Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers

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Abstract: Rivers and streams occupied by anadromous Atlantic salmon (*Salmo salar*) occur across a diverse array of landscapes. This article describes the general ecology of these rivers and streams, including many of the physical and biological variables that are important characteristics of all lotic systems. For analytical purposes, the geographic range of Atlantic salmon rivers is divided into five regions, based on geomorphology and climate. The physical habitat available to anadromous Atlantic salmon is diverse. The geology varies from granitic bedrock to volcanic and glacial substrates, which influence a broad array of other ecological variables, ranging from water chemistry to catchment morphology (e.g., river length). Flood regimes and system hydrology are dependent, as expected, on climate. Many of the catchments receive substantial precipitation in the form of snow; rivers in four of the five regions experience primarily spring freshets. Aquatic temperatures are also variable, representing close to the full range of thermal tolerance of *S. salar*, with lows just above 0°C in the northernmost latitudes to summer highs in western Europe approaching 25°C. Most rivers are best characterized as oligotrophic with relatively low annual primary productivity. However, physical factors such as availability of suitable spawning and rearing habitat, as well as aquatic temperature and flow regimes, may drive anadromous productivity. In general, most of the rivers have been modified by flow regulation and many suffer from impacts related to other anthropogenic disturbances, principally riparian forest clearing for agriculture, forestry, and urban development. We conclude that the rivers and streams occupied by anadromous Atlantic salmon are diverse across the species' range and have been heavily impacted by anthropogenic disturbances.

Résumé : On trouve les cours d'eau fréquentés par le saumon de l'Atlantique anadrome (*Salmo salar*) dans divers types de paysages. Le présent article décrit l'écologie générale de ces cours d'eau, dont bon nombre des variables physiques et biologiques qui sont d'importantes caractéristiques de tous les milieux lotiques. Aux fins de l'analyse, l'aire géographique dans laquelle on trouve les rivières à saumon est divisée en cinq régions sur la base de la géomorphologie et du climat. Le saumon atlantique anadrome fréquente des habitats physiques divers. Sur le plan géologique, on trouve aussi bien des substrats granitiques que des substrats volcaniques ou glaciaires, lesquels déterminent une vaste gamme d'autres variables écologiques, comme la chimie de l'eau et la morphologie du bassin versant (p. ex., la longueur des cours d'eau). Les régimes de crue et l'hydrologie des bassins dépendent, comme on peut s'y attendre, du climat. Bon nombre de bassins versants reçoivent une part substantielle de précipitation sous forme de neige; les cours d'eau de quatre des cinq régions connaissent principalement des crues nivales. Les températures de l'eau sont aussi variables : elles couvrent presque entièrement la plage de tolérance thermique de *S. salar*, avec des minimums juste supérieurs à 0°C sous les latitudes septentrionales et des maximums estivaux approchant 25°C en Europe de l'Ouest. La plupart des cours d'eau sont oligotrophes et montrent une productivité primaire annuelle relativement faible. Cependant, des facteurs physiques comme la présence d'habitats favorables pour la reproduction et l'alevinage, de même que la température de l'eau et les régimes d'écoulement, peuvent encourager la productivité du saumon anadrome. En général, la plupart des cours d'eau ont été modifiés par la régulation de leur débit, et bon nombre ont subi des impacts négatifs liés à d'autres perturbations anthropiques, principalement à la coupe des arbres sur leurs rives pour l'agriculture, l'exploitation forestière ou le développement urbain. Nous concluons que les cours d'eau fréquentés par le saumon atlantique anadrome montrent une grande diversité d'un endroit à l'autre de l'aire de répartition de ce poisson et ont été fortement perturbés par les activités humaines.

[Traduit par la Rédaction]

"And the star-stream of heaven flowed westward, to far beyond the ocean where salmon, moving from the deep water to the shallows of the islands, leapt — eager for immortality.

Henry Williamson (1935), excerpted from *Salar the Salmon*

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Introduction

The basic concept of rivers as a continuous series of integrating physical gradients and associated biotic adjustments has provided the holistic perspective needed for discovering and understanding how variations in the physical environment are ecologically relevant to widely distributed species (Vannote et al. 1980; Naiman et al. 1987). For some time it has been known that the characteristics of running waters reflect local geomorphology, climate, disturbance regimes, and features of the riparian ecotone (Décamps and Naiman 1989; Naiman and Bilby 1998). As a consequence, individual river segments acquire unique features related to position in the catchment, patterns of water movement, channel gradient, and accessibility to colonizing organisms. The ecological consequences of the physical variability within catchments, as well as between ecoregions, are expressed as variations in life history strategies, evolutionary processes, ecosystem integrity, and patterns of biodiversity. Variations in these ecological characteristics have, in turn, strong implications for management and restoration strategies.

This is especially true in the numerous Atlantic salmon (*Salmo salar*) rivers draining into the North Atlantic Ocean, the Norwegian Sea, and the Barents Sea. Strong gradients and contrasts in parent geology, topography, soils, temperature, and flow regime exist within these rivers, encompassed within 40° to 60° north latitude in North America and from 40° to 70° north latitude in Europe (Netboy 1973). Describing patterns in the physical environment and understanding processes creating and maintaining those patterns provides a fundamental foundation for interpreting trends in Atlantic salmon life histories and productivity and the biotic communities supporting them.

In this article, we investigate the breadth of this heterogeneity by examining the general biophysical characteristics of rivers within the natural range of Atlantic salmon. The objective is to provide an overview of regional patterns in geomorphology, climate, hydrology, water temperature and chemistry, aquatic biodiversity, and productivity, as well as riparian characteristics (Table 1). These patterns are described (in so far as possible) for natural rivers and discussed in light of recent land use changes, with several case studies provided as illustrations. In making connections between biophysical characteristics and salmon ecology and production, we seek to identify factors which may make certain rivers more productive than others and to elucidate differential vulnerability to various anthropogenic stresses. An understanding of these factors is essential to guiding management, conservation, and restoration strategies of salmon-bearing streams.

Regional analysis

The range of *S. salar* historically included every country with rivers draining into the North Atlantic Ocean, the Norwegian Sea, and the Barents Sea. Currently, the range of Atlantic salmon rivers extends from New England through the eastern seaboard of Canada, across to Greenland and Iceland, eastward through Scandinavia to Russia, and south and westward to the British Isles, France, Spain, and Portugal (MacCrimmon and Gots 1979).

For the purpose of analysis, we divided the range of *S. salar* into five major regions (Fig. 1) according to differences in geology, flow regime, and climate, coupled with geographic position (Fig. 2). Although based on catchment variables, the scheme is generally supported by studies which have clustered Atlantic salmon populations according to genetic and other characteristics (Davidson et al. 1989; Table 2).

Region I: New England, Nova Scotia, and Gaspé Peninsula

This region includes the Gaspé Peninsula, New Brunswick, and Nova Scotia in Canada, as well as the northeastern United States. Topography ranges from gentle, rolling granite uplands to areas with much greater relief such as the White Mountains in New Hampshire. The geology of New England is characterized by folded overthrust sediments with metamorphics and igneous intrusives (Strahler 1975). River channels bear evidence of extensive modification during the Pleistocene by glacial scour and deposition. The region has undergone recent glacial modification; glacial deposits overlying bedrock average 8–15 cm but can reach 120 m in some river valleys (Webster et al. 1995). The summer climate is mild (10–20°C) to hot (>20°C) with cool to cold winters (<10°C; National Geographic Society 1992).

Region II: Canadian Shield

The Canadian Shield extends from Labrador and Québec around Hudson Bay to central-eastern Canada (Sutton 1972; Mackay 1995). Underlain by Precambrian deposits, the region is characterized by granite bedrock either exposed or overlain by thin soils (Mackay 1995). Much of the region consists of a flattened plateau (<1000 m elevation) of low or undulating relief dissected by deep valleys with a few mountains penetrating above the plateau (Power 1981). Rivers flowing to the St. Lawrence River cut through the plateau, often resulting in very abrupt changes in elevation with rapids and falls presenting natural barriers to fish passage (Netboy 1980). In Labrador, areas rich in limestone and sandstone deposits also occur (Anderson 1985). Rivers in Labrador either flow over relatively flat topography or through deeply incised valleys to the Labrador Sea. Here the Shield is characterized by numerous areas of standing waters which form lakes, swamps, and bogs (Anderson 1985; Mackay 1995). Mild to cool summers and cold winters typify the climate, with mean daily temperatures ranging from –10 to –25°C in January to 10–15°C in July (Geographical Services Division 1985).

Region III: Northern Islands

The Northern Islands region is comprised of the harsh environments of Iceland and Greenland. The geology of Iceland is heavily influenced by volcanic activity with a plateau of volcanic rock forming the interior of the island (Petersen et al. 1995; Netboy 1980). Recent lava and palagonite formations comprise the interior of the island from the southwest through the central highlands to the northeast coast, with basalt lying to the west and east (Einarsson 1968). The

Table 1. Selected bophysical characteristics of Atlantic salmon rivers by region.

