increase sample sizes. Ratios of grilse in Year x to 2SW salmon in Year x+1 (hereinafter called ratios) were calculated and used in subsequent analyses.

The total Faroese catch was used as a variable, as was the Norwegian Sea catch. Faroese and Norwegian Sea catches were also combined in some analyses as one variable. Catches in Year x were related to grilse (Year x-1) to salmon (Year x) ratios for the 22 rivers.

The total West Greenland catch was also used as a variable and the catch in Year x was related to the ratios of grilse (Year x) to 2SW (Year x+1) salmon.

Sea temperatures

Data on sea temperatures were monthly mean surface values at Raufarhöfn, a station on Iceland's northeastern coast. Monthly means were based on several, usually equally spaced, measurements per month obtained through the Icelandic National Weather Office. Data used extended from 1947 to 1985. From 1952 to 1985, monthly data were continuous (408 monthly values), except for May 1965. This value was estimated from the mean of 10 monthly means from surrounding years, five before and five after. Three different combinations of temperatures were analyzed against ratios (Scarnecchia et al., 1989). The first temperature variable (T1) was the sum of monthly mean temperatures from May to December (Year x-1), corresponding to the time when smolts would enter the sea and begin rapid growth until their first winter at sea. The second variable (T2) was the sum of monthly mean temperatures from May (Year x) to April (Year x+1), corresponding to the time between when grilse would be returning to rivers and 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 prior to and during the time smolts would be entering the sea. It is hypothesized that higher than average temperatures during this period are associated with high primary and secondary production, and hence more food, during the smolts' first month or two at sea (Scarnecchia, 1984a). Peterman (1985) concluded that this period may be critical in influencing sea age at maturity of Bristol Bay sockeye salmon, and Scarnecchia (1984a) and others have also concluded that the time soon after the smolts enter the sea is important in determining year-class strength.

Statistical analyses

Pearson correlation coefficients were calculated for comparing grilse catches as well as ratios among rivers. Linear, multiple and stepwise regressions were used to identify if and how sea temperatures or salmon catches in the Faroese, Norwegian Sea and West Greenland fisheries related to ratios in the rivers. A P < 0.20 value was the criterion for entry into the model. Because both sea temperatures and salmon catch time series tend to be autocorrelated, residuals of linear relationships between variables entering selected stepwise models were analysed 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 selected stepwise models.

TABLE 3

Correlations among grilse catches for 22 Icelandic north coast rivers

		A	В	С	D _	E	F	G	Н	I	J
Hrútafjardará	Α	_								•	
Midfjardará (H)	В	0.70**	_								
Vídidalsá	C	0.79**	0.87**								
Vatnsdalsá	D	0.78**	0.83**	0.84**	_						
Laxá á Ásum	E	0.57**	0.65**	0.68**	0.67**	_					
Blanda-Svartá	F	0.84**	0.68**	0.83**	0.81**	0.74*	-				
Laxá-Ytri	G	0.37**	0.37	0.52*	0.40	0.35	0.30	_			
Saemundará	Н	0.48	0.59*	0.46	0.45	0.59*	0.38	0.06			
Húseyjarkvísl	Ĭ	0.38	0.52*	0.32	0.43	0.62*	0.42	0.34	0.69**	_	
Fljótaá	J	0.44	0.60*	0.66**	0.56*	0.65**	0.52*	0.06	0.89**	0.67**	_
Fnjóská	K	0.83**	0.64**	0.80**	0.77**	0.65**	0.82**	0.40	0.26	0.35	0.59*
Laxá í Adaldal	L	0.56**	0.59**	0.66**	0.76**	0.71**	0.67**	0.26	0.73**	0.73**	0.80*
Ormarsá	M	0.43	0.66*	0.14	0.50	0.50	0.35	0.13	0.88**	0.94**	0.69*
Deildará	N	0.68*	0.59*	0.29	0.58*	0.58*	0.56*	-0.08	0.71**	0.64*	0.59*
Svalbardsá	О	0.42	0.51*	0.15	0.37	0.48	0.41	-0.10	0.77**	0.72**	0.65**
Sandá	P	0.53*	0.69**	0.46*	0.62**	0.58**	0.63**	0.19	0.75**	0.72**	0.67**
Hölkná	Q	0.32	0.47	0.09	0.34	0.47	0.38	0.02	0.75**	0.81**	0.66**
Hafralónsá	Ŕ	0.42	0.56*	0.22	0.39	0.52	0.34	-0.03	0.87**	0.73**	0.79**
Midfjardará (B)	S	0.47	0.69**	0.33	0.49	0.39	0.34	-0.03	0.87**	0.73**	0.79**
Selá	T	0.48*	0.48*	0.32	0.62**	0.44*	0.45	0.18	0.77**	0.69**	0.70**
Vesturdalsá	U	0.37	0.59**	0.35	0.41	0.53	0.40	0.46*	0.72**	0.78**	0.65**
Hofsá	V	0.18	0.35	0.09	0.29	0.41	0.34	-0.00	0.74**	0.70**	0.57*

