Spatial and Temporal Variation in the Grilse Proportion of Atlantic Salmon in Norwegian Rivers

3 authors:

J. H. L'Abée-Lund
Norwegian Water Resources and Energy Directorate
83 PUBLICATIONS **1,958** CITATIONS

SEE PROFILE

Leif Asbjørn Vøllestad
University of Oslo
295 PUBLICATIONS **7,397** CITATIONS

SEE PROFILE

Stein Beldring
Norwegian Water Resources and Energy Directorate
29 PUBLICATIONS **715** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Understanding brown trout population structure: a Northern-European perspective. View project

fish evolution View project

Spatial and Temporal Variation in the Grilse Proportion of Atlantic Salmon in Norwegian Rivers

J. H. L'Abée-Lund*

*Norwegian Water Resources and Energy Directorate,
Post Office Box 5091, Majorsteun, N-0316 Oslo, Norway*

L. A. Vøllestad

*University of Oslo, Department of Biology,
Post Office Box 1050, Blindern, N-0316 Oslo, Norway*

S. Beldring

*Norwegian Water Resources and Energy Directorate,
Post Office Box 5091, Majorsteun, N-0301 Oslo, Norway*

Abstract.—Variation in the sea age at maturity of Atlantic salmon *Salmo salar* was studied in 158 Norwegian rivers over large spatial (58–71°N; 5–30°E) and temporal (1983–2000) scales. Age at sexual maturity was expressed as the proportion of grilse (fish with one sea winter) in the nominal salmon catch. No general temporal trend was found in the proportion of grilse in the catches. However, grilse proportion declined significantly in 10 rivers and increased significantly in 11 rivers out of the 55 rivers with data for all 18 years. There were no short-term cycles in grilse proportion within rivers. We found coherence and similarity in the temporal variation in grilse proportion for rivers draining into large fjord systems. Reasons for the temporal variation in grilse proportions must be sought at a river-specific or regional scale. River-specific factors (water discharge, river steepness, and presence of lakes) explained a large percentage of the spatial variation in grilse proportion. Grilse proportion increased with decreasing river size (measured as mean annual water discharge) and with increasing proportion of water discharge occurring during summer (i.e., the migration season). Grilse proportion was higher in rivers located nearer to the open ocean, probably indicating an effect of early feeding on growth and maturation. Even after accounting for environmental variation at the local scale, we found large regional differences in grilse proportion. Region captured this variation more efficiently than latitude, but grilse proportion was higher in the northern part of Norway than in the more southerly part. This variability may indicate large-scale differences in, for example, oceanic migration routes for fish originating from different regions.

Age at maturation is a pivotal trait in organisms, as fitness is more sensitive to changes in this trait than to changes in many other life history traits (Stearns 1992). This seems to be especially important for species with indeterminate growth (e.g., fish), as the fecundity of females and the fighting ability of males in many species is size dependent (for a review, see Roff [1992]). Early maturation increases the probability of surviving to maturity and reduces the generation time, but early maturing individuals reach only a small size and thus produce few or small offspring. Hence, the optimal trade-off solution will likely depend on age-specific growth and mortality rates (Stearns 1992).

Age at maturation in salmonid fishes has re-

ceived considerable attention for decades due to the wide variability both among and within populations. Differential survival and reproductive success due to environmental constraints largely shape this variability. Theoretical modeling and experimental and observational studies demonstrate that age at maturation is coupled with intrinsic (growth, age, and size at smolting; endocrine regulators) and extrinsic (breeding habitat, temperature, and interspecific competition) biological and physical factors (Alm 1959; Schaffer and Elson 1975; Stearns and Koella 1986; Quinn et al. 2001). Intrinsic factors are under some degree of genetic control, but will often vary as a function of environmental influences (plastic responses). The extrinsic factors will influence the individuals on different time scales, either through natural selection (evolutionary time scales and population scales) or through phenotypic plasticity leading to variability within short time spans (in-

* Corresponding author: lbl@nve.no

dividual scales). In general, environmental factors leading to rapid growth also tend to lead to an early age at maturity in salmonids (Alm 1959). However, the tendency for the fastest-growing individuals within a population to mature at an earlier age than slow-growing individuals is not unique to salmonid fishes. Day and Rowe (2002) theoretically showed an overall common negative reaction norm between the age at which various life history transitions occur and the growth conditions under which individuals develop.

Salmonids have complex life histories and great variation in age at maturity (Groot and Margolis 1991; Shearer 1992; Elliott 1994). Within species, the variation is due to local adaptation and phenotypic plasticity. Considerable evidence suggests adaptation to local environments in salmonids, although local adaptation is seldom directly documented (Taylor 1991). Local adaptation in sea age at maturity in Atlantic salmon *Salmo salar* may be coupled to predictable cues and various environmental traits in freshwater and marine habitats, such as water discharge and migratory arduousness (Schaffer and Elson 1975; Scarnecchia 1983). If marine conditions influence age at maturity, we would expect (1) covariation in temperature and maturation, as temperature, growth rate, and maturation are strongly correlated, and (2) synchronous variation in salmon populations utilizing the same oceanic habitats. The first statement is generally accepted (Saunders et al. 1983; Scarnecchia 1983; Friedland 1998). The second statement is more difficult to document, as the precise oceanic distribution of different salmon populations is not known. Our knowledge is restricted with regard to how various species of both Atlantic salmon and Pacific salmon *Oncorhynchus* spp. utilize different ocean regions. However, among-river covariation in sea age at maturity has been demonstrated for both these taxa, indicating that fish from rivers located in the same geographic area use the same areas in the ocean (Scarnecchia et al. 1991; Beamish and Bouillon 1983; Friedland et al. 1993; Friedland 1998; Pyper and Peterman 1999).

Atlantic salmon spawn in Norwegian rivers in October–January (Heggberget 1988). Parr stay for 1–6 years in the rivers before they transform into smolts and migrate to sea (Dahl 1916). They attain sexual maturity after 1–4 years at sea (Jensen et al. 1999) and return to freshwater in May–October (Jonsson et al. 1990; Hansen and Jonsson 1991) to spawn. Those fish that survive spawning migrate back to the ocean, feed, and subsequently return to the river to spawn again. However, most Atlantic

salmon spawn only once (Fleming 1996). Age at maturity varies widely among river populations, but what selective forces mold this variation?

There has been concern in recent years about a decline in the mean age of Atlantic salmon in British rivers (Shearer 1992; Crisp 2000). However, it is unclear whether the decline is due to a reduction in sea age at maturity or due to a change in population structure within rivers. Some rivers have several distinct groups of salmon, possibly originating from different subcatchments, with particular dynamics (see Youngson et al. [2002]). Most unusual are the salmon entering rivers in October of one year, but spawning the following October. A decline in age can be explained in several ways, either as a result of earlier maturation for all groups or as a result of a decline in subgroups (populations) of Atlantic salmon that normally mature at a later age. Salmon cannot enter many of the Norwegian rivers during winter due to ice and low discharge. Those entering a river during spring, summer, and autumn spawn in the autumn of the same year. Although salmon that spend multiple winters in the sea tend to ascend the rivers earlier in the season than do grilse (salmon maturing after 1 year in the sea), they are subjected to the same fishing pressure (Fiske and Aas 2001).

Here we document the spatial and temporal patterns in the grilse proportion of Atlantic salmon populations based on Norwegian official statistics of nominal catches from 158 Norwegian rivers covering a very large latitudinal range (58–71°N). Most rivers are relatively small and are characterized by low gradients. The data cover a time span of 18 years, for which information about size (and thus age) distribution of the catch is available. In Norway, all river catch is restricted to the summer season (usually June–August). In this paper, three questions are addressed. First, are there temporal patterns in the ratio of grilse to multiple-sea-winter (MSW) Atlantic salmon across Norway? Second, if such temporal variation exists, is it spatially synchronized? Third, what environmental variables at the global and local (river) scale are most important for determining age at maturity (sea age) in Atlantic salmon? These questions are of general interest, as knowledge of long-term trends in the life history of species subjected to climate change, human harvesting, and habitat perturbation is an essential prerequisite for their conservation and sustainable management.

Methods

Catch data.—The present study is based on the Norwegian official statistics of nominal catch

of adult Atlantic salmon from 158 Norwegian rivers situated over a wide geographical range ($58°28'−71°03'$N and $5°07'−30°32'$E; Table 1; Figure 1). This large spatial scale encompasses considerable variation in freshwater, coastal, and ocean conditions, and thus gives rise to a variety of different selection regimes. The considerable number of Atlantic salmon populations along the Skagerrak coastline that became extinct due to acidification (Hesthagen and Hansen 1991) was not included in this study.

In Norway, systematic collection of data on the different Atlantic salmon fisheries began in 1876 (Hansen 1986). For almost all rivers, the data contain recreational rod catches only. In three rivers (Numedalslågen, Tana, and Neiden), some commercial fishing with fixed nets and drifting nets is performed. The legal fishing season is restricted to summer and early autumn, but differs somewhat among rivers. Since 1876, local salmon management authorities have been required to collect and report total catches in each river. Starting in 1979, Atlantic salmon were differentiated into two weight categories (<3 kg and ≥3 kg). Starting in 1993, Atlantic salmon were categorized into three weight classes (<3 kg, 3–7 kg, and ≥7 kg). The smallest group (<3 kg) mainly corresponds to one-sea-winter (1-SW) fish (grilse), and the larger groups correspond to MSW fish (2-SW and 3-SW fish) (Martin and Mitchell 1985; Jensen et al. 1999). These age and weight categories are identical to those used by the International Council for the Exploration of the Sea (ICES) (Anonymous 2002). Some bias may be introduced by using this classification, but we believe this is of minor importance. In a regional Norwegian study, Dahl (1910) showed that small-sized Atlantic salmon (<3 kg) were chiefly 1-SW fish (96.3%, $n = 1,387$), and only a small fraction were 2-SW fish (3.7%, $n = 54$). Further, some 1-SW fish may exceed 3 kg. In a study of 17 Norwegian Atlantic salmon populations, the mean body length of 1-SW fish varied significantly among rivers (mean size = 55.4–69.0 cm) (Jonsson et al. 1991a); however, this cannot directly be transformed to weight classes. Unpublished data from four rivers (A. Jensen, Norwegian Institute for Nature Research, personal communication) showed that between 2.2% and 6.9% of 1-SW fish were larger than 3 kg (Strynselva 6.9%, $n = 246$; Saltdalselva 2.2%, $n = 603$; Orkla 4.4%, $n = 798$; Vefsna 3.0%, $n = 1,615$), whereas between 0.1% and 2.9% of 2-SW fish were smaller than 3 kg (Strynselva 0.1%, $n = 277$; Saltdalselva 0.2%, $n = 319$; Orkla

0.9%, $n = 573$; Vefsna 2.9%, $n = 970$). In the Alta during 1991–2000, 4.7% of 2,645 age-determined, 1-SW fish were between 3 and 4 kg (O. Ugedal, Norwegian Institute for Nature Research, personal communication). For the Gaula during 1987–1991, 6.6% of 1-SW fish were larger than 3 kg ($n = 534$), whereas 0.05% of 2-SW fish were smaller than 3 kg ($n = 388$) (J. H. L'Abée-Lund, unpublished data). In total, some bias may be introduced by classification of all fish smaller than 3 kg as grilse, but based on available data, the bias is probably of minor importance.

