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Variation in the timing of river entry of Atlantic salmon (*Salmo salar* L.) in the Baltic

Anna KUPARINEN[*], Juha MERILÄ

Department of Biological and Environmental Sciences, P. O. Box 65, FI-00014 University of Helsinki, Finland

Abstract The timing of river entry in the Atlantic salmon is known to depend on genetic, demographic and environmental factors, but little is known about the relative magnitude of among population and among year variation and covariation in this respect in natural state Atlantic salmon rives. To investigate this, variability in the timing of river entry in three historical Finnish Atlantic salmon populations were analyzed using salmon trap data collected during 1870 - 1902. The analyses reveled that 1) the timing of river entry differed substantially and consistently among the rivers, and that 2) variation among the rivers was much larger than variation among years. Annual variations were not explained by regional environmental conditions, whereas in one river the timing of the local flood peak was a significant predictor of the timing of river entry. Differences in the timing of salmon entry to geographically closely situated rivers suggests that a regionally fixed opening date for coastal fisheries might not be the best management strategy as it may lead to uneven exploitation of salmon populations from different rivers [*Current Zoology* 55 (5): 342 - 349, 2009].

Key words Atlantic salmon, Coastal fisheries, Fisheries management, Freshwater entry, Migration, River entry

The Atlantic salmon (*Salmo salar* L.) is an economically important anadromous fish distributed from southern Europe to arctic waters and North America (World Wildlife Fund, 2001; Hindar et al., 2007). Largely due to overfishing, Atlantic salmon populations have been seriously declining worldwide during the 20th century, and this trend is particularly pronounced in the Baltic Sea area (Karlsson and Karlström, 1994; World Wildlife Fund, 2001). One of the critical factors affecting viability of Atlantic salmon populations relates to the success of annual spawning migrations. Therefore, the challenge for coastal fisheries management is to ensure that sufficient number of spawners escape fisheries, which, in turn, requires detailed information about the timing of river entry of migrating salmon (e. g. Karlsson and Karlström, 1994; Jokikokko et al., 2004; Finstad et al., 2005).

Several anadromous iteroparous salmonids, including Atlantic salmon, enter freshwater in spring- or summertime, months before the actual spawning which takes place in autumn or early winter (e. g. Jonsson, 1991). The timing of river entry (later referred also as run timing) is known to vary both between populations and years. In general, as demonstrated by several mark-recapture experiments individual populations are genetically adapted to a run timing that is optimal for their local environments (Hansen and Jonsson, 1991; Smoker et al., 1998; Quinn et al., 2000, Stewart et al., 2002; Jonsson et al., 2007). Environmental conditions then induce annual variations around these population-specific average times, though demographic fluctuations may also play a role. For example in Atlantic salmon one sea-winter (1SW) salmon enter freshwater later than multi sea-winter (MSW) salmon (Fleming, 1996; Stewart et al., 2002; Jokikokko et al., 2004), so that the overall migration pattern may be postponed by a large proportion of 1SW salmon in the spawning stock.

Timing of spring/summertime flooding is an important environmental variable stimulating and even regulating river entry of migrating salmonids. Large discharge aids salmon to locate their natal rivers through olfactory cues (Jonsson, 1991) and shallow upstream spawning areas are better accessible during high water levels (e. g. Økland et al., 2001). In Atlantic salmon, flooding has been observed to stimulate river entry in several river systems (Erkinaro et al., 1999; Jonsson and Jonsson, 2002; Jonsson et al., 2007; Thorstad et al. 2008). It has also been further suggested that this effect is largest in rivers in which flow constrains migration (Lilja and Romakkaniemi, 2003; Tetzlaff et al., 2005; Jonsson et al., 2007). Also sea surface (SST) and river temperatures have been found to be correlated with the timing of river entry in salmonids (Karlsson and Karlström, 1994; Hodgson and Quinn, 2002; Jonsson and Jonsson, 2002; Dahl et al., 2004; Hodgson et al., 2006), but the temperature effect is typically only of secondary importance, playing a role in rivers with little seasonal variation in flow (Jonsson, 1991; Dahl et al., 2004).