^{*}P<0.05; **P<0.01.

TABLE 4

Correlations among ratios for 22 Icelandic north coast rivers

		A	В	С	D	E	F	G	H
Hrútafjardará	Α	-							
Midfjardará (H)	В	0.35	_						
Vídidalsá	C	0.66**	0.79**	_					
Vatnsdalsá	D	0.61**	0.52**	0.55**					
Laxá á Ásum	E	0.41	0.88**	0.80**	0.43*	-			
Blanda-Svartá	F	0.69**	0.86**	0.92**	0.72**	0.73**	-		
Laxá-Ytri	G	0.18	0.28	0.29	0.19	0.55*	0.29		
Saemundará	H	0.85**	0.75**	0.92**	0.69**	0.80**	0.78**	0.14	_
Húseyjarkvísl	I	-0.02	0.09	0.07	0.05	0.09	-0.03	-0.28	0.24
Fljótaá	J	0.81**	0.51*	0.72**	0.64**	0.47	0.74**	0.20	0.61*
Fnjóská	K	0.23	0.02	-0.01	0.11	0.06	0.24	0.37	0.01
Laxá í Adaldal	L	0.42	0.55**	0.77**	0.71**	0.63**	0.83**	0.01	0.78**
Ormarsá	M	0.38	-0.00	-0.02	0.28	-0.04	-0.12	0.56	0.18
Deildará	N	0.77*	0.77**	0.75**	0.76**	0.75**	0.77**	0.51	0.91**
Svalbardsá	О	0.84**	0.54*	0.71**	0.82**	0.62*	0.67*	0.70*	0.65*
Sandá	P	0.03	-0.48	-0.06	0.01	-0.10	-0.20	0.19	-0.21
Hölkná	Q	0.21	0.12	0.24	0.37	0.17	0.21	0.15	0.02
Hafralónsá	Ŕ	-0.14	0.35	0.03	0.01	-0.07	0.35	-0.39	-0.12
Midfjardará (B)	S	0.60	0.19	-0.09	0.11	-0.15	0.11	0.37	0.76
Selá	T	0.37	-0.12	-0.07	0.12	-0.02	0.24	0.18	0.12
Vesturdalsá	U	0.14	0.18	0.28	0.43	0.53*	0.24	0.44*	0.25
Hofsá	V	-0.17	0.07	-0.15	-0.12	-0.07	0.08	-0.13	-0.06

^{*}P<0.05; **P<0.01.

K	L	M	N	0	P	Q	R	S	T	U	v
				_		•					

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0.67**
         0.77**
0.29
         0.75**
                  0.89**
0.50
                            0.87**
                   0.90**
0.32
         0.60*
                   0.88**
                            0.85**
                                      0.92**
0.59
         0.79**
                                      0.96**
                                               0.92**
0.30
         0.66**
                   0.95**
                            0.87**
                                      0.88**
                                               0.82**
                                                         0.89**
0.31
         0.76**
                   0.89**
                            0.86**
                                                         0.88**
                                                                   0.91**
                                      0.88**
                                               0.90**
         0.74**
                   0.91**
                            0.81**
0.37
                                                         0.82**
                                                                   0.89**
                                                                             0.93**
                                      0.83**
         0.83**
                   0.94**
                            0.80**
                                               0.88**
0.43
                                                                            0.82**
                                               0.85**
                                                         0.88**
                                                                   0.88**
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         0.60**
                   0.89**
                            0.59*
                                      0.81**
0.32
                                                                            0.84**
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                                               0.94**
                                                         0.94**
                                                                                      0.78**
                                                                                                0.72**
                                      0.96**
0.19
         0.58**
                   0.89**
                            0.81**
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I	J	K	L	M	N	0	P	Q	R	S	T	U	V