All analyses were based on the proportion of grilse in the reported annual catch (numbers of fish) within each river. The official catch statistics do not distinguish between males and females, so sexes were treated together in the analyses. We only used grilse proportion in our analysis, and assumed that the reported proportion was based on a random sample of the total catch. Hansen (1986) stated that it is generally accepted that the data describe the fluctuations in catches and the development of the fisheries. Furthermore, studies from Iceland and northern Ireland demonstrate that catch statistics reflect the size of the spawning run (Gudjonsson et al. 1995; Crozier and Kennedy 2001). These and other comparable data are also used by the ICES to describe the status and development of Atlantic salmon in Norway and other countries (Anonymous 2002). The ICES aggregated the catch from all rivers into one national index, whereas we treat the data on a river-by-river basis. If aggregated data were used, any biological signal would be dominated by the large rivers, such as the Tana (constituting 16–25% of the Norwegian river catch in 1987–1992).

The study rivers varied considerably in size, as did the catches. In some rivers, catch was very low in some years, either because of small catches or because of problems with the reporting procedure. Rivers with reports from fewer than five seasons were not included in the analyses. A minimum required catch of 20 individuals per year was used; otherwise the report for that year and river was deleted from the database. After excluding all reports with less than 20 fish, 2,375 individual year × river observations remained (469, or 16.5%, year × river observations were missing or excluded). For the observations retained for analysis, the mean and median number of fish was 743 and 171, respectively (90th percentile = 1,785 fish; 10th percentile = 36 fish).

For some rivers, the data clearly indicated that the reporting of the various weight-groups was bi-

TABLE 1.—Characteristics of 158 Norwegian rivers where the grilse proportion (%) of Atlantic salmon populations was monitored, 1983–2000. Latitude (°N) and longitude (°E) give the geographical position of each river mouth. River length (km) and altitude (m above sea level) are maximum distance and maximum altitude of salmon ascent in each river. Coastal distance (km) is the distance from the river mouth to the coastal shelf. Summer discharge is the proportion of annual mean discharge (m^3/s) occurring in summer (May–August); N indicates number of years of observations; ND indicates no data.

River	Latitude	Longitude	River length	Altitude	Lake	Costal distance	Mean annual discharge	Summer discharge	Grilse	N
Skagerrak region										
Enningdalselva	58°59′	11°28′	24	45	Yes	50	2.6	0.18	33.73	18
Glomma	59°12′	10°57′	49	30	Yes	36	660.6	0.64	34.01	17
Sandvikselva	59°53′	10°31′	13	90	No	104	4.26	0.34	75.47	18
Åroselva	59°42′	10°31′	11	60	No	86	2	0.30	67.01	13
Lierelva	59°45′	10°17′	35	60	No	92	5.29	0.42	73.83	17
Drammenselva	59°44′	10°14′	39	40	No	106	308	0.65	48.59	18
Numedalslågen	59°02′	10°03′	69	60	Yes	20	111.78	0.61	47.68	17
Ogna	58°31′	5°48′	20	170	Yes	4	6.85	0.18	84.98	18
Fuglestadelva	58°33′	5°44′	16	70	Yes	1	2.29	0.17	89.64	17
Bjerkreimselva	58°28′	6°00′	15	63	Yes	12	53.58	0.25	83.22	18
Kvassheimelva	58°32′	5°48′	7.5	75	No	5	0.86	0.18	94.45	14
N. Varhaugelva	58°36′	5°47′	4	38	No	2	0.74	0.18	96.64	14
Håelva	58°41′	5°32′	32	150	Yes	2	7.96	0.17	84.57	18
Figgjo	58°48′	5°33′	29	130	Yes	5	10.32	0.16	78.43	18
Dirdalselva	58°50′	6°11′	9.5	170	No	60	12.82	0.31	84.97	16
Frafjordelva	58°51′	6°17′	7	100	Yes	66	16.28	0.34	78.42	13
Jørpelandselva	59°01′	6°03′	2	95	No	44	6	0.22	75.7	14
Årdalselva	59°09′	6°11′	13	130	Yes	56	45.78	0.42	58.34	18
Hjelmelandselva	59°14′	6°11′	2.5	15	Yes	58	2.67	0.20	47.48	12
Vorma	59°16′	6°20′	4	250	No	66	7.84	0.34	67.74	17
Hålandselva	59°21′	6°15′	3.5	115	No	138	4.51	0.34	53.94	16
Ulla	59°19′	6°27′	6.5	150	No	78	33.62	0.49	59.65	12
Suldalslågen	59°29′	6°15′	25	70	Yes	76	104.82	0.53	46.85	18
Rødneelva	59°33′	5°52′	3.5	50	No	72	4.95	0.31	79.91	11
Åmselva	59°28′	5°44′	4.5	15	Yes	72	2.53	0.19	73.4	9
Vikedalselva	59°30′	5°54′	11.5	80	No	68	10.68	0.40	80.14	15
Western Norway region										
Etneelva	59°40′	5°56′	9	71	Yes	64	23.11	0.44	63.96	18
Omvikelva	59°57′	5°59′	6.5	95	No	60	3.01	0.41	79.1	8
Rosendalselva	59°59′	6°01′	6.5	374	Yes	66	6.85	0.49	69.44	16
Æneselva	60°05′	6°07′	6.5	135	No	82	3.26	0.47	68.95	10
Jondalselva	60°07′	6°15′	1	40	No	108	9.14	0.48	87.15	6
Opo	60°04′	6°33′	1.5	70	No	172	35.69	0.55	35.84	16
Eio	60°27′	7°05′	77	160	Yes	174	45.99	0.69	34.37	14
Granvinselva	60°32′	6°43′	13	100	Yes	138	8.66	0.44	43.36	13
Øysteseelva	60°24′	6°12′	0.9	20	No	126	5.37	0.48	34.38	5
Steinsdalselva	60°23′	6°08′	4.5	20	Yes	126	9.25	0.41	62.68	15
Oselva	60°11′	5°28′	15	100	Yes	54	9.7	0.18	77.93	18
Eikefetelva	60°43′	5°33′	3	100	No	50	8.96	0.25	90.29	18
Ortnevikselva	61°07′	6°08′	3	125	Yes	94	5.08	0.49	95.04	6
Vikja	61°05′	6°35′	1.8	40	No	122	5.78	0.57	62.85	17
Nærøydalselva	60°53′	6°51′	11.5	130	No	180	15.56	0.57	42.07	15
Flåmselva	60°52′	7°08′	5	40	No	188	15.93	0.66	37.3	8
Lærdalselva	61°06′	7°28′	24.7	245	No	174	36.07	0.69	28.69	14
Sogndalselva	61°14′	7°06′	6	160	No	160	9.48	0.61	54.67	16
Årøyelva	61°16′	7°10′	1	50	No	166	17.44	0.61	29.43	17
Daleelva	61°03′	6°05′	7	140	No	94	14.92	0.59	77.13	18
Dalselva	61°22′	5°24′	4	40	No	54	6.7	0.26	86.49	11
Flekkeelva	61°18′	5°21′	9	40	Yes	52	24.72	0.25	34.82	13
Gaula	61°22′	5°41′	13.5	110	No	68	44.84	0.50	67.57	18
Nausta	61°31′	5°44′	12	70	No	64	24.18	0.51	82.96	18
Osenelva	61°33′	5°25′	13	59	Yes	48	25.89	0.30	57.33	18
Åelva	61°44′	5°55′	10	150	Yes	82	12.93	0.56	60.83	18
Ryggelva	61°47′	6°08′	1.5	100	No	74	4.66	0.55	65.92	9
Gloppenelva	61°46′	6°12′	5	55	No	78	31.39	0.62	44.14	18
Oldenelva	61°50′	6°48′	2.7	20	No	118	6.81	0.63	33.69	16

Table 1.—Continued.