Even though the timing and factors affecting

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[*] Corresponding author. E-mail: anna.kuparinen@helsinki.fi

salmonid river entry has been intensively studied，data from river systems without man-made migration obstacles，artificial flow changes，or other environmental or genetic disturbances（e. g. stocking）are rare（Finstad et al.，2005），and as in the case of the Baltic Sea Atlantic salmon，virtually lacking. This information is still highly relevant when designing management schemes to revive and promote natural reproduction of salmonids. Here，historical data on the timing of river entry of three natural，geographically closely situated（Fig.1）Atlantic salmon populations was analyzed. The aims of the study were to assess relative roles of 1）among population and 2）among year variation in the timing of river entry，and 3）further investigate whether annual variations could be assigned to any of the available environmental variables.

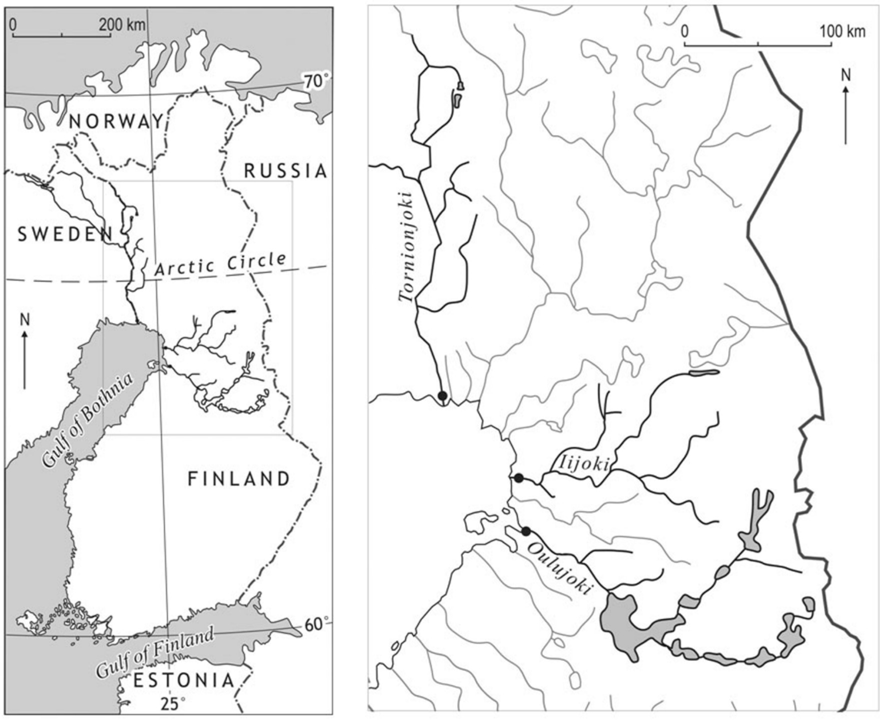

Fig.1 A map showing the locations of the rivers Tornionjoki，Iijoki and Oulujoki
The rivers run to the Gulf of Bothnia of the Baltic Sea. Locations of the traps at which daily salmon catches were recorded are denoted with black bullets.

1 Materials and Methods

1.1 Study rivers and annual catch records

The rivers Tornionjoki，Iijoki and Oulujoki are located in northern Finland and they run to the Baltic Sea at 65°45′N 24°08′E，65°20′N 25°16′E，and 65°01′N 25°27′E，respectively（Fig.1）. Hydromorphologically，river Oulujoki has substantially larger average flow than rivers Iijoki and Tornionjoki，but the flow in river Oulujoki is also buffered by several large lakes. In contrast，rapids are more common in river Iijoki（$n = 140$）and river Tornionjoki（$n = 35$；Hurme，1962）. Harvesting of salmon was typically done by using traps of fixed wooden lattice built crosswise to the stream（Fig.2）. As the traps were fixed structures，fishing effort within the rivers remained roughly constant over a migration season.

Daily salmon catches were recorded at the traps located close to the river mouths from May to August during the time periods 1881 – 1886 and 1898 – 1902 for river Tornionjoki，during 1896 and 1898 – 1902 in river Iijoki，and during 1870 and 1872 – 1901 in river Oulujoki. The raw data from the salmon catch in the three rivers originates from Nordqvist（1904）. During the recorded years，the investigated salmon populations could be characterized as natural in terms of abundance and migratory patterns，and the rivers were not fragmented or polluted（Nordqvist，1904）.