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-0.20
        0.22
-0.23
        0.74** -0.02
 0.20
               -0.01
                        0.10
 0.21
        0.16
 0.29
        0.56*
                 0.04
                        0.83** 0.38 -
        0.69**
                        0.66** 0.67* 0.75** -
 0.02
                 0.20
                               0.63 0.56
                                             0.72**
        0.03
                 0.27 - 0.03
 0.47
                                0.43 0.17
                                             0.55
                                                      0.55 -
                 0.07
                        0.29
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        0.13
                                             0.29
                                                      0.48 0.74*
                               0.21 0.22
                 0.14
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 0.48 - 0.38
                               0.29 0.19
                                             0.12
                                                    -0.02 0.17
                                                                   0.61
                 0.21 - 0.10
 0.15 - 0.19
                                                      0.61* 0.89** 0.80**
                                                                            0.23 -
                                0.36 0.13
                                             0.57*
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 0.07
        0.13
                 0.34
                                             0.69*
                                                      0.21 0.40
                                                                   0.19
                                                                          -0.22 0.43* -
                        0.16
                                0.33 0.39
-0.11 -0.08
                 0.08
                                                      0.56* 0.54
                                                                   0.84**
                                                                            0.38 0.80** 0.33 -
 0.22 - 0.15
                 0.18 - 0.19
                                0.10 0.01
                                             0.27
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RESULTS

Correlations among grilse catches and grilse to salmon ratios

Grilse catches were strongly correlated among the 22 rivers. Of the 231 Pearson correlation coefficients of grilse between pairs of rivers, 123 (53%) were positive and highly significant (P<0.01), 28 (12%) were positive and significant (P<0.05), and none were negatively significant at either P<0.05 or P<0.01 (Table 3). Correlations were particularly close among the northeastern rivers (from Saemundará eastward) as a group and among the northwestern rivers as a group (Hrútafjardará through Blanda), but somewhat less close between these groups.

Ratios were also correlated among themselves. Of the 231 correlations, 47 were positive and highly significant (P<0.01), and 19 were positive and significant (P<0.05). None were negatively significant at either P<0.05 or P<0.01 (Table 4). Correlations among grilse and among ratios were generally lowest for rivers such as Fnjóská and and Laxá-Ytri, whose catches were particularly low (often <100 fish year⁻¹). The significant correlations among ratios were particularly noteworthy inasmuch as all fishing, data collection and data analyses were conducted independently for each river.

Trend in grilse to salmon ratios over time

Four rivers – Hafralónsá, Midfjardará (Bakkaflóa), Selá and Hofsá – showed increasing ratios over time (P < 0.01 or P < 0.05; Fig. 2a-c; Table 5). All four of these rivers are in the northeast, and are among the closest rivers to the Faroese and Norwegian Sea fisheries. In contrast, two northwestern rivers, Midfjardará (Húnaflói) and Laxá á Ásum, showed significantly decreasing ratios with time (P < 0.05; Fig. 2d), which indicated that 2SW salmon became more abundant relative to grilse as time passed. The other 16 rivers showed no significant trends in ratios with time.