River	Latitude	Longitude	River length	Altitude	Lake	Costal distance	Mean annual discharge	Summer discharge	Grilse	N
Loelva	61°52′	6°52′	2.8	52	Yes	116	7.71	0.65	33.47	15
Strynselva	61°54′	6°43′	11	29	Yes	106	22.16	0.61	27.55	17
Eidselva	61°54′	5°59′	12	53	Yes	66	25.3	0.36	62.56	18
Ervikelva	62°10′	5°07′	10	60	Yes	4	1.97	0.19	83.98	18
Åheimselva	62°03′	5°37′	7	110	Yes	36	5.42	0.24	93.22	18
Oselva	62°05′	5°44′	5	95	No	40	3.14	0.30	84.98	18
Norddalselva	62°06′	5°45′	2.5	60	No	40	3.13	0.37	82.98	7
Austefjordelva	62°04′	6°19′	5.5	30	Yes	72	4.96	0.40	81.55	18
Kilselva	62°03′	6°02′	8.5	60	Yes	58	8.38	0.36	74.83	16
S. Vartdalselva	62°08′	6°15′	ND	ND	No	37	3.44	0.40	78.11	18
N. Vartdalselva	62°09′	6°19′	5	270	No	36	1.38	0.38	88.33	12
Barstadvikelva	62°16′	6°22′	5.5	230	No	38	2.37	0.42	85.97	15
Ørstaelva	62°11′	6°08′	12.5	170	Yes	48	11.24	0.37	84.28	16
Hareidselva	62°22′	6°04′	7	70	Yes	32	2	0.17	88.15	15
Bondalselva	62°12′	6°28′	18.5	255	No	62	7.01	0.43	80.71	17
Vikelva	62°06′	6°34′	9.5	145	Yes	76	2.9	0.43	70.25	15
Norangdalselva	62°02′	6°39′	11.5	120	No	72	3.45	0.50	77.72	12
Aureelva	62°24′	6°35′	7	100	Yes	46	2.66	0.31	96.46	12
Velledalselva	62°20′	6°36′	11	175	Yes	58	7.21	0.44	84.88	18
Strandaelva	62°18′	6°56′	11.5	240	No	86	11.94	0.50	76.03	18
Korsbrekkelva	62°05′	6°52′	3	100	No	124	8.07	0.56	74.53	17
Eidsdalselva	62°16′	7°10′	6	140	No	92	3.23	0.52	80.51	11
Stordalselva	62°27′	6°59′	10	140	No	72	10.48	0.52	73.59	18
Vagsvikelva	62°23′	6°53′	1	60	No	64	2.45	0.36	84.27	13
Valldalselva	62°18′	6°15′	17	230	No	92	15.08	0.62	54.2	12
Ørskogelva	62°28′	6°48′	3.5	60	No	66	2.87	0.31	90.99	15
Solnørelva	62°29′	6°43′	6	100	No	52	2.44	0.19	96.11	16
Tennfjordelva	62°32′	6°35′	3	46	Yes	40	2.28	0.15	95.25	12
Hildreelva	62°36′	6°21′	ND	ND	ND	20	0.71	0.19	88.27	12
Vågsbøelva	62°54′	7°26′	8	25	Yes	34	3.01	0.22	97.9	13
Usma	62°43′	8°25′	10	100	No	90	8.04	0.61	81.97	5
Driva	62°41′	8°33′	119	580	No	94	63.67	0.75	48.2	13
Søya	62°53′	8°32′	22	190	No	74	8.96	0.53	94.52	16
Todalselva	62°49′	8°42′	8.5	180	No	90	14.63	0.65	78.08	12
Surna	62°58′	8°40′	58	231	No	70	55.15	0.58	55.44	17
Central Norway region										
Orkla	63°18′	9°50′	88	260	No	126	65.57	0.63	47.63	18
Gaula	63°21′	10°14′	112	285	No	112	95.43	0.66	49.55	18
Homla	63°15′	10°48′	5	70	No	128	2.92	0.39	99.71	16
Nidelva	63°16′	10°22′	6	40	No	120	85.12	0.59	51.7	18
Stjørdalselva	63°26′	10°54′	55	120	No	138	74.52	0.50	62.7	18
Levangerelva	63°46′	11°18′	19	100	No	170	3.41	0.32	94.37	18
Verdalselva	63°48′	11°28′	58	140	No	180	51.26	0.44	67.22	18
Figga	64°01′	11°30′	26	70	Yes	190	8.89	0.26	78.96	9
Steinkjerelva	64°02′	11°30′	6	18	No	192	64.25	0.25	62.38	10
Skauga	63°36′	9°56′	40	100	No	86	14.21	0.25	97.53	18
Nordelva	63°46′	10°07′	12	115	No	58	13.64	0.29	95.11	16
Stordalselva	63°57′	10°13′	30	100	Yes	64	16.95	0.21	92.71	18
Steinsdalselva	64°18′	10°31′	3.5	20	No	36	11.5	0.20	96.03	17
Oksdøla	64°26′	11°12′	12	80	No	60	3.7	0.23	98.03	18
Aursunda	64°21′	11°22′	12	90	Yes	68	5.98	0.16	99.38	18
Bogna	64°23′	11°23′	20	100	No	68	19.29	0.24	96.29	18
Årgårdselva	64°18′	11°12′	9.5	60	No	78	24.54	0.20	97.45	18
Namsen	64°28′	11°35′	84	100	Yes	74	303.28	0.39	57.74	18
Salselva	64°42′	11°26′	1.2	9	No	46	25.15	0.30	90.99	18
Kongsmoelva	64°53′	12°27′	12	60	No	106	22.17	0.44	91.09	18
Åelva	65°05′	12°27′	16	60	No	90	42.2	0.51	88.71	14
Eideelva	65°15′	12°27′	18	70	Yes	78	7.2	0.36	90.64	12
Sauselva	65°23′	12°32′	21	105	Yes	86	7.2	0.29	86.54	13
Lomselva	65°27′	12°47′	7	120	No	80	18.99	0.56	65.96	8
Vefsna	65°50′	13°13′	28	35	No	110	180.75	0.59	56.11	17
Leirelva	66°05′	13°03′	12	120	Yes	74	5.02	0.53	70.49	12
Røssåga	66°08′	13°47′	16	50	No	106	100.62	0.58	48.36	13
Saltdalselva	67°06′	15°25′	42	125	No	158	43.87	0.66	48.36	10

TABLE 1.—Continued.

River	Latitude	Longitude	River length	Altitude	Lake	Costal distance	Mean annual discharge	Summer discharge	Grilse	N
				Northern Norway region						
Løksebotn	68°56′	17°43′	7	160	Yes	92	3.33	0.66	90.89	11
Salangselva	68°53′	17°52′	49	220	Yes	98	19.27	0.71	72.23	17
Skøelva	69°08′	18°03′	14	180	No	80	7.01	0.69	77.66	18
Lysbotnelva	69°25′	17°54′	16	90	Yes	42	9.23	0.57	84.36	18
Grasmyrelva	69°17′	17°54′	13	55	Yes	56	3.82	0.54	93.59	10
Laukhelleelva	69°14′	17°51′	29	130	Yes	68	11.12	0.55	82.07	18
Rossfjordelva	69°17′	18°13′	4.5	25	Yes	66	7.67	0.55	82.65	8
Lakselva	69°17′	18°43′	6	40	No	68	2.53	0.60	98.24	15
Målselva	69°14′	18°31′	108	150	No	70	158.44	0.74	62.61	18
Skogfjordelva	70°01′	19°04′	3	20	Yes	32	6.64	0.52	79.23	13
Breivikelva	69°40′	19°38′	34	70	No	88	10.4	0.67	86.94	17
Signaldalselva	69°16′	19°55′	27	90	No	141	14.56	0.76	71.78	13
Skibotnelva	69°23′	20°16′	20	140	No	140	17.61	0.78	55.58	9
Oksfjordelva	69°54′	21°19′	20	175	Yes	76	7.8	0.74	82.94	17
Reisa	69°46′	21°02′	100	200	No	94	81.17	0.78	61.04	18
Altaelva	69°58′	23°23′	46	100	No	114	90.77	0.75	55.62	18
Lakselva	70°07′	23°23′	7	90	No	106	4.03	0.72	92.67	9
Repparfjordelva	70°27′	24°20′	27	190	No	72	30.45	0.69	83.96	18
Russelva	70°37′	24°40′	7	40	No	64	9.47	0.59	87.04	13
Stabburselva	70°11′	24°54′	15	120	No	110	21.33	0.72	71.99	18
Lakselva	70°04′	24°55′	70	100	Yes	146	25.56	0.75	56.46	18
Børselva	70°18′	25°32′	63	220	No	120	18.32	0.73	76.83	18
Lille Porsangerelva	70°49′	26°18′	5	70	No	72	3.19	0.70	92.11	12
Veidneselva	70°39′	26°36′	30	200	No	62	5.16	0.76	90.73	14
Storelva	70°22′	26°28′	31	210	No	96	14.41	0.75	80.7	14
Sandfjordelva	71°03′	28°04′	21	180	No	6	1.79	0.63	92.43	15
Risfjordelva	70°58′	28°11′	4	31	Yes	12	2.25	0.69	78.87	14
Langfjordelva	70°37′	27°36′	35	280	No	64	7.99	0.75	88.57	16
Tanaelva	70°28′	28°20′	288	240	No	56	124.42	0.74	63.68	17
Kongsfjordelva	70°39′	29°15′	13	138	No	20	7.32	0.71	77.9	17
Vesterelva	70°32′	29°58′	50	225	No	22	15.49	0.75	81.12	18
Skallelva	70°12′	30°20′	19	135	Yes	28	5.51	0.74	74.39	18
Komagelva	70°14′	30°32′	39	200	No	22	8.28	0.74	79.54	18
Vestre Jakobselva	70°06′	29°20′	3.5	20	No	80	12.54	0.76	70.1	17
Vesterelva	70°09′	28°34′	11	20	No	95	2.44	0.73	74.77	16
Bergebyelva	70°09′	28°54′	1	25	No	94	4.2	0.75	80.86	11
Klokkerelva	69°52′	29°23′	5	15	No	72	1.22	0.70	95.52	15
Munkelva	69°39′	29°27′	14	70	No	74	1.37	0.69	92.46	17
Neidenelva	69°42′	29°24′	79	193	Yes	84	5.95	0.72	71.87	13
Karpelva	69°40′	30°23′	17	171	Yes	36	1.49	0.73	93.03	16

ased in the years 1979–1982. This can be exemplified by data from the Gaula, Namsen, and Alta rivers, where all salmon were recorded as grilse during these 4 years. In contrast, during the subsequent 18 years (1983–2000), the proportion of grilse varied annually between 27% and 85% for the Gaula, 42% and 71% for the Namsen, and 33% and 71% for the Alta. It is possible that the procedure of reporting the catch into weight-classes was not efficient in the earlier years. The change in reporting procedure probably was not effectively implemented in all rivers. The bias may not have been present in all rivers, but to reduce any effects of biased weight categorization, and to err on the conservative side, we based our statistical analyses on 1983–2000 data only.