In all three rivers，annual salmon catch records consist of daily numbers of salmon caught at a fixed trap. In total，the dataset contained 4375 daily salmon catches. As the fishing effort may have varied among years and among study sites，we focused on investigating variations in the cumulative pattern of the freshwater migration. To this end，year-specific dates by which 5%，50% and 95% of the annual salmon catch was caught were calculated for each study site. However，to provide background information about the catch sizes at the study sites，the annual catches ranged between 611 – 4249 individuals in river Iijoki，159 – 5336 in river Tornionjoki，and 969 – 6304 in river Oulujoki.

In river Oulujoki，age classification of returning salmon were done from scale samples. Scale samples were

Fig.2 A typical salmon trap used in historical salmon fisheries in Finland

This particular trap was situated in river Tornionjoki, and it was established in the same location from year to year (Vilkuna, 1974; Järvi, 1932). The picture is published with the courtesy Finnish National Museum.

collected years 1870 – 1901 and the sea-age of the salmon was identified based on scale growth patterns. The frequencies of the sea-age classes were reported by Järvi (1958) and as given as the annual proportions of 1SW and MSW salmon (Table Ⅰ).

1.2 Environmental conditions

SST measurements were available only from 1880 and onwards (Alm, 1924) and does not cover the entire study period. The analyses focused on SSTs in March and April as these have previously been found correlated with the timing of salmon river entry to the Baltic river Dalälven (Dahl et al., 2004). As springtime SSTs are expected to be correlated with the severity of the preceding winter (i. e. a cold winter is reflected in low springtime SSTs due to heavier ice cover), the impacts of winter time climatic patterns in the Baltic Sea region on salmon migration were investigated. Annual climatic oscillations were described by the Baltic winter index (WIBIX; Hagen and Feistel, 2005). This index summarizes annual wintertime (January-March) oscillations in the North Atlantic, and more local environmental patterns in the Baltic Sea area. A negative value of WIBIX reflects a severe winter whereas positive WIBIX indicates a mild, maritime type of winter. From 1890 to 1902, the maximum ice cover in Baltic Sea was recorded (data provided by the Finnish Marine Research Institute). This was used in the analyses as an additional measure of the harshness of winter.

Annual patterns in local environmental conditions were described by the date of ice break-up in the river, and the date at which spring/summertime-flooding of the river peaked, both observed close to river mouths. Date for the flood peak was derived from daily water level measurements over the migration season reported by Nordqvist (1904). Dates for the ice cover break-up in the river were available only for the river Oulujoki (Nordqvist, 1904) and for river Tornionjoki (data provided by Finnish Environmental Research Institute). All the available environmental variables are given in Table Ⅰ.

1.3 Statistical analyses

Annual, river-specific dates by which 5% and 50% of the annual salmon catch was caught were the response variables (converted into a running date index number starting at 1 on May 20. that was the first date salmon were ever caught at the traps). The goal of the analyses was to estimate differences in the initiation (5%) and median (50%) timing of the freshwater migration 1) among the rivers as well as 2) annual variations in these measures, and 3) whether these variations could be associated with any of the regional or local environmental variables available. To first explicitly estimate the relative amounts of variation in the timing of river entry among rivers and years, the timing of 5%/50% migrations in the three rivers were modeled jointly through a linear mixed-effect model, where river was set as a fixed factor and year constituted a random effect accounting for annual environmental variation from any source. The ability of regional environmental variables to explain annual variation in the 5%/50% migration was then investigated using a multiple linear regression with WIBIX, average SSTs in March and April, maximum ice cover in Baltic

Table Ⅰ Regional and within-river environmental conditions，and availability of salmon catch records in rivers Oulujoki（O），Iijoki（I）and Tornionjoki（T）