Influence of sea temperatures and catches of offshore fisheries on ratios

Stepwise analysis – ratios versus the three temperature variables (T1, T2, T3) and Faroese catch

The mean April-May temperature (variable T3) was significantly and positively related to ratios for eight of the 22 rivers – Hrútafjardará, Midfjardará, Vatnsdalsá, Laxá á Ásum, Saemundará, Fljótaá, Laxá í Adaldal and Svalbardsá (Table 6; Fig. 3a and b). One other river, Vídidalsá, had ratios significantly and positively related to May-December temperatures (variable T1; Fig. 3c). The Faroese catch was significantly related to ratios for two northeastern rivers, Hafralónsá and Hofsá. In addition, the Faroese catch entered

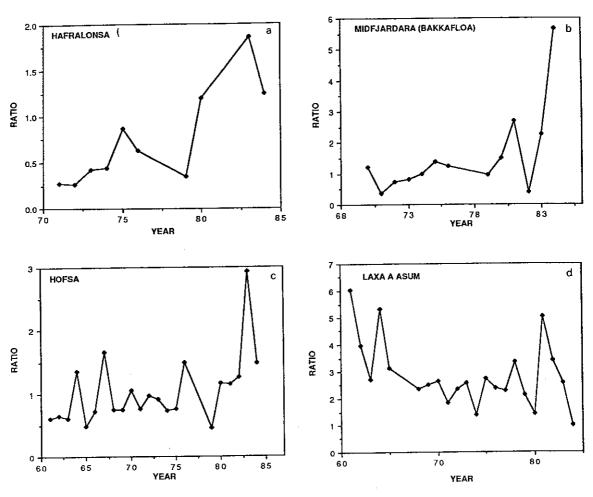


Fig. 2. Ratios of grilse (Year x) to 2SW salmon (Year x+1) for (a) Hafralónsá, ratio=-6.5943+0.0959 (year); (b) Midfjardará (Bakkaflóa), ratio=-12.0130+0.1765 (year); (c) Hofsá, ratio=-1.6968+0.0379 (year); (d) Laxá á Ásum, ratio=8.6063-0.0785 (year).

the stepwise model positively and May-April temperature (T2) entered negatively for Blanda/Svartá once mean April-May temperature had entered the model.

Only four of the rivers had no variables entering the stepwise models at P < 0.20 (Table 6). The Faroese catch entered models in nine of 22 rivers (eight positively, one negatively), including five of the nine most northeasterly rivers investigated. Ten of the 22 rivers had no variables enter the stepwise model at the P < 0.05 level. Thirteen of the 22 stepwise equations were significant (P < 0.05), but no equation with combinations of temperature and Faroese catch variables explained > 57% of the variation in ratios. This result indicated to us that the models were only moderately successful in explaining the observed variations in ratios. Residuals of all the stepwise models listed in Table 5 were analyzed to check regression assumptions and to determine if autocorrelation problems existed. Of the 18 rivers that had variables enter stepwise models, two (Húseyjarkvísl and Hofsá) had autocorrelation of re-

TABLE 5

Coefficients of determination for the relationship of ratios versus year, and for stepwise analyses of ratios (dependent variable) versus combined Faroese plus Norwegian Sea catches and three temperature variables (T1, T2, T3). Variables entered stepwise models at P < 0.20

River	Ratios vs. year	Variables entering stepwise model	Significance of equation (P<0.05)	Percentage of variation in ratios explained	Individual variables with significance of $P < 0.05$
Hrútafjardará	0.04(-)	T3(+),T2(-)	Yes	35	T3(+)
Midfjardará (H)	0.14*(-)	Catch(-)	Yes	18	Catch(-)
Vídidalsá	0.05(-)	TI(+)	Yes	48	T1(+)
Vatnsdalsá	0.01(-)	T3(+), T2(-)	Yes	52	T3(+)
Laxá á Ásum	$0.20^{+}(-)$	T3(+)	Yes	29	T3(+)
Blanda/Svartá	0.05(+)	T3(+),T2(-)	Yes	34	None
Laxá-Ytri	0.07(-)	T3(+),T1(-)	No	15	None
Saemundará	0.20(+)	T3(+)	Yes	33	T3(+)
Húseyjarkvísl	0.08(+)	Catch(+)	No	21	None
Fljótaá	0.01(+)	T3(+)	Yes	26	T3(+)
Fnjóská	0.17(+)	None	_	_	None
Laxá í Adaldal	0.00(+)	T3(+)	Yes	26	T3(+)
Ormarsá	0.18(-)	None	_	_	None
Deildará	0.04(+)	T3(+)	No	23	None
Svalbardsá	0.02(+)	T3(+)	Yes	35	T3(+)
Sandá	0.02(+)	None	_	_	None
Hölkná	0.12(+)	None	<u>-</u>	_	None
Hafralónsá	0.69**(+)	T1(-)	No	32	None
Midfjardará (B)	0.37*(+)	None	_	-	None
Selá	0.24*(+)	None	_	_	None
Vesturdalsá	0.00(-)	None	_	_	None
Hofsá	0.25*(+)	T3(-)	No	11	None