The incidence of escaped farmed Atlantic salmon in the recreational angling catch has been monitored annually since 1989 in several Norwegian rivers. Although considerable variation existed among rivers during 1989–2000, the grand mean incidence of escaped salmon was low ($<10\%$), and no significant time trend was observed (Fiske et al. 2001). The effects of escaped farmed salmon in the analyses were probably random and negligible. However, by use of data on proportion of escaped farmed salmon in a number of rivers together with estimated proportion of farmed salmon maturing as grilse, we tested whether our conclusions would change if the incidence of farmed salmon in the fisheries was adjusted for. For 27 rivers, we had access to 1–12 years of data on
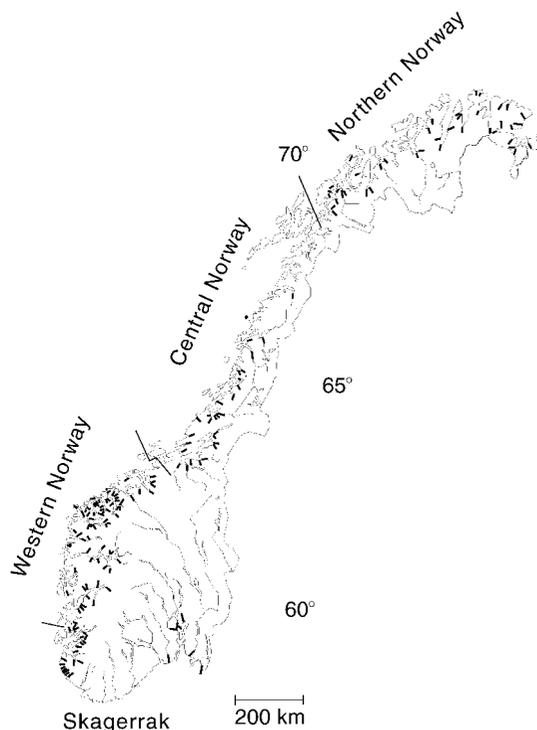
FIGURE 1.—Geographic locations of 158 Norwegian rivers where nominal catches of Atlantic salmon were recorded.

proportion of farmed salmon (Fiske et al. 2001). Mean incidence ($\pm$SD) of farmed salmon in rivers with more than 2 years of data varied between 0.3% $\pm$ 0.6% and 23.1% $\pm$ 10.1%. During 1997–2000, the proportion of grilse in the farmed fish caught during the fishing season was 39.8% (P. Fiske, Norwegian Institute of Nature Research, personal communication), and we used that number for all rivers and years. We examined the effect of adjusting for variation in the proportion of farmed salmon on the temporal variation in grilse proportion. However, since we only had estimates of farmed salmon incidence in a restricted number of rivers, we did not adjust the mean value for each river. Adjusting the mean values only for the rivers with data on incidence of farmed salmon would clearly introduce a bias of unknown magnitude to the analyses.

The proportion of Atlantic salmon returning as grilse was calculated in two ways based on available data. In the first method, the proportion of grilse was estimated as the fraction of returning fish from a smolt cohort that included the numeric grilse catch in year *x,* 2-SW fish (3–7 kg) in year *x* + 1, and 3-SW fish (>7 kg) in year *x* + 2. In

some rivers, the spawning run also included 4-SW fish, but their number is small compared to the other age-groups (Jensen et al. 1999). Thus, 4-SW fish had only minor importance in the calculations based on cohorts. We were only able to estimate a mean grilse proportion for the 1992–1998 smolt cohorts in 81 rivers. This period is too short to conduct formal testing for temporal variation in grilse occurrence. In the second calculation method, the mean grilse proportion was estimated directly from the annual catches of different-sized fish during 1983–2000. This method yielded data for 158 rivers. The correlation between the two different estimates of grilse proportion was highly significant ($r = 0.924$, $n = 81$, $P < 0.0001$). Thus, the statistical analyses regarding spatial variation were based on the total data set (158 rivers) of annual mean grilse proportion (hereafter referred to as the ''spatial data set'').

To test for temporal variation in grilse proportion within rivers, the 55 rivers containing complete data from all 18 years were selected (hereafter referred to as the ''temporal data set''). Both correlation analysis and formal time-series analysis were used to test for temporal trends within rivers. Correlation analysis was used to test for temporal covariation in the proportion of grilse among rivers. To remove possible artifacts due to different starting points (grilse proportions), all values were standardized ($x'_{ij} = [x_{ij} - \text{mean } x_j]/\text{SD}_j$; where x_{ij} is the observed grilse proportion in year *i* and river *j*).

Habitat Characteristics.—To test for large-scale environmental effects, two different approaches were used: either latitude was used as a covariate in the statistical models or region was set as a fixed effect. In the latter case, Norway was divided into four major geographic regions, namely Skagerrak (58°–59°35′N), Western Norway (59°40′–63°N), Central Norway (63°–68°N), and Northern Norway (68°–71°N). The first three regions are natural groupings based on geography and hydrology. For Northern Norway, recent studies indicate biological reasons for separating this region from Central Norway. Atlantic salmon from rivers in Northern Norway use areas close to the Barents Sea for feeding, whereas salmon from rivers in the other regions use the Norwegian Sea and adjacent areas (Jensen et al. 1999; Holm et al. 2000; Hansen and Jacobsen 2003).

A number of different habitat traits related to river size and migration arduousness were estimated for each river. River length (mainstem only) from the estuary to the uppermost accessible site
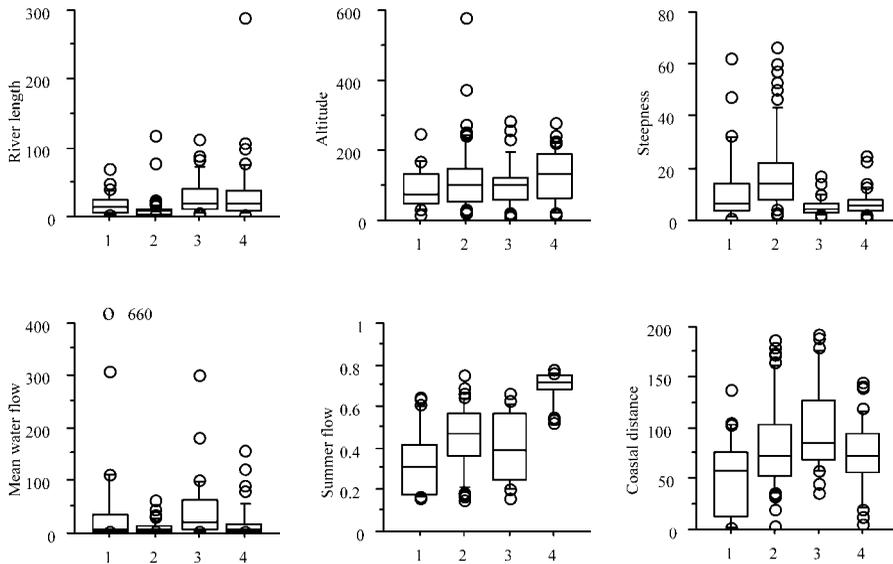
FIGURE 2.—Box plot showing the regional variation in river length (km), maximum altitude (m above sea level), steepness (m/km), annual mean water flow (m³/s), summer flow (proportion of annual mean discharge occurring in May–August), and coastal migration distance (km; distance from river mouth to the coastal shelf) for 158 Norwegian Atlantic salmon populations, 1983–2000. Regions are denoted as follows: 1, Skagerrak; 2, Western Norway; 3, Central Norway; and 4, Northern Norway.

for Atlantic salmon was measured on maps (1: 50,000) and the altitude (meters above sea level [asl]) of the latter was found. In 58 rivers, Atlantic salmon had access to a lake. Lakes situated within the river reach were included in the river length estimate. The length of lakes situated at the top of the accessible reach was not included in the total river length, as the tributaries to these lakes are usually of negligible reproductive importance. Most rivers in all four regions are short (<15 km), although one river (Tana in Northern Norway) has almost 300 km (tributaries not included) of productive river length (Figure 2). The altitude of the uppermost ascendable part of most rivers was less than 150 m asl for most rivers, but Atlantic salmon may reach 580 m asl in the Driva River in Western Norway (Figure 2). River steepness, the ratio between altitude and river length (m/km), was chiefly low, although some rivers demonstrated high values (>60 m/km; the Ryggelva and Vagsvikelva in Western Norway; Vorma in the Skagerrak region) (Figure 2). In general, rivers in Central Norway and Northern Norway are less steep than rivers located in Western Norway or along the Skagerrak coast.

Monthly discharge for each river catchment was calculated by a spatially distributed version of the HBV model developed by the water balance section of the Swedish Meteorological and Hydro-

logical Institute (Bergström 1995). The model performs water balance calculations for 1-km²-grid cell elements that are characterized by their altitude and land use. Each grid cell may be divided into two land-use zones with differing vegetation: a lake zone and a glacier zone. The algorithms used in the model are described by Sælthun (1996). The model was run with daily time steps, and data inputs were precipitation and air temperature. Daily runoff data for the individual grid cells were subsequently aggregated to monthly discharge for the respective catchments. A globally applicable set of model parameters determined by Beldring et al. (2003) was used. The calibration procedure rests on the hypothesis that model elements with common vegetation characteristics, land use, and pedological, topological, and geological conditions controlling their hydrological process dynamics should be assigned the same parameter values. The model was calibrated with available information about climate and hydrological processes from gauged catchments in different parts of Norway, and parameter values were transferred to other catchments based on a classification of landscape characteristics. The median of annual mean discharge was 8.5 m³/s; over 90% of the studied rivers had discharges lower than 65 m³/s, although large (>300 m³/s) rivers (Namsen, Dram-

menselva, and Glomma) were also included (Figure 2).

Norwegian Atlantic salmon ascend the rivers and are captured by recreational fishers during summer. The water flow during the migration season may therefore be more important for the ascending adult salmon than the mean annual water flow. However, mean annual discharge and mean discharge during summer (May–August) were strongly positively correlated ($r = 0.957$, $n = 158$, $P < 0.001$). Consequently, these two parameters could not be used in a multiple linear regression model simultaneously. We therefore used the mean annual discharge as our index of river size. A factor capturing the variability in water flow within a year is the fraction of water that flows during a particular season. The seasonal fraction will vary depending on climate and topography. The estimated proportion of mean annual discharge occurring during summer (May–August) was significantly correlated with mean annual discharge ($r = 0.311$, $n = 158$, $P < 0.001$), but with a relatively low correlation coefficient. We were therefore able to use both parameters within the same model. In general, between 30% and 60% of the total discharge was observed during summer (Figure 2). In the Northern Norway region, a very large fraction of the total water flow was discharged during summer.

The coastal migration distance for Atlantic salmon from the point of saltwater entry to the open ocean was estimated as the distance from the river mouth to the coastal shelf (a line drawn between the outermost islands along the coast) on maps (1:1,000,000). The coastal shelf line represents a theoretical border between coastal and offshore waters. Long migration distances indicate either long passages through fjords or a wide coastline, whereas short distances indicate rivers situated close to open-sea areas. Coastal migration distance was normally distributed, with some rivers located close to the coastal shelf and others located in the inner part of large fjord systems (>180 km; Trondheimsfjorden [Central Norway]: Verdalselva, Figgja, and Steinkjerelva; Sognefjorden [Western Norway]: Nærøydalselva and Flåmselva). In general, the coastal migration distance is greater for salmon migrating from rivers in Western Norway and Central Norway than from rivers in Northern Norway and Skagerrak.