Region	Geology	River length (km)	Flood regimes	Aquatic temperature regime[a] (°C)	Length of growing season	Role of ice	[DOC] mg C·L^{-1}	Productivity	Diversity	Riparian	Land uses/Major impacts
I	Glacial deposits overlying bedrock	5–552	March, April freshet	ND; 20–25+	150 to 170[b]	Not important	4	Low, variant		Significant hardwood component	Urbanization, agriculture, regulation
II	Exposed granitic bedrock	1–546	April, May freshet	0–0.4; 15–22	80 to 170[b]	Under ice cover from ~Dec. to ~March	10–15	Low, variant		Primarily boreal forest	Forestry
III	Volcanic, some glacial	93–320	Spring freshet	0–5; 3–5+	ND	Spring fed, volcanically–influenced rivers do not freeze over; arctic/alpine rivers will freeze over	?	A *f(n)* of arctic light regimes; minimal riparian cover		Low woody shrubs and grasses; little riparian cover	Few
IV	Calcareous or granite/gneiss substrate	94–1809	Winter freshet along coast of Denmark, Atlantic coast of Norway; boreal regions experience Spring freshet	0–5; 11–23	63 to 192[c]	Boreal/alpine streams freeze over; coastal systems remain clear	15–45	Low, variant		Primarily boreal forest	Regulation
V	Glacial deposits; chalk; boulders and rocks (uplands); alluvial in lowlands	19–1110	Winter freshet	0–4; 12–25	196 to >330[c]	Not important	5–7	Low, variant		Mixed forests; significant clearing for agriculture	Urbanization, agriculture, regulation

[a]Minima and maxima ranges, respectively.
[b]Number of days greater than 5.6°C.
[c]Number of days greater than 7.0°C.

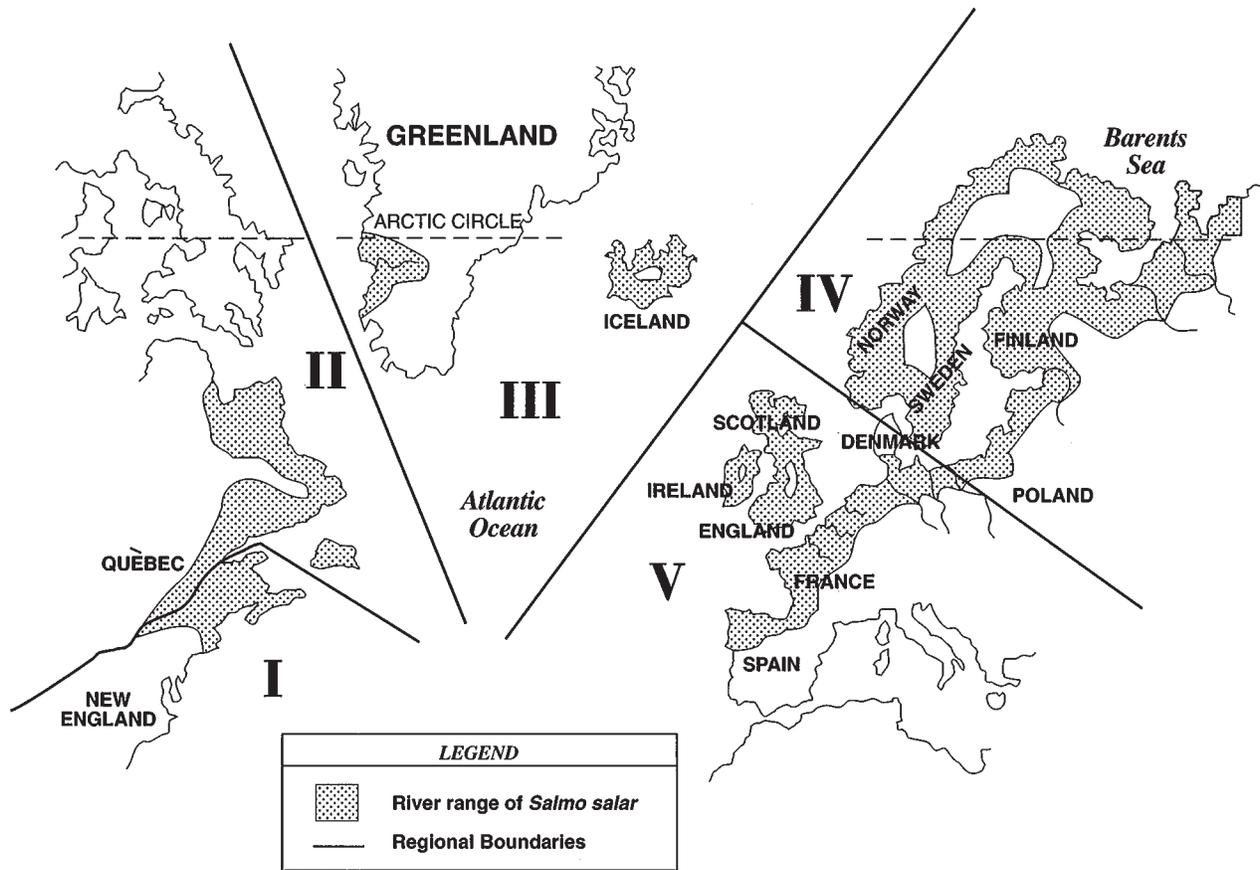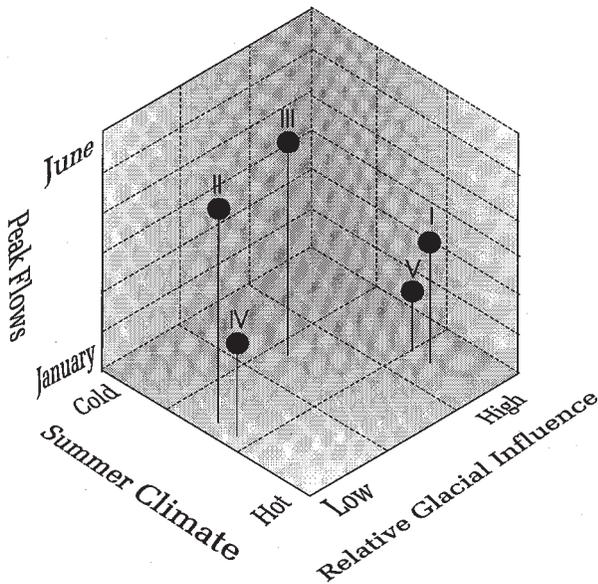**Fig. 1.** Natural geographic range of Atlantic salmon rivers.

Fig. 2. Clustering of regions according to climate, flow regime, and glacial influence.

regimes depending on source type: direct runoff, lake or standing water fed, spring fed, and glacier fed. Iceland has a humid and temperate climate (Netboy 1980). Mean monthly air temperature for middle Iceland ranges from –10°C in January to 6°C in July (Petersen et al. 1995). Atlantic salmon spawn in only one river in Greenland, the Kapisillit, on the southwest coast of the island (Shearer 1992).

Region IV: Scandinavia and Russia

Scandinavia includes Denmark, Finland, Norway, Sweden, and Poland. The geology of Scandinavia is of two distinct types: the first, encompassing Denmark and southern Sweden, consists primarily of glacial moraine deposits; the second is composed of Archaean crystalline rocks and dominated by the Fennoscandinavian Shield, a formation sloping gently toward the southeast. Low-gradient rivers in this region flow over calcareous or granite/gneiss substrates with thin soils while high-gradient streams exhibit bare granite geomorphology. Rivers range from low-gradient streams interspersed with lakes, ponds, and wetlands, to high-gradient mountain streams dominated by cascades and waterfalls. Generally, Nordic rivers are short in length and small in catchment area (Petersen et al. 1995). Salmon rivers in Russia are generally longer and drain greater areas (Netboy 1980) than Nordic rivers. The general climate is one of mild (10–20°C) summers and cold (<0°C) winters (National Geographic Society 1992); mean annual air temperature ranges

numerous rivers tend to be fast and large and are influenced by either glaciation or volcanism. Lakes and areas of standing water are also numerous. Rist (1956) identified four types of Icelandic rivers with different flow and temperature

Table 2. Genetic and geographic groupings of Atlantic salmon.

Region	Thorpe and Mitchell 1981		Stähl 1987		Møller 1970
I	North American		Canadian		New Brunswick/ Nova Scotia; Maine
II					Newfoundland/ Labrador
III	European	Western	European	Eastern Atlantic	
IV		Northern; Baltic		Baltic	
V		Western		Eastern Atlantic	

Note: Stähl 1987: Inferred from dendrogram constructed from genetic distance matrix based on allele frequencies at 38 loci. Møller 1970; Mitchell and Thorpe 1981: Based on differences in transferring allele (TF^4) frequencies.

from 8°C in southern Sweden to 2°C in the arctic region (Petersen et al. 1995).

Region V: Western Europe

The European countries of the United Kingdom, Ireland, Belgium, Netherlands, Germany, France, Spain, and Portugal present a wide diversity of Atlantic salmon habitat. Rivers in Britain, for example, are generally small relative to other rivers of the world (Ward 1981). They arise in chalk, sandstone, limestone, or from metamorphic or igneous rock in low elevation mountains and flow at low gradients through clay or alluvium (Ladle and Westlake 1995). Streams in the north and west are typically steep, fast, and rocky with little intervening floodplain while those of the south and east are slower and more meandering with pronounced floodplains (Newson 1981; Ladle and Westlake 1995). The area encompassing France, Belgium, and the Netherlands consists of two large plateaus of secondary and tertiary sedimentary rocks surrounded by three uplift Hercynian massifs (Billen et al. 1995). Rivers in the area tend also to be short with relatively small basins, although there are several major river systems which are substantially larger. The lowlands of this region often have well-developed alluvial plains (Billen et al. 1995). Salmon rivers in Spain and Portugal are confined to the north and northwest portions of the Iberian Peninsula, which receive substantial rainfall distributed somewhat evenly throughout the year. Streams arising in the mountains are short, fast, and cold, flowing through deeply incised valleys with numerous rocky ledges and cascades (Netboy 1980); they tend to be spate rivers, quick to rise and fall (Garcia de Leaniz and Martinez 1988) and drain granite and basalt formations (Sabater et al. 1995). Despite such variety in upland geomorphology, rivers of the western European region have somewhat similar climates. Mild (10–20°C) summers and cool (0–10°C) winters, while Spain and eastern Europe tend towards higher and lower temperatures, respectively (National Geographic Society 1992).