^{*}P<0.05; **P<0.01.

siduals (P<0.05). Four rivers had heteroscedastic residuals and three had residuals that seemed to deviate from normal. Inasmuch as these frequencies were only slightly greater than that expected by chance, no transformations were made on the data sets.

Stepwise analysis — ratios versus the three temperature variables and the combined Faroese and Norwegian Sea catch

Results for the combined Faroese–Norwegian Sea catch were similar to those for the Faroese catch considered alone. Mean April–May temperature entered the models significantly (P < 0.05) for seven rivers (Table 5). The combined Faroese–Norwegian Sea catch entered the models positively for only one river at the P < 0.20 level and for no rivers at the P < 0.05 level. Overall, the combined Faroese–Norwegian Sea catch was less effective in explaining variations in the ratios than was the Faroese catch alone. Ten of the 22 rivers had significant stepwise equations, but these equations explained no more than 52%, and usually much less, of the variation in ratios.

TABLE 6

Coefficients of determination for the relationship of Faroese-catch versus year, and for stepwise analyses of ratios (dependent variable) versus Faroese catch and three sea temperature variables (T1, T2, T3). Variables entered stepwise models at P < 0.20

River	Ratio vs. Faroe catch	Variables entering stepwise model (in order entered)	Significance of equation (P<0.05)	Percentage of variation in ratios explained	Individual variables with significance of $P < 0.05$
Hrútafjardará	0.00(-)	T3(+),T2(-)	Yes	35	T3(+)
Midfjardará	0.00(-)	T3(+)	Yes	16	T3(+)
Vídidalsá	0.00(-)	T1(+)	Yes	48	T1(+)
Vatnsdalsá	0.00(-)	T3(+),T2(-)	Yes	52	T3(+)
Laxá á Ásum	0.02(-)	T3(+)	Yes	29	T3(+)
Blanda/Svartá	0.12(+)	T3(+),Catch(+),T2(-)	Yes	57	Catch(+),T2(-)
Laxá-Ytri	0.06(-)	T3(+),T1(-)	No	15	None
Saemundará	0.07(+)	T3(+),Catch $(+)$	Yes	48	T3(+)
Húseyjarkvísl	0.21(+)	Catch(+)	No	21	None
Fljótaá	0.21(+)	T3(+)	Yes	26	T3(+)
-	0.02(-)	None	_	_	None
Fnjóská Laxá í Adaldal	0.03(+)	T3(+)	Yes	26	T3(+)
Ormarsá	0.00(+)	Catch(-)	No	23	None
Ormarsa Deildará	0.23(+)	T3(+),Catch(+)	Yes	37	None
Svalbardsá	0.00(-)	T3(+)	Yes	35	T3(+)
Sandá	0.00(-)	None	_	_	None
Hölkná	0.06(+)	None	_	_	None
Hafralónsá	0.46*(+)	Catch(+)	Yes	46	Catch(+)
	•	Catch $(+)$, $T2(+)$	No	34	Notic
Midfjardará (B)	0.18(+)	Catch(+)	No	13	None
Selá	$0.13(\pm)$ 0.00(-)	None	-	_	None
Vesturdalsá Hofsá	0.00(-)	Catch(+)	Yes	18	Catch(+)

^{*}P < 0.05.

Stepwise analysis — ratios versus three temperature variables, combined Faroese-Norwegian Sea catch and West Greenland catch

Mean April-May temperature again entered the models significantly (P<0.05) for seven rivers. The Greenland catch entered the models at P<0.05 for three rivers, all with signs opposite to the expected direction. The combined Faroese-Norwegian Sea catch entered only in two of the stepwise models at P<0.20 and none of the models at P<0.05.