During the study period, 20 study rivers were infested by the parasitic monogenean *Gyrodactylus salaris*. The infestation has led to rapid and dramatic declines in the Atlantic salmon populations in these rivers (Johnsen and Jensen 1986). Intensive surveys of most Norwegian rivers have documented that the parasite is not yet present in other rivers. We found no indication that the infested rivers were different from uninfested rivers in terms of grilse proportion ($F_{1,151} = 0.080$, $P = 0.77$). However, to determine the importance of the parasite, we performed all statistical tests with all rivers included, and then performed another complete set of tests that excluded the rivers with a *G. salaris* infection.

The North Atlantic Oscillation (NAO) is a north–south alternation in atmospheric mass between the subtropical, high-pressure center over the Azores and the subpolar, low-pressure center over Iceland (Hurrell et al. 2002). The NAO measures the strength of the westerly winds blowing across the North Atlantic Ocean between 40°N and 60°N (Hurrell et al. 2002). Variability in the direction and magnitude of the westerly winds is responsible for interannual and decadal fluctuations in winter temperatures and the balance of precipitation and evaporation across the Atlantic Ocean and the adjoining landmasses (Stenseth et al. 2002).

Statistics.—Variation in grilse proportion among rivers was analyzed by use of general linear models (GLM). Grilse proportion was arcsine-transformed to normalize variance. We used a large number of environmental variables as predictor variables in the models. A number of these variables were highly intercorrelated (Table 2), and could not be included in a statistical model at the same time. A number of separate models were therefore explored. Model selection was based on the Akaike information criterion (AIC) (Hurvich and Tsai 1989). Models with the lowest AIC value represent the best compromise between bias (including too few parameters) and lack of precision (including too many parameters) (Burnham and Anderson 1998). All model selections started by including all two-way interactions. Higher-level interactions were not included, mainly because most would be impossible to interpret biologically. Most predictor variables were highly skewed and thus were either $\log_e$-transformed (mean annual discharge, river length, altitude, and steepness) or arcsine-transformed (summer discharge expressed as a proportion of annual discharge).

Results

Temporal Variation

There was large temporal variation in the proportion of grilse both within and among rivers

TABLE 2.—Spearman's rank correlation coefficients (*r*-values, above diagonal; *P*-values, below diagonal) between environmental variables for 158 Norwegian rivers. Coastal distance (km) is the distance from the river mouth to the coastal shelf, River length and altitude are the maximum distance and maximum altitude of salmon ascent in each river. River steepness (m/km) is the ratio between river length and altitude. Summer discharge is the proportion of annual mean discharge occurring in summer (May–August).

Variable (km)	Coastal distance (km)	River length (km)	Altitude (m)	River steepness (m/km)	Annual mean discharge (m^3/s)	Summer discharge proportion
Coastal distance		0.069	0.008	−0.087	0.368	0.418
River length	0.391		0.495	−0.701	0.476	0.310
Altitude	0.923	<0.001		0.197	0.145	0.255
River steepness	0.279	<0.001	0.013		−0.423	−0.147
Annual mean discharge	<0.001	<0.001	0.070	<0.001		0.310
Summer discharge proportion	<0.001	<0.001	<0.001	0.065	<0.001	

(Figure 3), and there was a significant temporal trend (Spearman's rank correlation, $P < 0.05$) in 21 of the 55 rivers with complete data for all 18 years (Figure 4). The mean correlation coefficient was not significantly different from zero (mean ± SE = 0.01 ± 0.06; $t = 0.105$, $n = 55$, $P = 0.917$). The proportion of grilse increased significantly with time in 11 rivers and decreased significantly with time in 10 rivers. In other words, no overall global trend existed, but for specific rivers, there were some indications of a change in grilse proportion with time. The scatter plot in Figure 4,

however, demonstrates that the grilse proportion generally increased with time in those rivers with relatively low mean grilse proportions.

The proportion of grilse within rivers displayed no tendency to vary cyclically (time series analysis with different lags; all parameter estimates were nonsignificant at α = 0.05). To test whether a large-scale climatic effect influenced grilse proportion within rivers, the mean annual NAO index was correlated with the proportion of grilse within each river. A significant correlation with the NAO index was found for 1 of 55 rivers (Figgjo), and
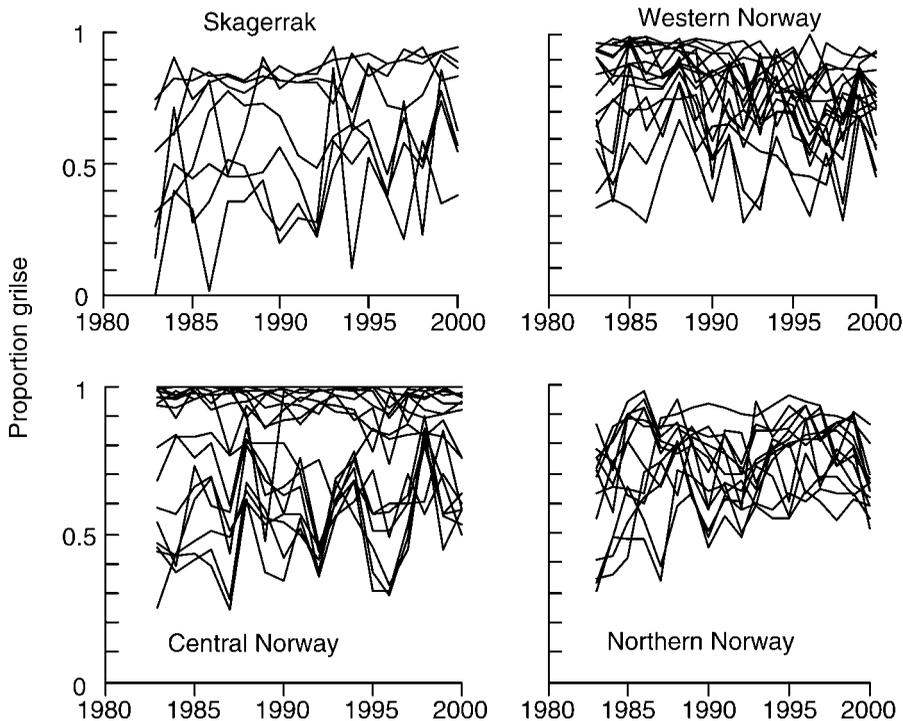
FIGURE 3.—Temporal variation in grilse proportion of Atlantic salmon (1983–2000) in 55 Norwegian rivers divided among four geographical regions.
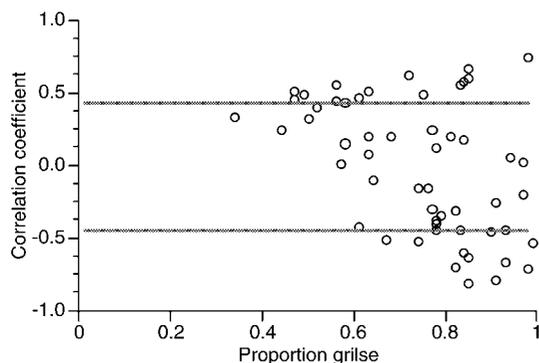
FIGURE 4.—The relationship between the observed mean grilse proportions in 55 Norwegian rivers (1983–2000) and the correlation coefficients of time versus grilse proportion. Points situated above the upper line or below the lower line indicate significant correlations.

this correlation was negative ($r = -0.505$, $n = 18$, $P = 0.033$). When the large number of tests was corrected for, this relationship was not significant ($\alpha = 0.05/55$).

We tested for any correlations between individual rivers in terms of the temporal changes in grilse proportion. In total, 1,485 individual correlation analyses were performed. Of these, 180 correlation coefficients were significantly positive ($P < 0.05$). This is a significantly higher number than would be expected by chance (74). A cluster analysis turned out not to be informative. However, when analyzing for correlation among rivers from the three larger fjords where multiple rivers were represented, we found a higher-than-expected proportion of significant correlations. In the Nordfjord (Western Norway), 5 of 15 correlations (33%) were significant. In the Trondheimsfjord (Central Norway), 7 of 15 correlations (45%) were significant. In the Porsangerfjord (Northern Norway), 3

of 3 correlations (100%) were significantly positive.

For 27 rivers, we were able to test whether the incidence of farmed salmon in the catches significantly influenced our results concerning time trends in the proportion of grilse. After adjusting for the incidence of farmed salmon (i.e., only analyzing ''native'' fish), the mean proportion of grilse was reduced in all rivers (mean reduction ± SD; 2.0% ± 2.7%), at most by 10.1%. The relationship between grilse proportion and time did not change significantly for any river. Thus, the incidence of farmed salmon in the catches in some rivers did not seriously bias our data.

Spatial Variation

The mean annual grilse proportion (±SD) varied between 27.6% ± 18.9% (Stryn) and 99.7% ± 0.9% (Homla River) among the rivers in the spatial data set. The selected GLM model (based on minimizing the AIC) containing factors related to marine and freshwater conditions explained 74.2% of the variation in grilse proportion (Table 3). Clearly, some large regional differences were not accounted for by the available environmental variables. Also, the significant interaction of region with both summer discharge proportion and coastal migration distance implies some important underlying environmental differences between regions. Latitude as a covariate did not capture this variability in grilse proportion as efficiently as did region (based on the AIC). In general, the estimated grilse proportions were low in the two southern regions and high in the two northern regions (least-squares means [LSM] ± SE [arcsine-transformed proportions]: Skagerrak, 0.79 ± 0.01; Western Norway, 0.76 ± 0.02; Central Norway, 0.95 ± 0.05; Northern Norway, 1.13 ± 0.08). The

TABLE 3.—Parameter estimates for the selected general linear model explaining the proportion of grilse (arcsine transformed) in 158 Norwegian populations of Atlantic salmon, 1983–2000.