The physical environment

Catchment morphology

Lengths of 70 rivers on the Gaspé Peninsula and in Nova Scotia and New Brunswick (Region I) range from 5 to 343 km ($\bar{x}$ = 59 km; Schaffer and Elson 1975). Combined river length data from Region II (Québec, Newfoundland, and Labrador; n = 17, 47, and 102, respectively; Schaffer and Elson 1975; Anderson 1985) yielded a greater range (1–

546 km) but a similar mean of 57 km. Comprehensive data sets such as these apparently are not available for other regions, where lengths for major river systems only were reported; in such cases, it may be more valid to compare upper levels in length ranges. Three of New England's (southern Region I) largest rivers, for example, are 340–552 km long (Unesco 1978), comparable to the upper level for rivers to the north of the region. Petersen et al. (1995) provide lengths for three representative rivers (from Regions III and IV) in each of five countries: Iceland (93–230 km), Denmark (94–146 km), Finland (507–560 km), Norway (302–601 km), and Sweden (450–720 km). Rivers in Russia extend in length from the relatively short rivers of the Kola Peninsula to the broad, slow-flowing Pechora River, the largest of Atlantic salmon rivers at 1809 km (Unesco 1978; Kuz'min and Smirnov 1982). In England (Region V), Atlantic salmon rivers range from 82 to 239 km (Ward 1981) with Scottish rivers substantially shorter (19–158 km, $\bar{x}$ = 26; Thorpe and Mitchell 1981). Salmon rivers in France are longer than in the United Kingdom, from the 650 km Garonne to the 1110 km Loire (Unesco 1978), while those in Spain are shorter, generally <50 km (Garcia de Leaniz and Martinez 1988).

Catchment size, or drainage area, is positively and strongly correlated with river length for all regions considered (Fig. 3). The slope of this relationship reflects patterns in geology and hydrology and might be expected to differ substantially among regions, yet there are no apparent regional patterns other than differences in absolute river and catchment sizes. The three large river systems in New England (southern Region I) drain 29 000 to 35 000 km^2 (Unesco 1978). Drainage areas range from 13 to 93 415 km^2 ($\bar{x}$ = 2225 km^2) for 102 Labrador rivers (Region II) (Anderson 1985). Similar data for river length is presented for drainage areas of Icelandic and Scandinavian rivers (Regions III and IV, respectively; Petersen et al. 1995): Iceland (2000–8000 km^2), Denmark (1000–3000 km^2), Norway (16 000–42 000 km^2), Sweden (32 000–50 000 km^2) and Finland (40 000–62 000 km^2). Values for Region V range from 1090 to 9950 km^2 for 20 Great Britain rivers (Ward 1981) with relatively large values evident for Belgium and France (13 489–120 000 km^2, n = 4; Unesco 1978). Drainage areas for 6 rivers in Asturias, Spain, however, are much smaller, only 467–2572 km^2 (Ventura 1988).

Catchment size has obvious implications for the ecology and life history strategies of Atlantic salmon. Smaller river systems tend to have lower discharges and more variable flow regimes, potentially confining upstream migration to a narrower time frame. Longer rivers are associated with lon-

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Fig. 3. Relationship between river length and drainage area for Atlantic salmon rivers. Regression equation: $y = 1.6921x - 0.0744$ ($r^2 = 0.8829$). — = Region 1 ($n = 5$); ▲ = Region II ($n = 105$); ● = Region III ($n = 3$); * = Region IV ($n = 31$); ○ = Region V ($n = 22$).
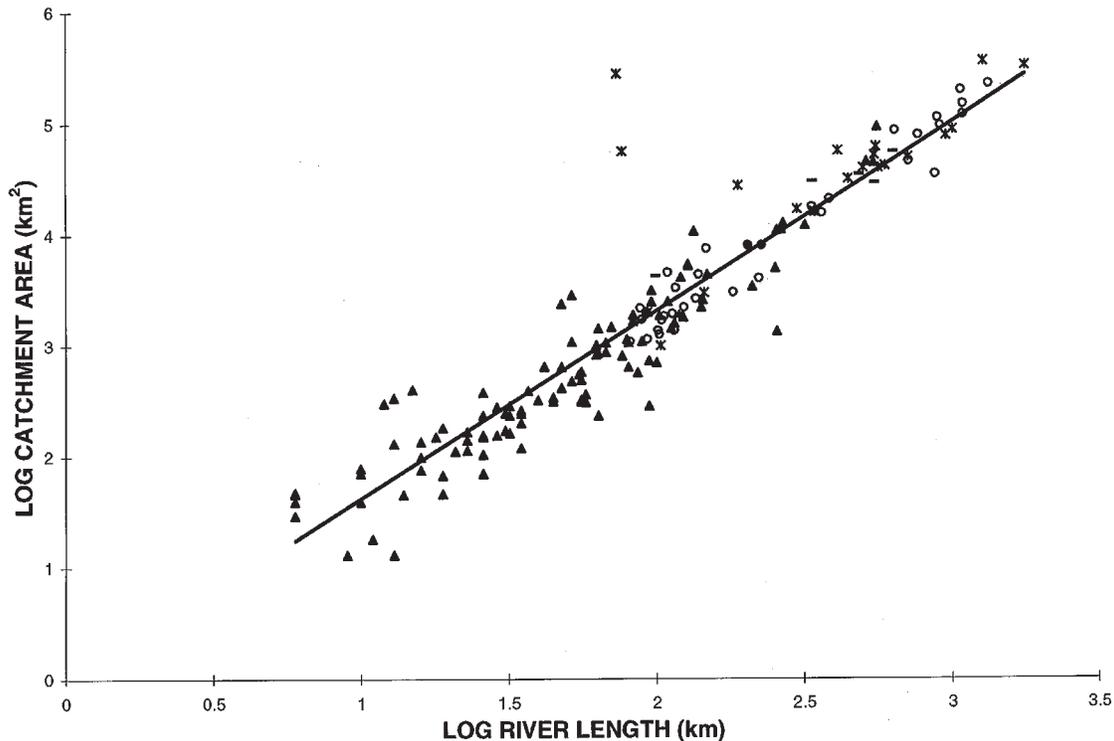
ger periods at sea and higher mean age of first spawning (Schaffer and Elson 1975), presumably due to the difficulty of upstream migration in such rivers. Difficult migrations in long, fast rivers may also lead to increased postspawning mortality and subsequent reduction in frequency of iteroparity. In any comparison, it is important to consider factors such as barriers to fish passage and availability of suitable habitat lower in the catchment which may reduce the length of river actually used by salmon.

Hydrology

In catchments unimpacted by human activities, hydrology is controlled by climate, precipitation, and geology. Accordingly, Atlantic salmon rivers tend to follow one of two generalized patterns of annual discharge. In cold regions, peak flow timing is determined by the extent to which runoff inputs are delayed in snow and ice. In warmer climates without appreciable snow or ice cover, peak flows are controlled by seasonal changes in rates of precipitation and evapotranspiration. Under these different hydrologic scenarios, different factors affect growth and survival rates of Atlantic salmon.

Where winter precipitation occurs primarily as snow, or where surface waters are frozen for some portion of the winter, discharge volumes are highest during spring melt. For example, an average of 54% of annual streamflow at Hubbard Brook, New Hampshire occurs between March and April (Likens et al. 1977). Similarly, 50% of annual discharge in subarctic Québec streams occurs during April and May freshets, whereas January and February flow volumes represent only 3–5% of annual maxima (Naiman and Link

1997). This pattern of snowmelt-driven peak flows in spring and relatively low flows in winter is evident throughout New England (Region I) and Québec (Region II), as well as in the boreal, arctic, and alpine regions of Iceland and Scandinavia (Regions III and IV, respectively) (Mackay 1995; Petersen et al. 1995; Webster et al. 1995; Naiman and Link 1997).

During winter and early spring, flood magnitudes in these areas are influenced by instream ice formations. Where high flows interact with ice cover at the time of spring breakup, ice jams can deflect flow onto the banks and exacerbate spring flooding (Prowse 1994; Scrimgeour et al. 1994). During winter, anchor ice on the river bed serves to elevate the effective river stage, while ice blockages may lead to rapid increases in water level immediately upstream and decreased flow in downstream reaches (Prowse 1994; Cunjak 1996). Anchor ice or partial ice blockages may also decrease channel cross-sectional area, resulting in localized increases in flow velocity and potentially increased bed scour.

Despite these effects, salmonids in snow and ice-influenced regions are more typically threatened by low flows in winter. During the winter low flow period, physical space is a major factor regulating stream fish populations. As overwintering habitat area decreases, fry may experience high rates of mortality due to stranding and subsequent suffocation, as well as freezing and increased predation pressure (Cunjak 1996). Low winter discharges also reduce percolation of water through redds, resulting in decreased delivery of dissolved oxygen and correspondingly decreased rates of survival for incubating eggs (Chadwick 1982). Moreover, reduced flows may result in lower temperatures

and egg mortality typically increases at temperatures below 4°C (Peterson et al. 1977). Accordingly, there is a positive correlation between winter discharge and survival of juvenile Atlantic salmon in boreal rivers of Newfoundland and New Brunswick (Gibson and Myers 1988).