	Data availability	Regional conditions in Baltic			Within-river conditions			
Year	Rivers	March SST（C°）	April SST（C°）	Max. ice cover（100 km²）	WIBIX*	Timing of ice-cover break-up	Timing of flood peak	Proportion of 1SW salmon
1870	O	–	–	–	–0.47	O：27. Apr.	–	O：20%
1871	–	–	–	–	0.17	–	–	O：7%
1872	O	–	–	–	1.2	O：14. May	–	O：11%
1873	O	–	–	–	–0.15	O：30. May	–	O：17%
1874	O	–	–	–	0.68	O：13. May	–	O：18%
1875	O	–	–	–	0.16	O：12. May	–	O：3%
1876	O	–	–	–	–0.1	O：11. May	–	O：6%
1877	O	–	–	–	0.74	O：20. May	–	O：12%
1878	O	–	–	–	0.54	O：5. May	–	O：45%
1879	O	–	–	–	–1.26	O：9. May	–	O：28%
1880	O	–	4.6	–	–0.04	O：6. May	–	O：13%
1881	O，T	–	2.0	–	–1.33	O：21. May，T：24. May	T：4. July	O：24%
1882	O，T	3.8	5.5	–	1.17	T：10. May	T：1. July	O：28%
1883	O，T	0.5	2.2	–	–0.11	O：3. May，T：10. May	T：16. June	O：31%
1884	O，T	2.6	3.9	–	1.1	O：8. May，T：24. May	T：1. July	O：25%
1885	O，T	2.1	4.3	–	0.01	O：7. May，T：21. May	T：28. June	O：25%
1886	O，T	–	3.5	–	–1.14	O：19. Apr.，T：11. May	T：30. June	O：20%
1887	O	2.0	4.0	–	–0.76	O：3. May	–	O：26%
1888	O	–	–	–	–1.08	O：16. May	–	O：7%
1889	O	–	2.1	–	–0.45	O：8. May	–	O：24%
1890	O	1.6	4.4	81	0.38	O：27. Apr	–	O：43%
1891	O	0.9	3.0	126	–0.9	O：9. May	–	O：37%
1892	O	0.6	3.7	252	–0.97	O：17. May	–	O：26%
1893	O	0.9	3.7	420	0.19	O：20. May	–	O：9%
1894	O	2.4	5.0	81	0.44	O：24. Apr.	–	O：17%
1895	O	–	2.7	282	–2.06	O：3. May	–	O：35%
1896	O，I	1.7	4.5	143	0.63	O：8. May	–	O：49%
1897	O	–	3.4	180	–0.47	O：2. May	O：10. July	O：17%
1898	O，I，T	2.4	3.1	140	0.56	O：13. May，T：13. May	O：2. June，I：30. May，T：7. June	O：26%
1899	O，I，T	2.6	4.2	183	0.32	T：27. May	O：25. June，I：17. June，T：22. June	O：10%
1900	O，I，T	1.0	4.3	330	–1.47	T：24. May	O：10. June，I：9. June，T：3. June	O：6%
1901	O，I，T	1.6	3.2	180	–0.5	T：11. May	O：10. June，I：31. May，T：17. June	O：11%
1902	I，T	1.6	2.9	360	–0.6	T：19. May	I：21. June	–

* = Baltic winter index

Sea and the river as predictors，and the migration date as the response variable.

For assessing in detail annual population specific variation in the timing of river entry，5%/50% migration dates were analyzed separately in each river. In river Tornionjoki，these dates were modeled by a linear regression with WIBIX，average SSTs in March and April，maximum ice cover in Baltic Sea，date of break-up of the ice or date of the flood peak as predictors. As the number of the observed migration patterns was 11，only one of the predictors could be applied at the same time in order to avoid over-fitting of the model（i. e. too large number of model parameters in relation to the degrees of freedom，leading model to fit the data unrealistically well）. Similar model fitting was carried out for 5%/50% migration in river Iijoki. The available predictors were

WIBIX，average SSTs in March and April，Baltic ice cover and date of the flood peak. For river Oulujoki，the available environmental covariates were WIBIX，average SSTs in March and April，Baltic ice cover，date for the ice break-up，flooding peak date and the annual sea-age class frequencies. In addition to these variables，it was also investigated whether interannual variations in the timing of the migration pattern could be assigned to variations in the proportion of 1SW salmon. All the analyses were performed using R 2.7.2 statistical package.