Parameter	Sum of squares	df	F	P
Region	0.739	3	10.62	<0.001
Presence or absence of lakes	0.286	1	12.34	<0.001
Coastal distance	0.938	1	40.47	<0.001
Annual mean discharge	0.932	1	40.17	<0.001
Summer discharge (proportion of annual)	0.365	1	15.72	<0.001
River steepness	0.141	1	6.09	0.015
Region × summer discharge	0.771	3	11.08	<0.001
Region × coastal distance	0.327	3	4.70	0.004
Presence/absence of lakes × river steepness	0.289	1	12.47	<0.001
Error	(3.270)	(141)		
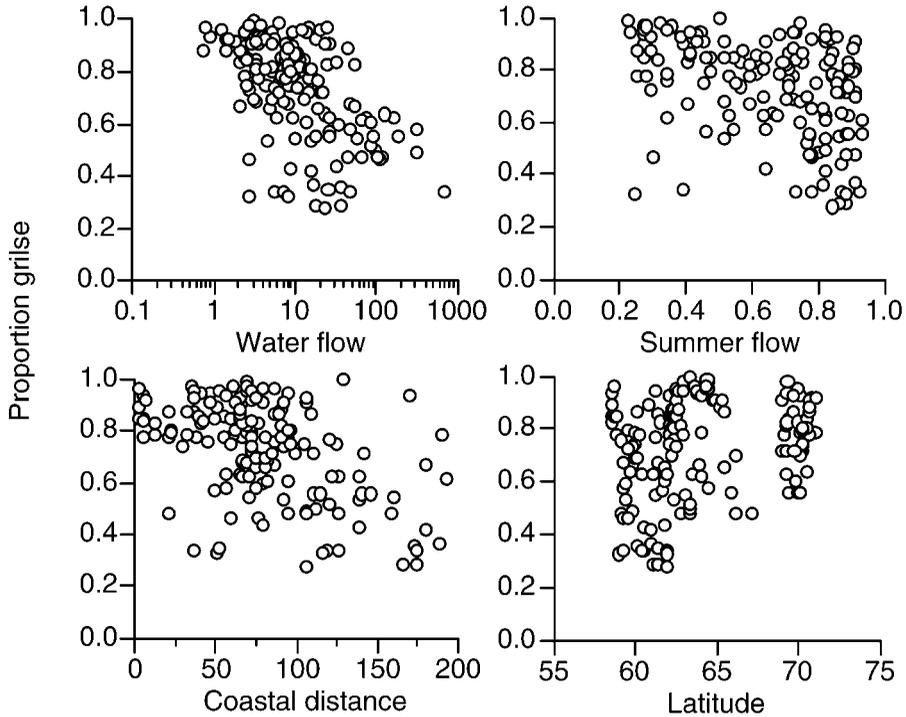
FIGURE 5.—The relationship between observed grilse proportions in 158 Norwegian rivers (1983–2000) and annual mean water flow (m³/s; $\log_e$-transformed), summer flow (proportion of annual mean discharge occurring in May–August), coastal distance (km; distance from river mouth to the coastal shelf), and latitude (°N).

regional mean estimates must be viewed with caution due to the significant interaction effects.

Grilse proportion displayed a significant negative correlation with both mean annual water discharge and the summer discharge proportion (Figure 5). That is, grilse were more abundant in small rivers with lower mean discharge and with a high proportion of the total discharge occurring during summer. The presence of a lake or lakes in the river system had a significant negative effect on grilse proportion (Table 1; LSM ± SE: with lakes, 0.85 ± 0.03; without lakes, 0.96 ± 0.03). River steepness was included as a factor in the selected model, and this combined factor captured the variation in migration arduousness better than either river length or river elevation as individual factors. A highly significant interaction effect existed between river steepness and the presence or absence of lakes. When analyzing this interaction in detail, we found that in rivers without lakes, the grilse proportion did not vary with steepness ($r = 0.052$, $n = 100$, $P = 0.603$), whereas in rivers with lakes, the grilse proportion increased significantly with increasing steepness ($r = 0.400$, $n = 57$, $P < 0.001$).

Norwegian Atlantic salmon populations demonstrated considerable variation in coastal migration distance (Figure 2). For Atlantic salmon that had a long coastal migration distance to the open ocean, the proportion of grilse in the catch was lower than for Atlantic salmon that had a short migration to the open ocean (Figure 5). The significant interaction between region and coastal migration distance indicates further the importance of other environmental effects that differ on large scales.

Analyses that excluded all rivers reportedly infested with the parasite *G. salaris* did not change any of our quantitative or qualitative results.

Discussion

Our study elucidated a significant effect of local conditions (annual river discharge, presence of lakes, coastal migration distance) as well as strong regional effects on the grilse proportion of Norwegian Atlantic salmon populations. Further, we showed that there was no consistent temporal trend in grilse proportion in the studied rivers.

Data Quality

The quality of long-term data series has undoubtedly been improved over time, introducing a possible bias. Despite this constraint, long-term data series are of crucial importance for scientific hypothesis making and for management decisions. The Norwegian official statistics of adult Atlantic salmon nominal catch have undergone several improvements since the program began in 1876. However, the data used in this study were recorded during a period of minor change in the statistics. Reporting procedures changed in 1992, but that change was only to introduce more detail into the statistics, and did not influence our data set. Fishing method, effort, and recording of river anglers' catch of anadromous salmonids changes over time. In this study, we focused on changes in the proportion of grilse. Our main assumption was that fishermen who report their catches are equally prone to report fish independently of fish size. That is, the reported fish are a random sample of the fish captured in a river during a given year. We could not test this assumption, as no data were available regarding the reporting behavior of Norwegian salmon anglers. We did not use actual numbers of captured fish, because actual numbers might be more vulnerable to temporal variation in reporting procedures and willingness, and thus could contain a measurement error of unknown size.

In 1989, the drift-net fishery for Atlantic salmon along the Norwegian coast was forbidden. Mean weights of salmon taken by drift nets in 1980–1988 varied between 3.0 and 3.6 kg (Jensen et al. 1999). Thus, the drift-net fishery mostly targeted 2-SW fish and large grilse, probably resulting in a relative increase in the MSW component in the rivers from 1990 onwards. This effect, if it was important, should have been observable in most of our time series, but this was not the case.

Temporal Variation and Coherence

The life history of Atlantic salmon varies among rivers and is anticipated to reflect local adaptation. The time span covered by our data was probably too short for any evolutionary changes to have occurred, at least without strong selection. Phenotypic plasticity may vary with time. However, without an external environmental force varying in a cyclic fashion, there is no reason to expect a cycle in the proportion of grilse within rivers. On the other hand, a succession of weak and strong year-classes may produce what looks like cyclic variation in grilse proportion for numeric reasons. Such cycles have been observed in Fraser River sockeye salmon *O. nerka* (Ricker 1997) and Atlantic salmon in the Baltic Sea (Svärdson 1954). Our data did not indicate any short-term oscillations in grilse proportion within populations. However, Summers (1995) demonstrated long-term (>150 years) oscillations in grilse proportion in Atlantic salmon in several Scottish rivers. The long-term oscillations may reflect large-scale variation in climatic conditions, and the relationship between growth and sexual maturity indicates that the environment can override the genetic factors that control age at maturity.

We observed no evidence of a general effect of the NAO index on time trends in grilse proportion in the 55 rivers with complete data for all 18 years. For 11 rivers, grilse proportion increased, whereas in another 10 rivers, grilse proportion decreased. In the remaining rivers, no significant linear temporal trend was detected. Grilse proportion tended to increase in rivers with a generally low proportion of grilse, indicating that the number of MSW fish may have been decreasing in those rivers. For rivers with a relatively high mean grilse proportion, both negative and positive correlations with time were observed. In the Imsa River, Norway, a significant increase in grilse proportion was observed for the same time period covered in our study (Jonsson et al. 2003). This river is not included in the official Norwegian catch statistics. A number of different explanations may be evoked to explain such variability in temporal trends; this variability indicates that we should seek river-specific or region-specific reasons rather than a global explanation. Candidate possibilities are variation in exploitation of different age- and size-classes of salmon, variation in climate, and major human encroachments, such as hydropower development.

A gradual decline in annual mean water discharge or summer discharge due to development of hydropower schemes could result in an increase in grilse proportion, as has been documented in the Norwegian river Eira (Jensen et al. 2003). However, in the 11 rivers that demonstrated a significant increase in grilse proportion in our study, five were not subjected to hydropower development. Of the remainder, five rivers were developed for hydropower production prior to 1974, and one river was developed in 1983 after being subjected to several constructions since 1908. Thus, hydropower development cannot explain the temporal increase in grilse proportion in these rivers.

In their review of North American and Icelandic

Atlantic salmon populations, Dempson et al. (1986) showed no detectable time effect on grilse proportion within populations. Further, they found no evidence that ocean temperature influences sea age at maturity in North American Atlantic salmon populations. Welton et al. (1999) reported a fundamental change in the age structure of Atlantic salmon in the River Frome, UK. Their data appear to indicate that this change was only due to short-term variability. Variation in sea temperature was, however, hypothesized to explain a 4-year periodicity in grilse catch in the vicinity of the River Dee, Scotland (Martin and Mitchell 1985). For Icelandic rivers, climatic changes may also explain short-term changes in sea age composition (Gudjonsson et al. 1995). Based on data from the early 1900s, river and ocean temperatures significantly affect the number of salmon and the grilse proportion in British and Scandinavian rivers (Svärdson 1954, and references therein). Grilse proportion particularly increased in the year following a warm summer. Although water temperatures have been recorded daily for years in several of our study rivers, the quality of these data was, unfortunately, not satisfactory enough to test for correlations with grilse variation.

Environment strongly influences growth rate, and growth rate often influences the transition between life history stages. For most fish species, age at maturity decreases with increasing growth rate (Alm 1959). For Atlantic salmon, the age at smolt transformation is usually reduced when growth rate increases (Thorpe 1989; Hutchings and Jones 1999). However, Jonsson et al. (2003) recently reported that the proportion of MSW, Imsa River Atlantic salmon increased with increasing growth rate during the first year at sea. The same result has been reported for male coho salmon *O. kisutch* (Vøllestad et al. 2004, this issue). If this observation turns out to be generally applicable, reductions in growth rate at sea would lead to an increase in grilse proportion in the river catches.

Smolt size may influence age at maturity of anadromous salmonids (Bilton et al. 1982; Chadwick et al. 1986). Large-sized male smolts of coho salmon and Chinook salmon *O. tshawytscha* have an increased probability of maturing at an early age compared to small-sized male smolts (Vøllestad et al. 2004, this issue). For hatchery-reared Atlantic salmon, age-1 smolts produced more 2-SW fish than did older smolts (Jonsson et al. 2003). Age-1 smolts are also smaller than older smolts. This means that environmental conditions both in the river and in the ocean may influence the temporal variation in grilse proportion in Atlantic salmon populations.