Ratios before and during the Faroese-Norwegian Sea fisheries

Twelve rivers had sufficiently long time series that ratios could be calculated for periods before and during the Norwegian Sea and, later, Faroese fisheries. Eight of the rivers had lower mean ratios during the fisheries (i.e. 1967 onward) than before the fisheries, the opposite of what would be ex-

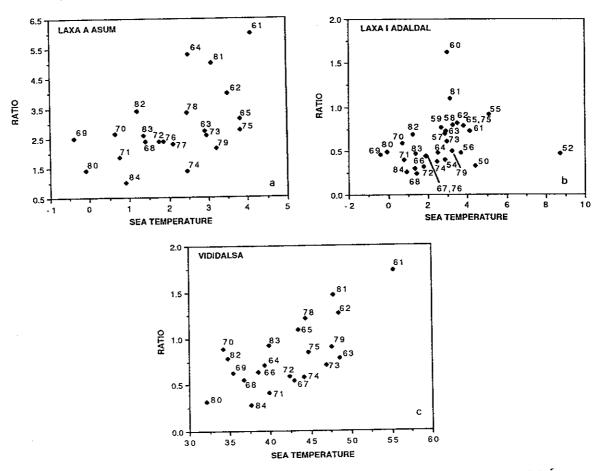


Fig. 3. Ratios versus mean sea temperatures (T1 and T3) in year (x-1) for (a) Laxá á Ásum, ratio=1.7594+0.5302 (T3); (b) Laxá í Adaldal, ratio=0.3434+0.1127 (T3); (c) Vídidalsá, ratio=-1.0140+0.0434 (T1).

pected if these fisheries were harvesting large numbers of MSW salmon. The mean ratios for Midfjardará (Húnafloí) and Laxá á Ásum showed highly significant decreases (P < 0.01) during the fishery; the mean ratio for Vídidalsa was significantly lower (P < 0.05) during the fishery than before the fishery (Table 7). Only for Sandá, a northeastern river, did the ratio increase significantly after fishing began (P < 0.05).

All 22 rivers had sufficiently long time series that mean ratios could be calculated for periods before 1979 and during the expanded Faroese fishery (1979–84). Of those 22 rivers, only four showed significantly different ratios before the fishery than after the Faroese fishery had expanded (P < 0.05). Only three of these rivers showed increasing ratios (as would be expected from Faroese harvest of MSW salmon), and those three rivers (Hafralónsá, Selá, and Hofsá) were in the northeast and were three of the four rivers that showed significantly increasing ratios with time (Table 5). A fourth northeastern river, Midfjardará (Bakkaflóa), showed higher ratios during the Faroese fishery at P < 0.10.

TABLE 7

Comparison of ratios of grilse (Year x) to 2SW salmon (Year x+1) before and after expansion of Faroese fishery for 22 Icelandic north coast rivers. Numbers of years of data are indicated in parentheses

River	Ratios		Comparison of means Prob < T
	Before expansion	After expansion	
Hrútafjardará	1.10 (17)	1.03 (3)	NS
Midfjardará	1.09 (23)	1.07 (6)	NS
Vídidalsá	0.82 (16)	0.78 (6)	NS
Vatnsdalsá	0.89 (18)	0.83 (6)	NS
Laxá á Ásum	2.98 (16)	2.60 (6)	NS
Blanda/Svartá	0.51 (14)	0.84 (5)	NS
Laxá-Ytri	1.57 (23)	1.13 (4)	NS
Saemundará	0.74 (10)	1.08 (4)	NS
Húseyjarkvísl	0.83 (9)	1.11 (6)	NS
Fljótaá	0.94 (11)	0.84 (6)	NS
Fnjóská	0.58 (10)	0.70 (6)	NS
Laxá í Adaldal	0.56 (28)	0.58 (6)	NS
Ormarsá	1.66 (3)	1.10 (6)	**
Deildará	0.98 (7)	1.35 (6)	NS
Svalbardsá	0.74 (8)	0.68 (6)	NS
Sandá	0.71 (13)	0.66 (4)	NS
Hölkná	0.89 (6)	1.19 (6)	NS
Hafralónsá	0.49 (6)	1.16 (4)	< 0.05
Midfjardará (B)	0.97 (7)	2.25 (6)	< 0.10
Selá	1.04 (18)	1.48 (6)	< 0.05
Vesturdalsá	1.10 (19)	1.01 (6)	NS
Hofsá	0.89 (16)	1.41 (6)	<0.05

^{**}Significant opposite of hypothesized direction (P < 0.05).