2 Results

The timing of 5% and 50% migration depended strongly on the river（Fig.3；for 5%：$F_{2,14} = 58.27$，$P < 0.01$；for 50%：$F_{2,14} = 67.47$，$P < 0.01$），and the date of both 5% and 50% migration occurred earliest in river Iijoki，followed by rivers Tornionjoki（Fig.3；5%：ca. 12.7 d later than in river Iijoki；50% ca. 13.3 d later than in river Iijoki），and river Oulujoki（Fig.3；5%：20.5 d later than in river Iijoki；50%：26.6 d later than in river Iijoki）. Standard deviation of the random effects of years was only 3.7 d for the timing of 5% migration and 2.5 d for the timing 50% migration，so that the timing of migration varied substantially more among rivers than among years. In all，the river effect alone explained 71.7% of the variation in the timing of 50% migration and 60.4% of the variation in the timing of 5% migration. WIBIX-index，SSTs and ice cover were not able to explain annual variations in the timing of 5%（WIBIX：$F_{1,14} = 0.01$，$P = 0.94$；March SST：$F_{1,14} = 2.08$，$P = 0.17$；April SST：$F_{1,14} = 2.09$，$P = 0.17$；ice cover：$F_{1,14} = 1.19$，$P = 0.29$）or 50% migration（WIBIX：$F_{1,14} = 0.02$，$P = 0.88$，March SST：$F_{1,14} = 1.09$，$P = 0.31$；April SST：$F_{1,14} = 0.31$，$P = 0.59$；ice cover：$F_{1,14} = 0.01$，$P = 0.91$）.

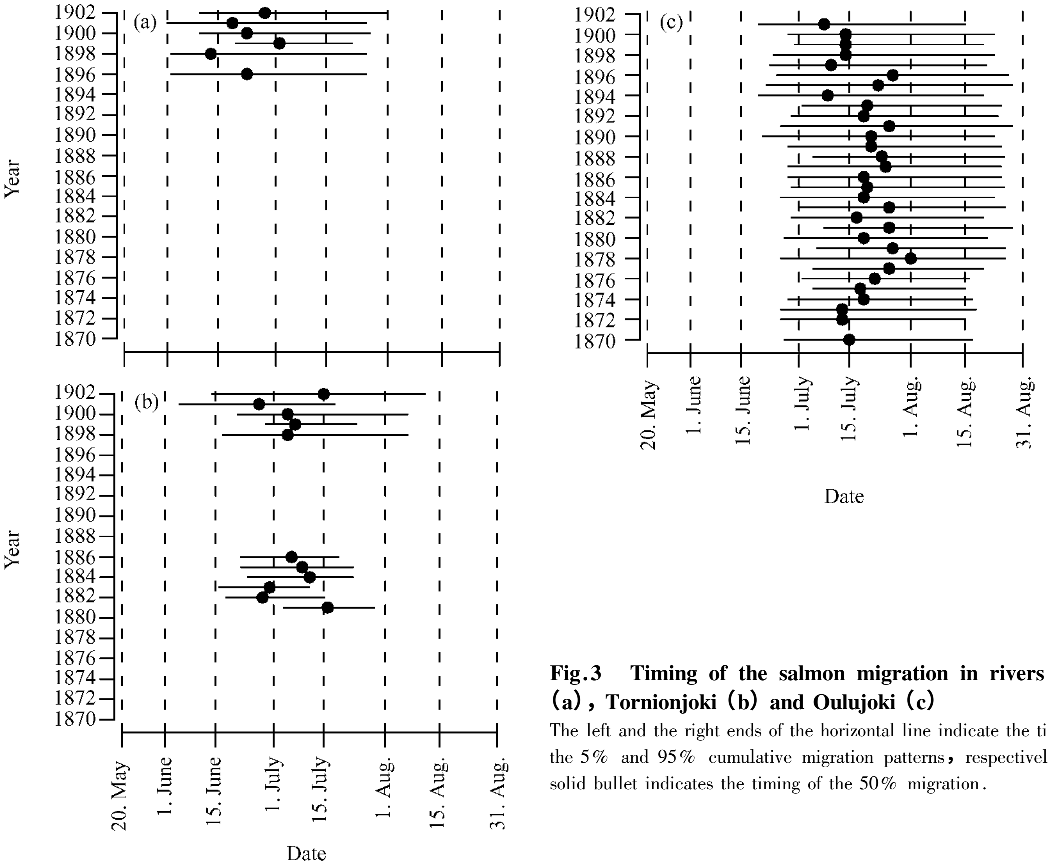

Fig.3 Timing of the salmon migration in rivers Iijoki（a），Tornionjoki（b）and Oulujoki（c）

The left and the right ends of the horizontal line indicate the timing of the 5% and 95% cumulative migration patterns，respectively. The solid bullet indicates the timing of the 50% migration.