Present knowledge indicates that Atlantic salmon populations from the same region intermingle at sea, and that salmon from different regions may utilize specific feeding areas in the ocean (Jensen et al. 1999; Holm et al. 2000; Hansen and Jacobsen 2003). Our data partly support this hypothesis. Similarity in temporal variation in grilse proportion from the rivers draining to three large fjords (Nordfjord, Trondheimsfjord, and Porsangerfjord) demonstrates that the populations are subjected to similar environmental selection pressures. Examinations of catch time series data have shown similarity in grilse proportions within regions in Iceland, but less so between rivers from different regions (Scarnecchia et al. 1991; Gudjonsson et al. 1995). This result may indicate that river conditions are more important than ocean conditions for explaining grilse proportion variation. River water temperature varies widely between years, and thus different growth conditions occur for the juveniles. A result of annual variation in temperature regime between rivers could be a corresponding variation in smolt size, as a close link exists between water temperature and juvenile growth (Metcalfe and Thorpe 1990; Jensen et al. 2000). This relationship may influence age at maturity (Bilton et al. 1982; Chadwick et al. 1986).

Spatial Variation

We have shown that several abiotic factors contribute to the overall spatial variation in age at maturity in Norwegian Atlantic salmon. These factors are connected to river conditions and coastal migration. River conditions may affect salmon size directly and indirectly. Water discharge and velocity may be critical factors for migrating anadromous species. Restriction in the amount of water will physically restrict large salmon from ascending the river; however, during periods when rivers were ascendable, we found as much variation in grilse proportion (33–100%) at 10 m³/s as we did over the whole range of water discharge. Atlantic salmon start to ascend Norwegian rivers in May–October, often in combination with snowmelt in spring and freshets in summer (Jonsson et al. 1990; Hansen and Jonsson 1991). We found that the correlation between discharge and grilse proportion was significantly negative, supporting a similar result given by Jonsson et al. (1991a); 16 of their 18 rivers are also included in our study. In Icelandic rivers, Scarnecchia (1983) also showed that water discharge was an important variable explain-

ing the proportion of grilse. Further evidence of the importance of water flow for the age composition and size composition of spawning Atlantic salmon can be found in the Eira River, Norway (Jensen et al. 2003). Since 1940, water has been diverted from the river due to hydropower development. The mean size of spawning salmon has decreased from 11.5 kg in 1953, when mean annual water flow was 40 m³/s, to 2.8 kg in 2002, when mean water flow was 15 m³/s. The Eira River has thus changed from producing mostly MSW fish in the 1950s to producing mainly grilse in recent times. This indicates that water flow may have a strong selective impact on adult body size; at low flow, a large fish may have problems in migrating upstream due to an insufficient water level, whereas a high flow may be to arduous to navigate for a small fish.

Water flow during migration and prespawning activity could also be a very important factor in the evolution of different reproductive strategies, such as the large, aggressive males and small, precocious males (Gross 1985). In rivers with high discharge, large and small salmon are both able to participate and have significant success during spawning. Thus, evolution of different life histories and reproductive strategies are possible. However, large-sized fish with a high age at maturity will have difficulties in entering and negotiating small rivers. Presence of lakes and habitat heterogeneity (variation between riffles and deep pools) probably act as modifying agents in the evolution of reproductive strategies, making the salmon population in small, heterogeneous systems more like populations in large rivers. Other factors being constant, the proportion of grilse in our study was reduced when lakes were present. The presence of lakes may also increase postspawning survival due to the presence of improved overwintering habitat. One consequence of increased postspawning survival would be a higher number of MSW fish, and thus a reduced proportion of grilse.

River steepness (an indicator of migration arduousness) was retained as a factor in the statistical model, and interacted significantly with presence or absence of lakes. We expected that a steep river would select for larger and older salmon due to the higher energetic costs of migration (Schaffer and Elson 1975; Scarnecchia 1983). However, the opposite effect was observed, although only when lakes were present. Energetic cost during upstream migration and spawning of Atlantic salmon has been studied in a short, Norwegian river of low elevation (Jonsson et al. 1997). The combination

of upstream migration and the holding of territories caused an energy loss of 60–70%; higher losses were sustained in large salmon compared to small salmon. Further, the total energy cost of spawning has been estimated as 50% of the total prespawning energy reserve (Jonsson et al. 1991b). Thus, the energetic cost of upstream migration is estimated at 10–20% of the total energy cost during spawning in small rivers. Our results seem to contradict results from studies in North American and Icelandic rivers (Schaffer and Elson 1975; Scarnecchia 1983). Our results may be due to the low variation in steepness among Norwegian rivers and the covariation of river steepness with river size (mean discharge).

Grilse proportion decreased with increasing coastal migration distance. We attribute this result to reduced food intake during the early phase of migration, and thus reduced postsmolt growth. Smolts from rivers situated in the inner part of Norwegian fjord systems tend to leave their rivers later than smolts from rivers situated further out (Arne J. Jensen, Norwegian Institute for Nature Research, personal communication). Thus, Atlantic salmon originating from rivers near the coastal shelf likely reach marine feeding areas earlier than salmon from rivers situated in the inner parts of large fjords. One consequence of this may be reduced postsmolt growth rates and postponed age at maturity in salmon with long coastal migrations. Furthermore, a long coastal migration introduces an extra cost that may select for an increased body size. Nevertheless, the distance migrated in coastal areas by Atlantic salmon from Norwegian rivers is short compared to the migration distance in the ocean. We therefore do not consider the energetic costs of coastal migration to have a major effect on grilse proportion.

We found large variation in grilse proportion among the four regions in Norway, even after adjusting for variability in a number of environmental variables. A negative latitudinal cline in sea age at maturity was also observed, but the classification of Norway into regions better captured the variability in grilse proportion. The grilse proportion in the southern regions (Skagerrak, Western Norway) was generally lower than in the more northerly regions (Central Norway, Northern Norway) after adjusting for variation in environmental factors. However, this north–south difference is contrary to what has been observed in studies by Scarnecchia (1983) and Salo (1991) on Atlantic salmon and chum salmon *O. keta*, respectively. These very different results indicate that latitude

per se is not important, but rather that certain mac-roclimatic effects are related to latitude in differing ways in different regions. For example, there were significant interactions between region and coastal migration distance, and between region and dis-charge during the migration season (summer). There are a number of possible reasons for the significant difference in grilse proportion between northern and southern Norway.

Firstly, climatic conditions along the Norwegian coast vary greatly. The most striking variation oc-curs off the Lofoten area (69°N). The warm North Atlantic drift secures relatively high (although re-duced in a northerly direction) and stable water temperatures along the Norwegian coast. However, north of Lofoten, the effect of the drift is consid-erably weakened, and sea temperatures are more variable (L'Abée-Lund et al. 1989; Orvik et al. 1995). Although the sea temperature is low in the Barents Sea, the density of zooplankton is still relatively high (Dalpadado et al. 2003) and gives rise to important marine fisheries. The feeding ar-eas are situated near the mainland, indicating that Atlantic salmon reach their marine feeding areas soon after leaving their natal northern Norway riv-ers as smolts. The exact marine distribution of salmon from rivers in northern Norway is un-known, although available data indicate a north-erly distribution compared to populations from southern Norway during the first year at sea (Han-sen and Jacobsen 2003). In their second year at sea, however, northern Atlantic salmon may un-dertake a migration further south and intermingle with southern populations (Hansen and Jacobsen 2003). This geographical distribution hypothesis and partly different distribution pattern of salmon from northern Norway are supported by anecdotal observations and catches of sexually immature salmon in the fjords of northern Norway during winter (Abrahamsen 1968). Similar observations in coastal areas in southern Norway have not been documented, possibly because of the long distance to suitable feeding areas. During their first year at sea, the Atlantic salmon seem to follow the main surface currents northwards into the Norwegian Sea and then spread out over wide areas (Holm et al. 2000). However, the sampling effort has been very low in the Barents Sea and in the Greenland Sea. Secondly, sea temperature may also affect the fraction of the population returning as grilse.

Jensen and Johnsen (1986) hypothesized that Atlantic salmon may adopt two different strategies with respect to smolt size. When low sea temper-atures limit salmon distribution (rivers in northern Canada and Russia), large smolt size is selected for because the osmoregulatory capacity is better at low temperatures (Hoar 1976; Knutsson and Grav 1976). In contrast, when river temperature limits salmon distribution, smolts are relatively small (Jensen and Johnsen 1986). North of 69°N, along the Norwegian coast, the sea temperature is considerably lower than in areas farther south, and river temperatures in summer are higher than sea temperatures (L'Abée-Lund et al. 1989). This sug-gests that the Atlantic salmon smolts should be larger in northern compared to southern rivers. No data on this is available for Norwegian Atlantic salmon populations. In the closely related anad-romous brown trout *S. trutta*, smolt size increases with latitude (L'Abée-Lund et al. 1989). For At-lantic salmon and Pacific salmon, negative cor-relations have been found between smolt size and age at maturity (Nævdal et al. 1978; Bilton et al. 1982; Chadwick et al. 1986; Ritter et al. 1986).

Atlantic salmon demonstrate great plasticity in life history characteristics like grilse proportion. The mechanisms behind this variation may be dif-ficult to detect with few populations or with data series covering short time periods. In this study, we have used a multiple-scale approach both spa-tially and temporally, and even this approach has shown that much of the variation in grilse pro-portion among Atlantic salmon populations re-mains unexplained. We look forward to seeing more innovative and insightful approaches for bet-ter understanding the variation in basic life history traits in this valuable fish. Pattern-oriented studies like ours are a prerequisite for further experimental and theoretical studies.

Acknowledgments

References

Abrahamsen, B. 1968. Undersøkelser over laks i Finnmark. Jakt- Fiske- Friluftsliv 9/10:1–12 [In Norwegian]

Alm, G. 1959. Connection between maturity, size, and age in fishes. Report of the Institute of Freshwater Research, Drottningholm 40:5–145.

Anon 2002. Report of the working group on North Atlantic salmon. International Council for the exploration of the Sea CM 2000/ACFM:14, Copenhagen.

Beamish, R. J., and D. R. Bouillon. 1983. Pacific salmon production trends in relation to climate. Canadian Journal of Fisheries and Aquatic Sciences 50:1002–1016.