Another factor that may affect salmonid reproduction in ice-influenced areas is the potentially limited spawning season. In spring, migrating salmon will not enter the river until after breakup and its associated freshets, yet spawning must occur earlier in fall, before tributaries are closed by ice. For example, few salmon enter the Nepisiguit River in northern New Brunswick (Region I) before late June or early July, and spawning typically ends in late October or early November (Nepisiguit Salmon Association 1995), whereas salmon may enter more temperate British Rivers (Region V) at all seasons of the year (Netboy 1968).

In more temperate, coastal regions, where almost all winter precipitation occurs as rain, seasonal patterns of discharge tend to reflect increased precipitation during winter and increased evapotranspiration in summer. In the coastal, deciduous regions of Denmark and the Atlantic coast of Norway (Region IV), where periods of below-freezing temperatures are relatively short, high flows occur in winter, and low flows occur in late spring through summer (Petersen et al. 1995). Similarly, peak flows in British streams (Region V) occur in winter and low flows occur in summer through early fall (Ward 1981; Ladle and Westlake 1995). In these regions, high winter flows may result in increased scouring of salmonid redds and correspondingly increased mortality of incubating eggs. These effects are exacerbated by rain-on-snow events where periodic snowfall is followed by warm rains, resulting in pulses of snowmelt during winter. Whereas summer discharge appears to be unrelated to survival in boreal rivers (Gibson and Myers 1988), low summer flows and stranding may have significant effects on survival rates for juveniles in these warmer regions of the Atlantic salmon's range. Positive correlations have been reported between summer discharge and survival of underyearling salmonids in coastal rivers of Britain (Elliott 1984; Solomon and Paterson 1980).

Discrepancies between flow maxima and minima are influenced by sources and pathways of water from the landscape to the stream channel, which are in turn influenced by catchment geology and topography. In catchments with high infiltrative capacities, a higher proportion of streamflow will be groundwater fed and annual discharge is more evenly distributed in time. For example, in the calcareous chalk areas of southern and eastern England, infiltration rates are high and up to 90% of discharge can be from groundwater (Paolillo 1969). Maximum:minimum discharge ratios of chalk streams range from 5 to 10, as compared with ratios of 30:300 in northwestern British streams draining more impervious, rocky basins (Ladle and Westlake 1995).

Aquatic temperature regimes

Given the considerable latitudinal gradient in the range of Atlantic salmon, variation in annual temperature ranges among rivers of different regions is not surprising. Two streams in New Brunswick (Region I) showed maximum annual water temperatures in the range of 20–22°C (Riddell and Leggett 1981) while two rivers in Maine, U.S.A., exceeded 25°C for 4–5 d·yr^{-1} (Hulbert 1978). The typically cool winters in Region I suggest temperatures do not normally result in extreme ice conditions. Rivers in Québec and Labrador (Region II), on the other hand, tend to be under extensive ice cover from December through March and are considerably cooler year round (Mackay 1995), as reflected in the mean annual air temperature of only 6°C for the region. Minimum water temperatures are near 0°C while summer maxima range from about 22°C in southern Québec (Naiman et al. 1987) to just 15°C in Ungava Bay, northern Québec (Jensen and Johnsen 1986). Temperatures in Icelandic rivers (Region III) are influenced by source type. Spring-fed rivers in the volcanic zone do not freeze in winter and, moreover, maintain fairly constant temperatures of 3–5°C year round (Rist 1956; Petersen et al. 1995). Those draining high mountain areas, however, are more variable and, due to influence of snowmelt in spring and early summer, remain cold even during the short growing season (Rist 1956). Jensen and Johnsen (1986) list annual ranges of 1–11°C for two rivers in northern Norway (Region IV) and 4–13°C for a river in western Norway, while rivers in central Scandinavia reach maximum temperatures of >14°C (Petersen et al. 1995). The Pechora River in northwestern Russia exhibits considerably higher temperatures than the coldest Norwegian rivers, reaching 23°C in summer (Jensen and Johnsen 1986). The annual temperature range for British rivers (Region V) is 1–20°C; the range varies for different streams in the same region: 0–25°C for low-order streams in general (Walling and Webb 1981), but only 11–12°C for chalk streams (Ladle and Westlake 1995). Belgium's Meuse exhibits a similar range (0–23°C) with mean 7–9°C annually (Descy and Empain 1984) while in Spain, river temperatures fall below 7°C only 1–2 mo·yr^{-1} (Garcia de Leaniz and Martinez 1988).

Growing season also varies considerably among Atlantic salmon rivers although comparison is somewhat confounded by differences in units reported in the literature. When expressed as number of days (d) air temperature exceeds 5.6°C (Power 1981), growing season among Regions I and II is greatest for the tip of Gaspé (150–170 d), followed by insular Newfoundland (120–170 d), southern Québec (120–160 d), and central and northern Québec and Labrador (80–120 d). A similar measure of growing season is the number of days that water temperature exceeds 7°C and is comparable only when river temperatures closely track air temperatures; growing season expressed thus for a New Brunswick river (146 d water temperature > 7°C, Symons 1979) was similar to that given above for Gaspé. Data are unavailable for Region III, although it is expected that the values might be similar to, if not slightly less than, alpine Norway (see below). Growing seasons in Region IV are also influenced by latitudinal effects, with 192 d (water temperature > 7°C) for a Swedish river, 149 d (average; 119–178 d range) for a river in western Norway, and 63 d (averaged; 54–87 d range) for a river in northern Norway (Jensen and Johnsen 1986). Higher growing seasons (expressed in this same form) have been reported for rivers in Region V, with 196, 262, 315, and >330 d for a river in each of Scotland, France, England, and Spain, respectively (Symons 1979; Garcia de Leaniz and Martinez 1988).

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Perhaps a better indicator of growing season, however, is the growth opportunity index (G) which integrates both temperature and daylength with the equation:

$$G = \sum T_i D_i$$

where T_i is mean air temperature $>5.5°C$ and D_i is the hours of daylight in month i (Metcalfe and Thorpe 1990). This index facilitates direct comparison of rivers across latitudes without the need to correct for photoperiod. Indeed, growth opportunity index explained 82.3% of the variance in mean smolt age among 182 rivers throughout the geographical range of Atlantic salmon, whereas latitude alone (a proxy for temperature) accounted for only 6.1% (Metcalfe and Thorpe 1990). The study compared rivers of the eastern Atlantic coast of Canada (Region II; $G = 3–23°C·h·10^3$; $n = 52$) to those in western Europe (Regions IV and V; $G = 7–39°C·h·10^3$; $n = 101$) and those draining into the Baltic and White Seas (Region IV; $G = 10–24°C·h·10^3$; $n = 29$).

Temperature range and length of growing season have obvious implications for salmonids. Low mean temperatures and short growing season result in lowered annual growth rates for rearing juveniles (Jensen and Johnson 1986) and hence higher mean age of smolts (Power 1981). Temperature also influences length of egg incubation period and longer incubation periods in colder rivers may lead to earlier spawning by adult salmon to ensure emergence at optimal times. High summer water temperatures may also approach upper lethal limits for salmon, especially in the southern regions.

The biological environment

Productivity

Most, if not all rivers within the range of Atlantic salmon are best characterized as oligotrophic, with net primary productivity (NPP) data reflecting relatively low annual productivity (Naumann 1932; Ladle and Westlake 1995). A study on the Fort River in Massachusetts yielded an average periphyton NPP of 0.38 g $C·m^{-2}·yr^{-1}$, with a range of 0.003–0.76 g $C·m^{-2}·yr^{-1}$ (Fisher and Carpenter 1976), while periphyton NPP values calculated on salmon rivers in southern Québec show values ranging from 0.3 to 1.0 g $C·m^{-2}·yr^{-1}$ (Naiman 1983). Data for productivity for Iceland and Greenland (Region III) are not available, but accessible information suggests that algal communities thrive in these harsh lotic systems and that primary production is important (Petersen et al. 1995). Perhaps this is related to this region's minimal riparian cover, as gross primary productivity (GPP) is significantly related to percent canopy cover (Lamberti and Steinman 1997). A study in southeastern Finland (Region IV) indicated low productivity, with values ranging from 0.09 to 0.8 g $C·m^{-2}·yr^{-1}$ (Holopainen et al. 1988). NPP data from the Meuse River basin (Region V) were somewhat analogous to the Massachusetts data (Region I) (Scailteur 1982). Even though these data reflect low annual productivity, some environmental factors (e.g., a seasonally variable photoperiod) may account for high productivity during certain periods of the year. In some of the northernmost areas, for example, productivity may be quite high during the summer months when the photoperiod is extended and average

daily water temperatures reach an annual peak. This small "burst" of productivity may be of critical importance to the trophic base supporting juvenile *S. salar*.

In boreal catchments where humic and fulvic materials are leached from peat bogs, DOC concentrations may be as high as 10–45 mg $C·L^{-1}$ (Naiman and Link 1997; Petersen et al. 1995), as opposed to deciduous regions where concentrations are typically <10 mg $C·L^{-1}$ (Webster et al. 1995; Meybeck 1985). Studies of blackwater rivers in the Amazon (e.g., Devol 1984) suggest that primary productivity may be limited by light extinction in these darker, high-DOC waters. Enhanced microbial activity associated with high DOC inputs may also result in increased community respiration in bottom and subsurface sediments (Findlay 1995). Accordingly, salmon eggs incubating in boreal rivers may be at greater risk of oxygen depletion.