DISCUSSION

In a related paper, Scarnecchia et al. (1989) categorized the effects of selective removal of MSW Atlantic salmon by fisheries into three cases, based on progressively higher harvest rates of MSW fish. In Case 1, there is a shift toward younger fish that results from direct, selective annual removal of MSW fish. This shift may be short term and need not substantially change the genetic composition of the next generation if sufficient MSW salmon spawn and if these spawners leave offspring more effectively than grilse. In Case 2, greater depletion of MSW salmon results in long-term intergenerational genetic change in a stock toward younger age at maturity (i.e. higher frequencies of grilse spawning and leaving offspring). In Case 3, in addition to the genetic changes, excessive harvest of MSW salmon results in a shortage of spawners, underutilization of stream habitat by their progeny, rapid growth of parr and earlier maturation, either precociously in the stream (for some males) or as grilse instead of MSW salmon. Case 3 is a life history response to high harvest rates

that has been identified by Gibson (1978) and Montgomery (1983) in the Matamek River, Quebec.

The northwestern and north-central Icelandic rivers show no trends towards declines in the number of MSW salmon characteristic of any of the three cases. We interpret the stability or increases in frequency of MSW salmon in these stocks during periods of offshore fishing to indicate that these stocks are not suffering significant numerical (Case 1) or genetic (Case 2) depletion from fisheries. In addition, the conservative in-river fisheries (with harvest rates usually 25–50%; Gudjónsson, 1988) have not had a negative impact on age structure through shortages of spawners (Case 3), as Gibson (1978) and Montgomery (1983) found in the Matamek River. This result differs markedly from reported decreases in MSW salmon in non-Icelandic stocks (Paloheimo and Elson, 1974; Bielak and Power, 1986) associated with fishing off West Greenland, the Faroe Islands and nearshore commercial fisheries.

However, four rivers in the northeast (Hafralónsá, Midfjardará (Bakkaflóa), Selá and Hofsá) showed increasing ratios over time, as well as significantly higher ratios after the expansion of the Faroese fishery in 1979 (P < 0.05 and P < 0.10). These rivers are some of the closest geographically to the Faroese and Norwegian Sea fisheries, and logically would be the rivers most likely to be affected by harvest of MSW salmon off the Faroe Islands. These declines in ratios in the four northeastern rivers are not accounted for by variations in sea temperatures. All four of these rivers had Faroese catch enter stepwise analyses as the first variable (P < 0.20). For two of the rivers, the Faroese catch entered significantly (P < 0.05).

Recent recoveries of microtagged salmon from north coast stocks, along with evidence of declining ratios in the northeast, support the idea that the Faroese fishery may be harvesting significant numbers of Icelandic salmon from northeastern stocks. The situation on the north-central and northwestern coasts is more ambiguous. Despite recoveries of microtagged salmon from several north-central stocks in 1988, stable or decreasing ratios for these stocks indicate that total harvest must not be great. In addition, the absence of longline hooks on salmon caught in Icelandic rivers supports the view that Faroese fishing is not significantly depleting these stocks. Such hooks frequently occur in Norwegian salmon, which are known to be caught off of the Faroes (ICES, 1986b). Scarnecchia et al. (1989) noted that observed annual variations in ratios make it difficult or impossible to detect low harvest rates with this approach. The indirect approach used in this paper is no substitute for more detailed tagging studies over several years and the recovery of long-line hooks from salmon caught in the rivers. It should be established that the stocks contribute consistently to the fisheries.

The remarkably close correlations between grilse catches in these rivers indicate to us that a widespread environmental factor (or factors) is affecting the abundance of Icelandic salmon. Although close correlations exist among

ICELANDIC SALMON 225

the entire 22 rivers as a group, the correlations are particularly strong among northeastern rivers from Saemundará eastward and among those rivers flowing into Húnaflói, i.e. from Blanda/Svartá westward (Table 3). Similar close correlations among catches from rivers have been reported for western Icelandic rivers (Scarnecchia et al., 1989), as well as for Scottish stocks (Thorpe and Mitchell, 1981).