Beldring, S., K. Engeland, L. A. Roald, N. R. Sælthun, and A. Voksø. 2003. Estimation of parameters in a distributed precipitation–runoff model for Norway. Hydrology and Earth System Sciences 7:304–316.

Bergström, S. 1995. The HBV model. Pages 443–476 in V. P. Singh, editor. Computer models of watershed hydrology. Water Resources Publications, Highlands Ranch, Colorado.

Bilton, H. T., D. F. Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Canadian Journal of Fisheries and Aquatic Sciences 39:426–447.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer Verlag, New York.

Chadwick, E. M. P., R. G. Randall, and C. Léger. 1986. Ovarian development of Atlantic salmon (*Salmo salar*) smolts and age at first maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89:15–18.

Crisp, D. T. 2000. Trout and salmon. Ecology, conservation and rehabilitation. Fishing News Books, Oxford.

Dahl, K. 1910. Alder og vekst hos laks og ørret belyst ved studiet av deres skjæl. Centraltrykkeriet, Kristiania. [In Norwegian]

Dahl, K. 1916. Salmon and trout: a handbook. The Salmon and Trout Association, London.

Dalpadado, P., R. Ingvaldsen, and A. Hassel. 2003. Zooplankton biomass variation in relation to climatic conditions in the Barents Sea. Polar Biology 26: 233–241.

Day, T., and L. Rowe. 2002. Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. American Naturalist 159: 338–350.

Dempson, J. B., R. A. Myers, and D. G. Reddin. 1986. Age at first maturity of Atlantic salmon (*Salmo salar*)—influences of the marine environment. Canadian Special Publication of Fisheries and Aquatic Sciences 89:79–89.

Elliott, J. M. 1994. Quantitative Ecology and the Brown Trout. Oxford University Press, Oxford,

Fiske, P., and Ø. Aas, editors. 2001. Laksefiskeboka. Om sammenhenger mellom beskatning, fiske og verdiskapning ved elvefiske etter laks, sjøaure og sjørøye. Norwegian Institute of Nature Research, Temahefte 20, Trondheim.

Fiske, P., R. A. Lund, G. Østborg, and L. Fløystad. 2001. Escapees of reared salmon in coastal and riverine fisheries in the period 1989–2000. NINA, Oppdragsmelding 704:1–26 [in Norwegian].

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379–416.

Friedland, K. D. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):119–130.

Friedland, K. D., D. G. Reddin, and J. F. Kocik. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. ICES Journal of Marine Science 50:481–492.

Groot, C., and L. Margolis, editors. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47–48.

Gudjonsson, S., S. M. Einarsson, T. Antonsson, and G. Gudbergsson. 1995. Relation of grilse to salmon ratio to environmental changes in several wild stocks of Atlantic salmon (*Salmo salar*) in Iceland. Canadian Journal of Fisheries and Aquatic Sciences 52:1385–1398.

Hansen, L. P. 1986. The data on salmon catches available for analysis in Norway. Pages 79–83 in D. Jenkins and W. M. Shearer, editors. The status of the Atlantic salmon in Scotland. ITE Symposium 15, Institute of Terrestrial Ecology, Monks Wood, UK.

Hansen, L. P., and J. A. Jacobsen. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands ICE Journal of Marine Science 60:110–119.

Hansen, L. P., and B. Jonsson. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 38:251–258.

Heggberget, T. G. 1988. Timing of spawning in Norwegian Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 45:845–849.

Hesthagen, T., and L. P. Hansen. 1991. Estimates of annual loss of Atlantic salmon, *Salmo salar* L., in Norway due to acidification Aquaculture and Fisheries Management 22:85–91.

Hoar, W. S. 1976. Smolt transformation: evolution, behavior, and physiology. Journal of the Fisheries Research Board of Canada 33:1233–1252.

Holm, M., J. C. Holst, and L. P. Hansen. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. ICES Journal of Marine Science 57: 955–964.

Hurrell, J. W., Y. Kushnir, G. Ottersen, and M. Visbeck. 2002. The North Atlantic oscillation. Climatic Sig-

nificance and Environmental Impact. American Geophysical Union, Washington D.C.

Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

Hutchings, J. A., and M. E. B. Jones. 1999. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1): 22–47.

Jensen, A. T., B. Finstad, N. A. Hvidsten, J. G. Jensås, B. O. Johnsen, E. Lund, and A. Moen. 2003. Fish biology surveys in the Aura watercourse. Annual report 2002. Norwegian Institute for Nature Research, Oppdragsmelding No. 781, Norway.

Jensen, A. J., T. Forseth, and B. O. Johnsen. 2000. Latitudinal variation on growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69:1010–1020.

Jensen, A. J., and B. O. Johnsen. 1986. Different adaptation strategies of Atlantic salmon (*Salmo salar*) populations to extreme climates with special reference to some cold Norwegian rivers. Canadian Journal of Fisheries and Aquatic Sciences 43:980–984.

Jensen, A. J., A. V. Zubchenko, T. G. Heggberget, N. A. Hvidsten, B. O. Johnsen, O. Kuzmin, A. A. Loenko, R. A. Lund, V. G. Martynov, T. F. Næsje, A. F. Sharov, and F. Økland. 1999. Cessation of the Norwegian drift net fishery: changes observed in Norwegian and Russian populations of Atlantic salmon. ICES Journal of Marine Science 56:84–95.

Johnsen, B. O., and A. J. Jensen. 1986. Infestations of Atlantic salmon, *Salmo salar* L., by *Gyrodactylus salaris* in Norwegian rivers Journal of Fish Biology 29:233–241.

Jonsson, N., L. P. Hansen, and B. Jonsson. 1991a. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. Journal of Animal Ecology 69:937–947.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1990. Partial segregation in the timing of migration of Atlantic salmon of different ages. Animal Behaviour 40: 313–321.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1991b. Energetic costs of spawning in male and female Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology 39:739–744.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. Journal of Animal Ecology 66:425–436.

Jonsson, N., B. Jonsson, and L. P. Hansen. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. Journal of Applied Ecology 40:900–911.

Knutsson, S., and T. Grav. 1976. Seawater adaptation in Atlantic salmon (*Salmo salar* L.) at different experimental temperatures and photoperiods. Aquaculture 8:169–187.

L'Abée-Lund, J. H., B. Jonsson, A. J. Jensen, L. M. Sættem, T. G. Heggberget, B. O. Johnsen, and T. F. Næsje. 1989. Latitudinal variation in life history characteristics of sea-run migrant brown trout *Salmo trutta*. Journal of Animal Ecology 58:525–542.

Martin, J. H. A., and K. A. Mitchell. 1985. Influence of sea temperature upon the number of grilse and multi-sea-winter Atlantic salmon (*Salmo salar*) caught in the vicinity of the River Dee (Aberdeenshire). Canadian Journal of Fisheries and Aquatic Sciences 42:1513–1521.

Metcalfe, N. B., and J. E. Thorpe. 1990. Determinants of geographical variation in the age of seaward-migrating salmon, *Salmo salar*. Journal of Animal Ecology 59:135–145.

Nævdal, G., M. Holm, O. Ingebrigtsen, and D. Møller. 1978. Variation in age at first spawning in Atlantic salmon (*Salmo salar*). Journal of Fisheries Research Board of Canada 35:145–147.

Orvik, K. A., L. Lundberg, and M. Mork. 1995. Topological influence and the flow field off Lofoten-Vesterålen. Pages 165.175 in H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas, editors. Ecology of fjords and coastal waters. Elsevier, Amsterdam.

Pyper, B. J., and R. M. Peterman. 1999. Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*), 1967–1997. Canadian Journal of Fisheries and Aquatic Sciences 56:1716–1720.

Quinn, T. P., L. Wetzel, S. Bishop, K. Overberg, and D. E. Rogers. 2001. Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. Canadian Journal of Zoology 79:1782–1793.

Ricker, W. E. 1997. Cycles in abundance among Fraser River sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 54:950–968.

Ritter, J. A., G. J. Farmer, R. K. Misra, T. R. Goff, J. K. Bailey, and E. Baum. 1986. Parental influences and smolt size and sex ratio effects on sea age at first maturity of Atlantic salmon (*Salmo salar*). Canadian Special Publication of Fisheries and Aquatic Sciences 89:30–38.

Roff, D. E. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Sælthun, N. R. 1996. The Nordic HBV model. Norwegian Water Resources and Energy Administration Publication 7:1–26.

Salo, E. O. 1991. Life history of chum salmon (*Oncorhynchus keta*). Pages 233–309 in C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Saunders, R. L., E. B. Henderson, B. D. Glebe, and E. J. Loudenslager. 1983. Evidence of a major environmental component in determination of grilse: large salmon ratio in Atlantic salmon (*Salmo salar*). Aquaculture 33:107–118.

Scarnecchia, D. L. 1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). Ca-

nadian Journal of Fisheries and Aquatic Sciences 40:1456–1468.

Scarnecchia, D. L., Á. Ísaksson, and S. E. White. 1991. 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*). Fisheries Research 10:207–228.

Schaffer, W. M., and P. F. Elson. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56:577–590.

Shearer, W. M. 1992. The Atlantic salmon—natural history, exploitation and future management. Fishing News Books, Oxford.

Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40:893–913.

Summers, D. W. 1995. Long-term changes in sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers Aquaculture and Fisheries Management 25:77–87.

Svärdson, G. 1954. Salmon stock fluctuations in the Baltic Sea. Institute of Freshwater Research Drottningholm Report 36:226–262.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207.

Thorpe, J. E. 1989. Developmental variation in salmonid populations. Journal of Fish Biology 35(Supplement A):295–303.

Vøllestad, L. A., J. Peterson, and T. P. Quinn. 2004. Effects of fresh water and marine growth rates on early maturity in male coho and Chinook salmon. Transactions of the American Fisheries Society 133: 495–503.

Welton, J. S., W. R. C. Beaumont, and M. Ladle. 1999. Timing of migration and changes in age structure of Atlantic salmon, Salmo salar L., in the River Frome, a Dorset chalk stream, over a 24-year period Fisheries Management and Ecology 6:437–458.

Youngson, A. F., J. C. MacLean, and R. J. Fryer. 2002. Rod catch trends for early-running MSW salmon in Scottich rivers (1952–1997): divergence among stock components. ICES Journal of Marine Science 59:836–849.