In general, productivity rates do not provide clear regional or latitudinal patterns; specific production rates appear to be primarily influenced by individual system parameters. Studies within regions show that production rates generally increase in a downstream direction (e.g., Naiman 1983), but are suspected to decline in large, deep rivers (Dodge 1989). One might expect productivity to be lowest in the northernmost river systems and greatest in the southernmost systems, but the scant data fail to either confirm or refute this trend. While most stream ecosystems exhibit a strong link between primary and secondary productivity, riverine "production" and success of anadromous fish may be more closely linked with factors such as quality of spawning substrate and hydrologic conditions, not to mention the various limitations expressed within the marine portions of the life history of *S. salar*.

Diversity

For these systems, there are very few data related to biological diversity, an important and popular topic. Unfortunately, few, if any, comprehensive surveys have been done on regional diversity trends. O'Connell and Andrews (1996) remarked on the "paucity" of information on benthic macroinvertebrates in Newfoundland river systems and Petersen et al. (1995) noted that "no detailed benthic community studies" had been done on Icelandic and Nordic-alpine rivers. Stout and Vandermeer (1975) reported on the lack of any trend related to species richness of rheophilic insects in mid-latitudinal systems, but data revealing any trends (or lack thereof) across the entire range of *S. salar* remain inaccessible. Furthermore, anthropogenic disturbances have made it difficult to ascertain natural variations in biological diversity.

Riparian zones

Riparian zones serve as vital links between terrestrial and aquatic ecosystems. For the purposes of this paper, the riparian zone is defined as the terrestrial area within which soil and vegetation are influenced by river water on an annual basis (Naiman and Décamps 1990, 1997; Naiman et al. 1998*a*). These zones serve a variety of ecological functions and processes including bank stabilization, control of material movement, regulation of streamside microclimates, fil-

Table 3. Selected major land uses and their impacts on lotic ecosystems.

Major land use	Impact	Location/example
Forestry and agriculture	Increased temperature; erosion; decrease in allochthonous inputs; increase in streamflow; dissolved nutrient concentration is correlated with cultivation and fertilizer application	European forests along Atlantic salmon rivers have been cleared extensively for agriculture since the Middle Ages
Industrialization and regulation	Temperature modification; eutrophication; overall reduction in discharge and sediment delivery	By 1860, 50% of salmon habitat in eastern North America (Region I) has been eliminated by damming and pollution associated with industrialization; another 25% has seen appreciable reductions in fish production capacity
Urban development	Frequency/magnitude of flooding is altered; increase in contaminant inputs; channel morphology is altered leading to simplification and loss of spawning and rearing habitat	>75% of the human population in the U.S.A., Canada and western Europe live in urban areas; urbanization is a major impact in Regions I and V

tration of nutrients, and the provision of allochthonous inputs (e.g., leaves, needles, and coarse wood). Along Atlantic salmon rivers, riparian vegetation reflects primarily the disturbance-oriented nature of the active channel and the floodplain and secondarily local forest vegetation. Species occurrence and relative abundance in many of the riparian zones depend primarily on life history characteristics of individual tree species (e.g., tolerance to inundation, capacity of damaged trees to regenerate, branch flexibility, root form, leaf form, season of productivity, duration of seed germinability) and the physical habitat conditions of the flood plain (soil condition, soil type, temperature, flood duration, season, current velocity, and flood force; Ellenberg 1982; Dister 1983; Krause 1985; Naiman and Décamps 1997). *Salix* (willow), *Alnus* (alder), *Betula* (birch), *Populus* (cottonwood, aspen, and other poplars), *Fraxinus* (ash), and *Fagus* (beech) represent typical riparian tree genera, many of which exhibit life history strategies (e.g., flexible stems, asexual reproduction) which allow them to persist in areas of varying disturbance. All regions maintain riparian tree cover with populations of many of the above species, except Region III (Iceland and Greenland), which is composed primarily of low growing woody shrubs and grasses.

A number of other generalities can be drawn regarding Atlantic salmon river riparian zones. The surrounding forests range from coniferous to broad-leaved deciduous forest. In general, the proportion of coniferous species increases as one moves north in latitude. This has implications for food webs given the differential in litter and woody debris decomposition rates and in detrital food quality between deciduous and coniferous stands. Organic matter from deciduous trees is generally more labile than coniferous-based detritus (Melillo et al. 1983; Webster et al. 1987). Accordingly, coniferous species, at least within the range of *S. salar*, are generally more decay resistant than deciduous members. As such, coniferous species may represent a more refractory source of organic matter but a more stable source of structurally important large woody debris (LWD).

Much of the natural riparian component of Atlantic salmon river systems has been altered considerably by human activities. Shifts in relative abundance of certain size-classes and species of riparian trees may have long-term implications for the structure and function of Atlantic salmon

rivers. For instance, riparian systems which have been altered may be heavily represented by early-successional species which are typically a less important source of LWD.

Land use and impacts

Many Atlantic salmon rivers have received extensive anthropogenic modifications (Dynesius and Nilsson 1994). The catchments of western Europe and New England are heavily populated and have been affected by a range of stresses associated with agriculture, industrialization, and urbanization. Land use practices have resulted in increasingly rapid and long-lasting changes in channel morphology, hydrology, and water quality (Table 3). Although there are significant differences in climatic, physiographic, and ecological conditions among different regions, certain patterns of anthropogenic disturbance (e.g., forest clearing, urbanization, river regulation, etc.) are ubiquitous.

Forestry and agriculture. Forest clearing has been widespread throughout western Europe and eastern North America, to the extent that few Atlantic salmon rivers drain catchments with intact natural or late-successional forests. European forests have been cleared extensively for agriculture and timber since the Middle Ages and approximately 1×10^5 km^2 were cleared in northeastern North America by 1776 (Williams 1990). Between 1860 and 1978, an additional (estimated) 1.6×10^6 km^2 were converted to regular cropping in North America and 2.2×10^5 km^2 were converted in Europe (Richards 1990). Conversion of forest to cropland decreases vegetative cover and reduces infiltrative capacities, particularly where fields are tilled in fall and left bare throughout the winter and early spring months during peak flow season (Miller 1990). Associated increases in surface runoff entail increased stormflow peaks and decreased baseflow, as well as increases in temperature, siltation, and nutrient flux (Bormann et al. 1969; Likens et al. 1970; Likens 1984). Export of dissolved nutrients is correlated with area under cultivation and rates of fertilizer application (Hill 1978; Miller et al. 1982; Neilsen et al. 1982). Pesticides typically occur in agricultural streams during spray season, but some compounds are persistent enough in soils to leach continually throughout the year (Frank et al. 1982).

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Surface runoff represents the most important pathway for agricultural pollutant inputs (Frank et al. 1982; Miller et al. 1982) and effects are therefore likely to be greatest in areas where clay soils or thin soils overlay rocky terrain.

Industrialization and hydroelectric power. With factories, mills, and foundries typically built near flowing water, salmon rivers of Europe and North America have been further impacted by industrialization. Industrial production and power generation have resulted in point and nonpoint source pollution and extensive damming and diversion of rivers. Rivers of western Europe and Scandinavia have been dammed for centuries (Ladle and Westlake 1995; Petersen et al. 1995), to the extent that, as early as the 17th and 18th centuries, legislation such as the French Bearnais statute (1662) and the edicts of Spain's Carlos IV (1790s) were deemed necessary to protect migratory passage for salmon (Netboy 1968). The scale of European river modification increased significantly with the Industrial Revolution (Allan 1995) and dam-building technologies were then transported to North America. By 1850, an estimated 50% of salmon habitat in eastern North America was eliminated by damming and pollution associated with agriculture and industry, with an additional 25% being appreciably reduced in production capacity for salmon (Legget 1975). Today there are more regulated rivers than naturally flowing ones in the United States (Benke 1990; Hydrodata 1995; Naiman et al. 1998*b*. Similarly, the majority of watercourses in western Europe (Region V) and Scandinavia (Region IV) are regulated (Petts 1984; Petersen et al. 1995).

The effects of major impoundments include overall reductions in discharge and sediment delivery downstream, as well as dampening of temperature and flow variability (Ward and Stanford 1979; Richards 1992; Allan 1995). Specific impacts will vary according to the location, size, and nature of the reservoir (e.g., hypolimnetic vs. epilimnetic), as well the natural hydrologic regime and sedimentology of

the river. Effects may be felt many kilometres downstream from dams (Webster et al. 1995).

Urban development. Urbanization has resulted in massive changes in the physical landscapes and hydrologic regimes of western Europe and North America. The removal of natural vegetative cover in favor of impervious surfaces, the installation of storm sewer systems, and the channelization of streams entail a more severe manifestation of the hydrologic symptoms of forest clearing. Accordingly, frequency and magnitude of flooding in urban streams increase with percent catchment imperviousness (Leopold 1968; Klein 1979). Hydrologic effects are compounded by contaminant inputs from urban runoff and sewer outfalls, which contain a complex mixture of conventional, metal, and organic contaminants (Marsalek 1986, 1990). In the United States, Canada, and most of the western European nations, greater than 75% of the population lives in urban areas (Berry 1990). As trends toward increased urbanization and suburban sprawl continue, salmon rivers will be increasingly impacted.

Within the natural range of Atlantic salmon, only the most northern rivers have been relatively unaffected by forestry, agricultural, industrial, and urban development. However, these rivers may be particularly susceptible to effects of climate change (Minns et al. 1992) and long range transport of atmospheric pollutants (Wania and Mackay 1993).