In river Tornionjoki，timing of the ice break-up explained about half of the variation in both the timing of 5% and 50% migration（5%：$F_{1,9} = 7.69$，$P = 0.02$，$R^2 = 0.46$；50%：$F_{1,9} = 8.23$，$P = 0.02$，$R^2 = 0.48$），but timing of flood peak had no effect（5%：$F_{1,8} = 1.99$，$P = 0.20$；50%：$F_{1,8} = 1.45$，$P = 0.26$，Fig.4）. WIBIX，SSTs and maximum ice cover in the Baltic Sea did not explain any variation either（Table Ⅱ）.

Timing of the flood peak had a considerable effect on the timing of 50% migration in river Iijoki（$F_{1,3} = 14.87$，$P < 0.01$；$R^2 = 0.83$；Fig.4），but not on the timing of 5% migration（$F_{1,3} = 5.39$，$P = 0.10$）. Even though the number of data points in these analyses is low，the strong effect of the timing of the flood peak does not

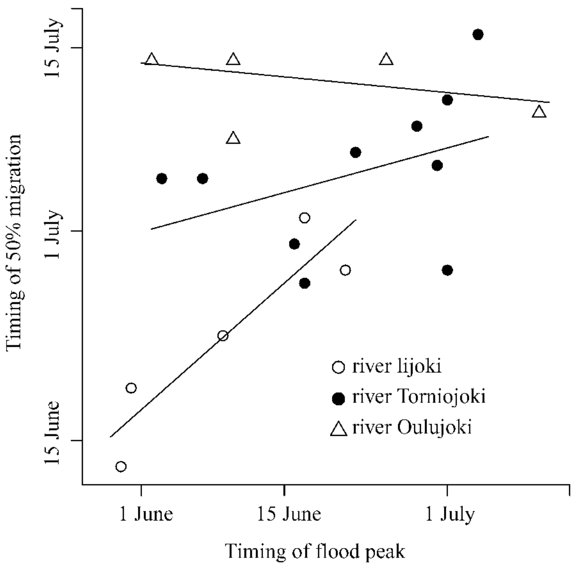

Fig.4 Timing of the 50% migration，plotted against the timing of the flood peak in rivers Iijoki，Tornionjoki，and Oulujoki

Linear regression lines are given to illustrate the relationships.

result from over-fitting of the model. Namely，when restricting data to those years from which catches were available from all the rivers and modeling the timing of 50% migration jointly in all the rivers（and having the interaction of the timing of the flood peak and the river as a predictor），the flood peak effect estimated for river Iijoki was approximately seven times as large as in the two other rivers（see also Fig.4）. As in the case of river Tornionjoki，WIBIX，SSTs and maximum ice cover in Baltic Sea did not affect the timing of migration in river Iijoki（Table Ⅱ）.

Table Ⅱ Summary of the factors detected to affect the timing of river entry

River*	Migration quantile	Factors affecting timing of migration	$R^{2\dagger}$
Tornionjoki（$n = 11$）	5%	Break-up of ice	46.1%
	50%	Break-up of ice	47.8%
Iijoki（$n = 6$）	5%	–	–
	50%	Timing of flood peak	83.2%
Oulujoki（$n = 31$）	5%	Proportion of 1SW salmon	10.9%
	50%	Proportion of 1SW salmon	27.7%
All	5%	River	60.4%
	50%	River	71.7%

* n = number of observations，† R^2 = explanatory power

In river Oulujoki，the proportion of 1SW salmon in the catch had a significant effect on the timing of 50% migration（$F_{1,29} = 11.20$，$P < 0.01$），and alone it explained 27.9% of the variation in the timing of migration. For the timing of 5% migrations this effect remained non-significant（$F_{1,29} = 3.54$，$P = 0.07$；$R^2 = 0.11$）. Other environmental covariates did not affect the timing of migration.

3 Discussion

Comparison of the migration patterns of Atlantic salmon in three Baltic rivers revealed that the timing of river entry varied substantially and consistently among the rivers，whereas annual variations were on a much smaller scale. Salmon entered first in river Iijoki，followed by rivers Tornionjoki and Oulujoki，respectively. One possible explanation for the observed fixed differences between the rivers is that the timing of river entry might be a trait that is under genetic control，being locally adapted to average within-river conditions（e. g. Quinn and Adams，1996）. However，as in case of any correlative study with no genetic evidence of adaptive differentiation between populations，it cannot be ruled out that the detected among river differences in run timing were due to differences in some local environmental factors not accounted for in this study. Differences between the rivers were still very consistent over time with little annual variation about them. Hence，any environmental factor able to account for this variation should still be very stable，such as differences in some geomorphological or hydrological features unique to each river. Therefore，it seems most likely that the among river differences were due to genetics，and supports the view that genetic differences are considered as one of the main ultimate determinants controlling timing of run timing between other Atlantic salmon rivers（e. g. Jonsson et al.，2007）.