Analogously, there are more significant correlations among ratios in these rivers than would be expected by chance, which indicates that some large-scale environmental factor is affecting annual variations in ratios. This factor could be affecting age at maturity per se, or it could merely be inducing differential natural mortality or differential in-river catchability between grilse and MSW salmon consistently among a large number of rivers. Because many of these rivers have close relations between the number of grilse caught in one year and the number of 2SW salmon caught the next year (Kristjánsson, 1982; Scarnecchia, 1984b), the effects of any environmental factors on ratios are probably small compared with the effects on yields of grilse and 2SW salmon from a given smolt class. Our results agree 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.

The relations between mean April–May sea temperatures and ratios for eight rivers support the idea that age at maturity for an individual fish may be altered early in its life at sea according to environmental conditions. Although these eight results seem to occur with much greater frequency than would appear by chance, observed correlations between ratios make these results not independent of each other. Nevertheless, similar significant correlations between ratios from western Icelandic rivers (Scarnecchia et al., 1989) also support the idea that ocean conditions during the first year at sea influence grilse to salmon ratios.

An explanation for this conclusion is that warmer sea conditions are associated with better conditions for feeding, growth and survival of smolts. There is evidence that warmer temperatures in spring and early summer off northern Iceland are associated with greater primary and secondary production, and more adult fish resulting from a given smolt class (Scarnecchia, 1984a). If these smolts survived better in part because they grew faster, more of them might make a physiological decision (Thorpe, 1986) to mature as grilse rather than MSW salmon. In cooler years associated with less Atlantic water on Iceland's north coast (Stefánsson, 1969), a lower abundance of food and suboptimum temperatures would be less conducive to rapid growth, relatively fewer smolts would mature as grilse and relatively more MSW salmon would result. These effects would be small relative to the observed wide natural fluctuations in both grilse and MSW salmon (Scarnecchia, 1984a).

We have argued (Scarnecchia et al., 1989) that evidence of this process can be clearly in the results of pen-rearing experiments with Atlantic salmon

(summarized by Dempson et al., 1986). Numerous studies (e.g. Simpson and Thorpe, 1976; Naevdal, 1983; Gjerde, 1984) have indicated that marine growth was more rapid in earlier maturing salmon than in later maturing salmon. We also argued (Scarnecchia et al., 1989) that results from wild fish do not contradict results from pen-rearing experiments.

Peterman (1985) concluded that early rather than late ocean life was the major source of the variation in ratios among Bristol Bay stocks of sockeye salmon. Our results support his conclusion. Ratios for none of the 22 northern Icelandic rivers showed any relationship to sea temperatures between the grilse and 2SW salmon stages (Table 5).

Declines in abundance of northern Icelandic stocks in the early 1980s were usually assumed by laymen and the popular press to be solely a result of Faroese fishing. By the mid-1980s, evidence had accumulated that the highly variable climatic and oceanic conditions during the smolts' first year at sea (Year x) may strongly influence the size of the grilse run the following year (Year x+1) and the 2SW salmon run in Year x+2 (Scarnecchia, 1984a). Evidently, the declines in the runs of major salmon rivers, such as Laxá í Adaldal and Vídidalsa, in the early 1980s were mainly a result of climatic and oceanic conditions, with some harvest by the Faroese fishery.

Although more detailed tagging studies are badly needed to more accurately identify the effects of the Faroese fishery on the north coast stocks, financial costs associated with marking and recovering large numbers of wild smolts from small stocks may severely limit investigations. Continued releases of large groups of hatchery reared, microtagged smolts may provide the best information on harvest. If the mixed-stock oceanic fishery persists, the next-best solution might be to continue monitoring age structure and abundance of the stocks for signs of overharvest. We support the idea of using a stable age structure (relative to the historical age structure) as one of several phenotypic indicators of sufficient numbers of spawners, of sufficient genetic diversity, and thus, of a "safe biological limit" for harvest in salmon fisheries (ICES, 1986a; Scarnecchia et al., 1989).

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