Case studies

The following case studies are provided as illustrations of typical systems within the natural range of *S. salar*. These rivers are certainly not representative of all rivers within each region and may not be the most important. They were, however, selected to show real examples of salmon-bearing systems within three of the regions reviewed in this article.

The River North Esk, England

While there is considerable variation among the rivers of western Europe (Region IV), it is useful to select examples which provide contrast to rivers of other regions. The River North Esk is a small river system which arises in Invermark Forest in northeast Scotland and flows eastward about 50 km to enter the North Sea between Aberdeen and Dundee. Despite its small size, it is one of Scotland's major salmon rivers and, indeed, has been a site for extensive research into natural history and stock dynamics (Shearer 1992).

The River North Esk and its 75 total tributaries drain 732 km^2 with an elevation drop of 750 m. Average flow is 13 m$^3 \cdot$s^{-1} with a range of 2–280 m$^3 \cdot$s^{-1}; peak flows occur in December with low flows in July (Ward 1981). Lining the riverbanks of the upper reaches are scattered patches of birch (*Betula pendula*) and alder (*Alnus glutinosa*) which give way to beech (*Fagus sylvatica*) in the middle reaches. The lower third of the river is largely agricultural.

During the years 1985 and 1986, water temperature in the river ranged from 2 to 16°C ($\bar{x} = 7.7$°C) while pH ranged from 6.9 to 8.8 ($\bar{x}= 7.65$). Two year ranges and means (reported in parentheses) for other water quality parameters were 87.2–123.0% (99.7) for dissolved oxygen (DO), 0.0–4.8 mg O$_2 \cdot$L^{-1} (2.2) for

biological oxygen demand (BOD) and 0–11 mg O$_2 \cdot$L^{-1} (4.0) for suspended solids. Ranges for nitrogen concentrations were 0–0.11 mg N$\cdot$L^{-1} (0.03) for ammonia and 0.75–3.78 mg N$\cdot$L^{-1} (1.97) for total oxidized forms (i.e., NO$_3$ and NO$_2$; Shearer 1992).

Agriculture and water withdrawal are the primary human impacts on the catchment. Silage effluent and pesticide discharge from extensive agriculture in the lower reaches occasionally causes fish kills and soil erosion resulting from land uses occasionally deposit layers of silt over gravel. Water is abstracted in the upper reaches at Loch Lee, which has been converted to a reservoir, as well as pumped from along the length of the river for irrigation. Industry on the river is slight (two distilleries) and there has been little forestry development.

Rivers in Scotland typically have yielded more Atlantic salmon than elsewhere in Great Britain (Netboy 1980). The River North Esk itself is the most productive on the east coast (catch per kilometre), a fact attributed to the high availability of spawning gravel in the mainstream and tributaries (Shearer 1992). High water quality and lack of substantial human impact relative to other rivers in Region V may also be important. As long as agriculture remains the primary human impact, water quality monitoring and bank erosion control may be the most effective management strategies in the catchment.

Rickleån River, Sweden

Located roughly 80 km north of the town of Umeå, Sweden, the Rickleån River flows into the Gulf of Bothnia. This medium-sized river has an average discharge of 16 $m^3 \cdot s^{-1}$ (range of 3–180 $m^3 \cdot s^{-1}$) and flows within a boreal forest zone (as defined by Sjörs 1963) dominated by spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The primary floodplain tree species are typical of other Atlantic salmon rivers, including alder (*Alnus incana*), birch (*Betula pubescens*), and willow (*Salix* spp.).

With a PO_4–P range of 1–12 $\mu g \cdot L$ and a NO_3–N range of 0–0.03 $\mu g \cdot L$, the Rickleån is best described as oligotrophic (Karlström 1976; R.C. Petersen, Jr., unpublished data). Rickleån pH ranges between 6.0 and 7.0 (Göthberg and Karlström 1975). Water in the Rickleån is clear and flows over a granite/gneiss crystalline rock substrate. This river maintains a 0.3% gradient, considered quite steep (Södergren 1974). Several rivers within the vicinity of the Rickleån are also quite steep and many, including the Rickleån, have been regulated, both factors contributing to the region's "Staircase of Power" nickname.

As a result of the steep gradient, the river has little floodplain and minimal sinuousity (Ulfstrand 1968). Turbulent, abrasive currents seem to be cause for high organic matter decomposition rates (0.83–0.95% d^{-1}). R.C. Petersen, Jr. (unpublished data) measured gross primary production in the Rickleån as approximately 98 mg $C \cdot m^{-2} \cdot d^{-1}$ in August and approximately 87 mg $C \cdot^{-2} \cdot d^{-1}$ in September, generally considered low.

Anthropogenic disturbance plays an important role in Rickleån ecology. The river itself consists of three tributaries emptying into a lake, the Bygdeträsket, regulated by a dam. From there, the Rickleån proper flows to the sea, with five power stations along its course. In addition to being regulated, this system suffers from heavy metal pollution in its lower reaches (Södergren 1974). Nonanadromous brown trout (*Salmo trutta*) and anadromous *S. salar* dominate the fish community.

The Rickleån provides an example of the factors which often dictate success in anadromous salmonids. The system does not exhibit high primary productivity but does consistently provide desirable spawning substrates, moderate flows, and clear, oxygen-rich water. While regulation has compromised unabated access, the river continues to summon the annual return of *S. salar*.

Moisie River, Québec

The biophysical characteristics of the Moisie River, Québec, have been well documented (Naiman 1982, 1983; Naiman et al. 1987; Naiman and Link 1997). The Moisie River empties into the north shore of the Gulf of St. Lawrence, draining a catchment of 19 871 km^2. This subarctic, precambrian Shield region is forested with typical boreal species: black and white spruce (*Picea mariana, P. glauca*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), speckled alder (*Alnus rugosa*), and willow (*Salix* spp.). The area receives approximately 1.2 m of precipitation annually, which is evenly distributed throughout the year and occurs primarily as snow from October through April. Mean annual air temperature is 1°C and growing season (mean daily temperature > 5.6°C) is 105 d. The Moisie is a relatively pristine river, as less than 1% of catchment area has been subjected to anthropogenic disturbance.

Mean annual discharge on the main stem of the Moisie (stream order 9) is 466.1 $m^3 \cdot s^{-1}$ and the gradient is 0.16%. High flows representing 50% of annual discharge occur during April and May freshets, whereas January and February flow volumes represent only 3–5% of annual maxima. Water temperatures range from 0.1 to 21.8°C and substrate is primarily sand and cobble. Alkalinity ranges from 0.0 to 17.0 mg·L^{-1} as $CaCO_3$ and pH values range from 6.3 to 7.1. Streams in this area have relatively low concentrations of NO_3–N (20–43 g·L^{-1}) and phosphorus (11–29 g·L^{-1}) and relatively high concentrations of DOC (10–15 mg $C \cdot L^{-1}$).

Naiman et al. (1987) reported significant trends with stream order for organic carbon dynamics, as related to changes in physical gradients, channel dimensions, hydrology, and riparian influences. As stream order increased, total C inputs (i.e., precipitation, throughfall, primary production, and allochthonous matertials) decreased, followed by a gradual increase due to greater primary production in streams >6th order.

Standing stock of C decreased exponentially downstream and total C outputs (i.e., respiration, leaching, methane evasion, and insect emergence) increased slightly. Most organic C was stored in 1st–3rd order streams, whereas the majority of C was metabolized in 7–9th order rivers. Percentage transmission of PAR to benthic substrates are significantly correlated with stream order, due to the fact that shading decreases, yet mean depth remains constant (<2 m) (Naiman and Link 1997). The majority of organic matter inputs result from autotrophic production, although fluvial transport of organic C to the Gulf of St. Lawrence was nearly three times that of total annual inputs, demonstrating that groundwater inputs of DOC are exceedingly important (Naiman et al. 1987).

Concluding remarks

The preceding case studies describe typical Atlantic salmon rivers in three of the five regions discussed in this paper. With the possible exception of the Moisie, these studies analyze rivers which have experienced marked declines in natural salmon production. Still, even the Rickleån, with a reportedly meager run of salmon and a series of dams, continues to provide some of the necessary ecological parameters which beckon the return of the fish. This paper has addressed some of the biophysical factors which provide the template upon which *S. salar* relies.

We have addressed patterns in biophysical influences on river systems within each of five regions. Among the various influences, biotic processes, such as primary production, may explain some regional variation in salmon abundance and success. However, success in anadromy and riverine "production" of anadromous salmonids is also reliant on factors such as discharge, substrate, and temperature regimes. A fundamental understanding of the natural variation of riverine conditions is necessary for the development of a restoration strategy guided toward life history and evolutionary strategies of *S. salar*; the most effective strategies will be those that consider the unique behavioral and physiological adaptations of local salmon populations.

Salmo salar has evolved to river conditions over a period best measured in tens of thousands of years. Over a relatively short time, anthropogenic disturbances have altered

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many of the biological and physical conditions upon which Atlantic salmon adaptations have been based. Monitoring riverine conditions against a background of a highly variable biophysical environment remains a major challenge for managers and researchers alike — one that must be resolved on a broad spatial scale if the long-term integrity of Atlantic salmon rivers is to be maintained.

The ecological consequences of regional differences in catchment characteristics, as well as latitudinal gradients in discharge patterns and temperature, have important implications for the management, restoration, and conservation of Atlantic salmon rivers. The North Atlantic Ocean (and its adjacent seas) is a heterogeneous region with substantial biophysical variability both within and among catchments. Management philosophies and restoration and conservation strategies embracing this natural variation will be the most successful in the long term.