In addition to the systematic differences in the timing of salmon entry to the three study rivers，some interannual variation in the timing of river entry was also observed（Fig.4）. However，this could not be associated with any of the analyzed regional environmental variables，and local factors explaining this variation differed between the rivers（Table Ⅱ）. This may be expected as different environmental factors have been found to be critical for regulating migration in different river systems（Jonsson，1991）. For example，water flow has been found to have the largest impact on run timing in rivers rich of rapids and highly fluctuating water levels during the migration season（e. g. Jonsson，1991；Tetzlaff et al.，2005；Jonsson et al.，2007）. This study gives support to these observations：timing of the flood peak had a pronounced impact on the timing of salmon river entry in river Iijoki（Fig.4，Table Ⅰ），which is the steepest of the three rivers and is characterized by more rapids compared to the other rivers and fewer lakes to buffer the water flow（Nordqvist，1904；Hurme，1962）. In the presence of such hydromorphological structures，shallow rapids may act as partial barriers during low waters，so that some spawning areas are only accessible during high flows. The variance in the timing of 95% migration was significantly smaller in river Iijoki compared to rivers Torniojoki and Oulujoki (Bartlett's $K^2 = 16.9$, $P < 0.01$), suggesting that salmon migration in river Iijoki may indeed have been impeded during the late summer.

The regional environmental variables and the timing of the flood peak were the only variables available from all of the rivers. Hence, comparison of relative importance of different environmental factors as determinants of river entry patterns is meaningful only for these variables (such as shown in Fig.4). For the other local variables, available only for one or two rivers, results must be viewed in the light of the available observations: environmental variable effects on run timing within a river (Table Ⅱ) only explore the relative importance of variables known for that river (Table Ⅰ), but they do not exclude the possibility that some unknown variable would explain a significant amount of variation in run timing and even encompass variation now associated to another, known variable. In particular, in river Oulujoki an increase in the proportion of 1SW salmon among the migrants was reflected as a delay in the timing of median migration pattern (Table Ⅱ). Information about the 1SW and MSW proportions was not available for rivers Iijoki and Tornionjoki, but annual variations in relative proportions of these age classes could account for at least some of the annual variation in run timing in these rivers.

Whether of genetic or environmental origin, substantial and consistent differences in the timing of river entry, such as those seen here, can make different salmon populations differently prone to human induced disturbances. Fixed regional opening time for coastal fisheries, through which Atlantic salmon fishery is currently regulated e. g. in the Baltic Sea, does not take into account differences in the run timing between the rivers, and can lead to over-exploitation of late running stocks. Likewise, the fixed opening date for fisheries can cause considerable fluctuations in the size of the breeding population and in juvenile recruitment due to interannual variations in the timing of migration (e. g. Karlsson and Karlström, 1994; Jokikokko et al., 2004). To avoid such negative effects, fisheries should be adjusted to river-specific differences in run timing and annual variations in those. A recent management program of sockeye salmon fisheries in the Fraser River in Canada provides an example of successful implementation of molecular genetic methods for detecting runs of different stocks and stock components and rapidly adjusting mixed-stock fisheries accordingly (Beacham et al., 2004; Schwarz et al., 2006).

In conclusion, the analysis of the timing of river entry in three Finnish Atlantic salmon rivers suggests that the timing of this important life-history event was to a high degree river specific and the differences between the rivers were consistent. Although already beyond reach of any further studies due to the extinction of original river Oulujoki and river Iijoki salmon stocks, it seems likely that the three different stocks were locally adapted to their respective river environments in terms of timing of their river entry. Particularly intriguing was the case of the early running river Iijoki stock which appears to have evolved to meet the challenge of timing their migration with the short flood peak to successfully negotiate numerous rapids to get access to and distribute between the spawning grounds in this rapidly discharging river.

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