References

Allan, J.D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, New York, N.Y.

Anderson, T.C. 1985. The rivers of Labrador. Can. Spec. Publ. Fish. Aquat. Sci. 81.

Benke, A.C. 1990. A perspective on America's vanishing streams. J. N. Am. Benth. Soc. **9**: 77–88.

Berry, B.J.L. 1990. Urbanization. *In* The Earth as transformed by human action. *Edited by* B.L. Turner II, W.C. Clark, R.W. Kates, J.F. Richards, J.T. Mathews, and W.B. Meyer. Cambridge University Press, Cambridge, Mass. pp. 103–119.

Billen, G., Décamps, H., Garnier, J., Boet, P., Meybeck, M., and Servais, P. 1995. Atlantic river systems of Europe (France, Belgium, The Netherlands). *In* Ecosystems of the world 22: river and stream ecosystems. *Edited by* C.E. Cushing, K.W. Cummins, and G.W. Minshall. Elsevier, Amsterdam. pp. 389–418.

Bormann, F.H., Likens, G.E., and Eaton, J.S. 1969. Biotic regulation of particulate and solution losses from a forest ecosystem. BioScience, **19**: 600–610.

Chadwick, E.M.P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Can. J. Fish. Aquat. Sci. **39**: 1496–1501.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Can J. Fish. Aquat. Sci. **53**(Suppl. 1): 267–282.

Davidson, W.S., Birt, T.P., and Green, J.M. 1989. A review of genetic variation in Atlantic salmon, *Salmo salar* L., and its importance for stock identification, enhancement programmes and aquaculture. J. Fish. Biol. **34**: 547–560.

Décamps, H., and Naiman, R.J. 1989. L'ecologie des fleuves. La Recherche, **20**: 310–319.

Descy, J.P., and Empain, A. 1984. Meuse. *In* Ecology of European rivers. *Edited by* B.A. Whitton. Blackwell Scientific Publications, Oxford, England. pp. 1–23.

Devol, A.H. 1984. Nutrient addition experiments in Lago Jacaretinga, Central Amazon, Brazil: 2. The effect of humic and fulvic acids. Hydrobiologia, **109**: 97–103.

Dister, E. 1983. Zur Hochwassertoleranz von Auenwaldbäumen an lehmigen Standorten. Verh. Ges. Okol. **10**: 325–336.

Dodge, D.P. (*Editor*). 1989. Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Dynesius, M., and Nilsson, C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. Science (Washington, D.C.), **266**: 753–762.

Einarsson, T. 1968. Jardfrcdi. Saga Bergs og Lands. Heimskringla, Reykjavik, Iceland.

Ellenberg, H. 1982. Vegetation Mitteleuropas mit den Alpen (3rd Edition). Ulmer, Stuttgart, Germany.

Elliott, J.M. 1984. Numerical changes and population regulations in young migrating trout, *Salmo trutta*, in a lake district stream. J. Anim. Ecol. **53**: 979–994.

Findlay, S. 1995. Importance of surface-subsurface exchange in stream ecosystems: the hyporheic zone. Limnol. Oceanogr. **40**: 159–164.

Fisher, S.G., and Carpenter, S.R. 1976. Ecosystem and macrophyte primary production of the Fort River, Massachusetts. Hydrobiologia, **49**(2): 175–187.

Frank, R., Braun, H.E., Van Hove Holdrinet, M., Sirons, G.J., and Ripley, B.D. 1982. Agriculture and water quality in the Canadian Great Lakes basin: V. Pesticide use in 11 agricultural watersheds and presence in stream water, 1975–1977. J. Environ. Qual. **11**: 497–505.

Garcia de Leaniz, C., and Martinez, J.J. 1988. The Atlantic salmon in the rivers of Spain with particular reference to Cantabria. *In* Atlantic salmon: planning for the future. Proceedings of the Third International Atlantic Salmon Symposium, Biarritz, France, October 21–23, 1986. *Edited by* D. Mills and D. Piggins. Timber Press, Portland, Oreg. pp. 179–209.

Geographical Services Division. 1985. Canada Temperature — January and July. National Atlas of Canada. 5th ed. Surveys and Mapping Branch, Energy, Mines, and Resources, Canada. Ottawa, Ont.

Gibson, R.J., and Myers, R.A. 1988. Influence of seasonal river discharge on survival of juvenile Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. **45**: 344–348.

Göthberg, A., and Karlström, U. 1975. Ecological research in running waters in northern Sweden. Rapport från Rickleå Fältstation, University of Umeå, Stockholm, Sweden. No. 64.

Hill, A.R. 1978. Factors affecting the export of nitrate-nitrogen from drainage basins in southern Ontario. Water Res. **12**: 1045–1057.

Holopainen, A.L., Hovi, A., and Roenkkoe, J. 1988. Lotic algal communities and their metabolism in small forest brooks in the Nurmes area of eastern Finland. Aquat. Fenn. **18**: 29–46.

Hulbert, P.J. 1978. Biological and physical factors bearing on restoration of Atlantic salmon in Mattawamkeag River, Penobscot River system, Maine. Mattawamkeag River Studies. University of Maine Migratory Fish Res. Inst. and Maine Coop. Fish. Res. Unit, Orono, Maine.

Hvidsten, N.A. 1993. High winter discharge after regulation increases production of Atlantic salmon (*Salmo salar*) smolts in the River Orkla, Norway. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci. 118. pp. 175–177.

Hydrodata. 1995. USGS Daily Values. West 2. Hydrosphere, Inc. and U.S. Geological Survey, Boulder, Col.

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

Karlström, U. 1976. Effects of nitrogen fertilization on the decomposition rate of organic materials in running waters. Vatten, **3**: 76.

Klein, R.D. 1979. Urbanization and stream quality impairment. Water Res. Bull. **15**: 948–963.

Krause, A. 1985. Bewuchs an Wasserläufen. Auswertungs- und Informationdienst für Ernährung, Landwirtschaft und Forsten, Bonn.

Kuz'min, O.G., and Smirnov, Y.A. 1982. Environmental factors and growth of young Atlantic salmon, *Salmo salar* (Salmonidae), in small rivers of the Kola Peninsula. J. Ichthyol. **22**: 42–51.

Ladle, M., and Westlake, D.F. 1995. Rivers and stream ecosystems of Great Britain. *In* Ecosystems of the world 22: river and stream ecosystems. *Edited by* C.E. Cushing, K.W. Cummins, and G.W. Minshall. Elsevier, New York, N.Y. pp. 343–388.

Lamberti, G.A., and Steinman, A.D. 1997. A comparison of primary production in streams. *In* Stream organic matter budgets. *Edited by* J.R. Webster and J.L. Meyer. J. N. Am. Benth. Soc. **16**(1): 95–104.

Legget, R. 1975. Ottawa waterway. University of Toronto Press, Toronto, Ont.

Leopold, L.B. 1968. Hydrology for urban land use planning: a guidebook on the hydrologic effects of urban land use. USGS Circular 554, Washington, D.C.

Likens, G.E. 1984. Beyond the shoreline: A watershed-ecosystem approach. Verh. Int. Verein. Limnol. **22**: 1–22.

Likens, G.E., Bormann, F.H., Johnson, N.M., Pierce, R.S., Fisher, D.W., and Reiners, W.A. 1970. The effect of forest cutting and herbicide treatment on nutrient budgets at Hubbard Brook watershed-ecosystem. Ecol. Monogr. **40**: 23–37.

Likens, G.E., Bormann, F.H., Pierce, R.S., Eaton, J.S., and Johnson, N.M. 1977. Biogeochemistry of a forested ecosystem. Springer, New York, N.Y.

MacCrimmon, H.R., and Gots, B.L. 1979. World distribution of Atlantic salmon, *Salmo salar*. J. Fish. Res. Board Can. **36**: 422–457.

Mackay, R.J. 1995. River and stream ecosystems of Canada. *In* Ecosystems of the world 22: river and stream ecosystems. *Edited by* C.E. Cushing, K.W. Cummins, and G.W. Minshall. Elsevier, Amsterdam. pp. 33–60.

Marsalek, J. 1986. Toxic contaminants in urban runoff: A case study. *In* Urban runoff pollution. NATO ASI Series G. Vol. 10. *Edited by* H.C. Torno et al. Springer-Verlag, New York, N.Y. pp. 39–57.

Marsalek, J. 1990. Evaluation of pollutant loads from urban non-point sources. Water Sci. Technol. **22**: 23–30.

Melillo, J.M., Naiman, R.J., Aber, J.D., and Eshlemann, K.N. 1983. The influence of substrate quality and stream size on wood decomposition dynamics. Oecologia, **62**: 150–155.

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

Meybeck, M. 1985. Composition chemique naturelle des ruisseaux non pollues en France. Sci. Geol. Bull. **39**: 3–77.

Miller, G.T., Jr. 1990. Living in the Environment: An Introduction to Environmental Science, Sixth Edition. Wadsworth Publishing Company, Belmont, Calif.

Miller, M.H., Robinson, J.B., Coote, D.R., Spires, A.C., and Draper, D.W. 1982. Agriculture and water quality in the Canadian Great Lakes basin: III. Phosphorus. J. Environ. Qual. **11**: 487–493.

Minns, C.K., Randall, R.G., Chadwick, E.M.P., Moore, J.E., and Green, R. 1992. Potential impact of climate change on the habitat and population dynamics of juvenile Atlantic salmon (*Salmo salar*) in eastern Canada. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat.Sci. 121. pp. 699–708.

Møller, D. 1970. Transferrin polymorphism in Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. **27**: 1617–1625.

Morin, R., and Naiman, R.J. 1990. The relation of stream order to fish community dynamics in boreal forest watersheds. Pol. Arch. Hydrobiol. **37**: 135–150.

Naiman, R.J. 1982. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Can. J. Fish. Aquat. Sci. **39**: 1699–1718.

Naiman, R.J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecol. Monogr. **53**: 73–94.

Naiman, R.J., and Bilby, R.E. (*Editors*). 1998. The ecology and management of rivers and streams: lessons from the Pacific Northwest Coastal Ecoregion. Springer-Verlag, New York, N.Y.

Naiman, R.J., and Décamps, H. (*Editors*). 1990. The ecology and management of aquatic–terrestrial ecotones. UNESCO, Paris and Parthenon Publishing Group, Carnforth.

Naiman, R.J., and Décamps, H. 1997. The ecology of interfaces — riparian zones. Ann. Rev. Ecol. Syst. **28**: 621–658.

Naiman, R.J., and Link, G.L. 1997. Organic matter dynamics in five subarctic streams, Québec, Canada. J. N. Am. Bethol. Soc. **16**: 33–39.

Naiman, R.J., Melillo, J.M., Lock, M.A., Ford, T.E., and Reice, S.R. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology, **68**: 1139–1156.

Naiman, R.J., Fetherston, K.L., McKay, S.J., and Chen, J. 1998*a*. Riparian Forests. *In* The ecology and management of rivers and streams: lessons from the Pacific Northwest Coastal Ecoregion. *Edited by* R.J. Naiman and R.E. Bilby. Springer-Verlag, New York. pp. 289–323.

Naiman, R.J., Magnuson, J.J. and Firth, P.L. 1998*b*. Integrating cultural, economic, and environmental requirements for fresh water. Ecol. Applic. (In press).

National Geographic Society. 1992. National Geographic atlas of the world. Rev. 6th ed. National Geographic Society, Washington, D.C.

Naumann, E. 1932. Grundzüge der regionalen Limnologie. Die Binnengewässer, Vol. 11. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Neilsen, G.H., Culley, J.L.B., and Cameron, D.R. 1982. Agriculture and water quality in the Canadian Great Lakes basin: IV. Nitrogen. J. Environ. Qual. **11**: 493–497.

Nepisiguit Salmon Association (NSA). 1995. Salmon enhancement on the Nepisiguit River: a cooperative approach. Nepisiguit Salmon Association, Bathurst, N.B.

Netboy, A. 1968. The Atlantic salmon: a vanishing species? Houghton Mifflin Company, Boston, Mass.

Netboy, A. 1973. The salmon: their fight for survival. Houghton-Mifflin Co., Boston, Mass.

Netboy, A. 1980. Salmon: the world's most harrassed fish. Winchester Press, Tulsa, Okla.

Newson, M.D. 1981. Mountain streams. *In* British rivers. *Edited by* J. Lewin. George Allen and Unwin, London. pp. 59–89.

O'Connell, M.F., and Andrews, C.W. 1996. A survey of benthic macroinvertebrates in rivers in Placentia Bay, Newfoundland. Can. Manuscr. Rep. Fish. Aquat. Sci. 2344.

Paolillo, S.A.C. 1969. Hydrogeology of the River Frome catchment (southern England). Mem. Note Inst. Geol. Apl., Napoli. **11**: 1–69.

Petersen, R.C., Jr., G.M. Gislason, and L.B.-M. Petersen. 1995. Rivers of the nordic countries. *In* River and stream ecosystems, ecosystems of the world. Vol. 22. *Edited by* C.E. Cushing, K.W. Cummins, and G.W. Minshall. Elsvier, Amsterdam. pp. 295–341.

Petts, G.E. 1984. Impounded rivers: perspectives for ecological management. Wiley-Interscience, Chichester, U.K.

Power, G. 1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Québec, and Newfoundland and Labra-

dor in relation to environmental barriers. Can. J. Fish. Aquat. Sci. **38**: 1601–1611.

Prowse, T.D. 1994. Environmental significance of ice to streamflow in cold regions. Freshwater Biol. **32**: 241–259.

Richards, J.F. 1990. Land transformation. *In* The earth as transformed by human action. *Edited by* B.L. Turner II, W.C. Clark, R.W. Kates, J.F. Richards, J.T. Mathews, and W.B. Meyer. Cambridge University Press, Cambridge. pp. 163–178.

Richards, K. 1992. Rivers: form and process in alluvial channels. Methuen, London, England.

Riddell, B.E., and Leggett, W.C. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **38**: 308–320.

Rist, S. 1956. Icelandic fresh waters. Hydrological Survey State Electricity Authority, Reykjavik.

Sabater, F., Guasch, H., Marti, E., Armengol, J., and Sabater, S. 1995. The Ter: a Mediterranean river case-study in Spain. *In* Ecosystems of the world 22: river and stream ecosystems. *Edited by* C.E. Cushing, K.W. Cummins, and G.W. Minshall. Elsevier, Amsterdam. pp. 419–438.

Scailteur, Y. 1982. Etude du mêtabolisme dún ecosystême lotique. Thesis. Université Libre de Bruxelles, Faculté des Sciences, Bruxelles.

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

Scrimgeour, G.J., Prowse, T.D., Culp, J.M., and Chambers, P.A. 1994. Ecological effects of river ice break-up: a review and perspective. Freshwater Biol. **32**: 261–275.

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

Sjörs, H. 1963. Amphi-Atlantic zonation. Nemoral to Arctic. *In* North Atlantic biota and their history. *Edited by* A. Löve and D. Löve. Permagon Press, Oxford, England. pp. 109–125.

Södergren, S. 1974. Ecological effects of heavy metal discharge in a salmon river. Ph.D. thesis. Department of Ecological Zoology, University of Umeå, Umeå, Sweden.

Solomon, D.J., and Paterson, D. 1980. Influence of natural and regulated stream flow on survival of brown trout (*Salmo trutta* L.) in a chalkstream. Environ. Biol. Fishes. **5**: 379–382.

Stähl, G. 1987. Genetic population structure of Atlantic salmon. *In* Population genetics and fishery management. *Edited by* N. Ryman and F. Utter. University of Washington Press, Seattle, Wash. pp. 121–140.

Stout, J., and Vandermeer, J. 1975. Comparison of species richness for stream-inhabiting insects in tropical and mid-latitudinal streams. Am. Nat. **109**: 263–280.

Strahler, A.N. 1975. Physical geography. Wiley, New York, N.Y.

Sutton, J.S. 1972. Notes on the geology of Labrador. Mem. Univ. Nfld. Geol. Rep. Vol. 5.

Symons, P.E.K. 1979. Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity. J. Fish. Res. Board Can. **36**: 32–140.

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

Thurman, E.M. 1985. Organic geochemistry of natural waters. Martinus Nijhoff/W. Junk, Dodrecht.

Ulfstrand, S. 1968. Benthic animal communities in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, and Diptera Simuliidae). Oikos, Suppl. **10**: 1–120.

UNESCO. 1978. World water balance and water resources of the earth. Stud. Rep. Hydrol. 25.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**: 130–137.

Ventura, J.A.M. 1988. The Atlantic salmon in Asturias, Spain: Analysis of catches: 1985–1986. Inventory of juvenile densities. *In* Atlantic salmon: planning for the future. Proceedings of the Third International Atlantic Salmon Symposium, Biarritz, France, October 21–23, 1986. *Edited by* D. Mills and D. Piggins. Timber Press, Portland, Oreg. pp. 210–227.

Walling, D.E., and Webb, B.W. 1981. Water quality. *In* British Rivers. *Edited by* J. Lewin. George Allen and Unwin, London. pp. 126–169.

Wania, F., and Mackay, D. 1993. Global fractionation and cold condensation of low volatility organochlorine compounds in polar regions. Ambio, **22**: 10–18.

Ward, J.V. 1981. River systems and river regimes. *In* British rivers. *Edited by* J. Lewin. G. Allen and Unwin, London. pp. 1–33.

Ward, J.V., and Stanford, J.A. 1979. The ecology of regulated streams. Plenum Press, New York, N.Y.

Ward, R.C. 1981. River systems and river regimes. *In* British rivers. *Edited by* J. Lewin. George Allen and Unwin, London. pp. 1–33.

Webster, J.R., Benfield, E.F., Golladay, S.W., Hill, B.H., Hornick, L.E., Kazmierczak, R.F., and Perry, W.B. 1987. Experimental studies of physical factors affecting seston transport in streams. Limnol. Oceanogr. **32**(4): 848–863.

Webster, J.R., Wallace, J.B., and Benfield, E.F. 1995. Organic processes in streams of the eastern United States. *In* Ecosystems of the world 22: river and stream ecosystems. *Edited by* C.E. Cushing, K.W. Cummins, and G.W. Minshall. Elsevier, Amsterdam. pp. 117–187.

Williams, M. 1990. Forests. *In* The earth as transformed by human action. *Edited by* B.L. Turner II, W.C. Clark, R.W. Kates, J.F. Richards, J.T. Mathews, and W.B. Meyer. Cambridge University Press, Cambridge, U.K. pp. 179–201.

Williamson, H. 1935. Salar the salmon. David R. Godine, Publisher, Inc., Boston, Mass.