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Spawning Migration of Salmon (*Salmo salar*) in the  
River Tornionjoki and in the Bothnian Bay on the  
Basis of Catch Data from 1920's till 1950's

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Abstract

The spawning migration of adult salmon was studied from historical catch data from the River Tornionjoki and Bothnian Bay. Data on salmon catches in the Tornionjoki and Bothnian Bay were collected in 1933-1957 and 1926-1961, respectively. The report also reviews the literature on the migratory behaviour of adult salmon.

Salmon were caught in the Tornionjoki mainly in June, July and August. The run was more intensive early than late in the season, and its timing depended on the size and therefore presumably on the age of the salmon. The catch of multi-sea-winter (MSW) sized salmon usually peaked in the period July 1-10 and the catch of one-sea-winter (1SW) sized salmon in the period July 21-31. The annual mean time of the spawning migration of MSW sized salmon varied within 2-3 weeks in the Tornionjoki. The large MSW salmon were caught, on average, 10-20 days later in the Tornionjoki than in the sea at the Iijoki estuary. The size of the caught salmon decreased steadily throughout the summer except that some large salmon appeared again very late in the season. The present findings support the view that the largest salmon start their homeward migration in the Baltic Sea first in the season and that they also ascend the river earlier than small salmon.

The timing of catches of MSW sized salmon correlated positively with the annual ice breakup date and negatively with the sea water temperature measured during June 10-20. Salmon thus ascend the river earlier during warm springs than cold ones. In the Tornionjoki, the water level had already passed its spring peak when the salmon catches peaked. However, the catch data for the river were based on fishing, which was to some extent dependent on conditions in the river. The mean timing of the salmon run estimated from the catches is therefore probably biased towards late season.

The mean weight of the salmon caught decreased over the observation period. The decrease in size was observed concomitantly with a delay in the annual mean time of upstream migration. The annual mean weight of spawners declined in several salmon stocks of the Gulf of Bothnia during that time. We can reasonably assume that similar changes in salmon stocks at the same time are affected by some common factors in the sea.

Key words

The River Tornionjoki, Bothnian Bay, salmon, spawning migration, migratory behaviour

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Irma Kallio-Nyberg ja Atso Romakkaniemi

**Lohen (*Salmo salar*) kutuvaellus Tornionjoessa ja Perämerellä 1920-luvulta 1950-luvulle kerättyjen saalisaineistojen mukaan**

Tutkimusraportti

Riista- ja kalatalouden tutkimuslaitos

Tornionjokeen nousevan lohikannan arviointi, 202250

Lohen kutuvaellusta tutkittiin Tornionjoelta vuosina 1933-1957 sekä Perämereltä vuosina 1926-1961 kerätystä saalisaineistosta. Lisäksi tehtiin kirjallisuuskatsaus lohen kutuvaelluskäyttäytymisestä.

Tornionjoessa lohisaalis pyydystettiin lähinnä kesä-, heinä- ja elokuun aikana. Saaliit olivat suurimmillaan alkukaudesta. Vaellushuippu riippui nousukalan koosta ja siten oletettavasti myös sen iästä. Usean merivuoden kokoisilla lohilla suurimmat saaliit ajoittuivat yleensä ajanjaksolle 1.-10. heinäkuuta ja yhden merivuoden kokoisilla lohilla jaksolle 21.-31. heinäkuuta. Usean merivuoden kokoisilla lohilla keskimääräinen vaellusajankohta Tornionjoessa vaihteli 2-3 viikon sisällä. Suurikokoiset (yli 6 kg painavat) usean merivuoden lohet pyydystettiin Tornionjoesta keskimäärin 10-20 päivää myöhemmin kuin merestä liikisuulta. Saalislohien keskipaino laski tasaisesti vaelluskauden loppua kohti, mutta hyvin myöhään kauden lopulla saadussa vähäisessä saaliissa kalojen keskikoko jälleen kasvoi. Saadut tulokset tukevat aiempaa käsitystä, että suuret lohet aloittavat kutuvaelluksensa jo Itämerellä ensimmäisinä ja myös nousevat keväällä kutujokiin aikaisemmin kuin pienet lohet.

Usean merivuoden kokoisten lohien saaliiden ajoittuminen korreloi positiivisesti vuosittaisen merijään lähtöajankohdan kanssa ja negatiivisesti 10.-20. kesäkuuta Perämerellä mitatun meriveden keskimääräisen lämpötilan kanssa. Nämä tulokset viittaavat siihen, että lohi vaelttaa kudulle lämpiminä keväänä aiemmin kuin kylminä keväänä. Tornionjoessa suurimmat lohisaaliit saatiin kevään tulvahuipun jälkeisenä aikana. Jokikalastus oli kuitenkin joessa vallinneista pyyntiolosuhteista riippuvaa. Tästä johtuen saaliin perusteella arvioitu lohen vaelluksen keskimääräinen ajoittuminen todennäköisesti aliarvioi alkukauden vaellusmääriä suhteessa loppukauden vaellusmääriin.

Saalisaineistojen keruuvuosina lohen keskimääräinen koko pieneni jakson loppua kohden. Yhtäaikaisesti keskikoon pienenemisen kanssa vuosittainen vaellusajankohta siirtyi myöhemmäksi. Nousulohen keskikoon pieneneminen tarkastelujaksolla on havaittu myös muissa Pohjanlahden lohikannoissa. On oletettavaa, että tämä ilmiö johtuu joistakin lohen syönnösvaellukseen Itämerellä liittyvistä tekijöistä.

Tornionjoki, Perämeri, lohi, kutuvaellus, vaelluskäyttäytyminen

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# 1. INTRODUCTION

Till the middle of this century, traditional salmon fishing methods were frequently used in catching salmon in the Bothnian Bay rivers. Large salmon weirs made of wood, stones and nets were characteristic of that time, and also drifting nets and dipnets were used in river fishing. Daily booked information on the catches and their composition were obligatory in this fishery. No similar follow-up was established in the coastal trapnet fishery of salmon. However, some documents of fish markets can be used for a coarse follow-up of the daily coastal salmon catches and their composition. In this report, the spawning migration of adult salmon has been studied by utilising the above mentioned historical catch data from the River Tornionjoki and Bothnian Bay. The report also reviews the literature of the migratory behaviour of adult salmon.

The Finnish Game and Fisheries Research Institute has been exploring methods to provide adult salmon passage estimates in the Tornionjoki. The most promising results to date have been achieved with hydroacoustics. Funding for a project to establish monitoring by hydroacoustic means is being provided by the EC from 1997 to 1999. As part of the project this report provides some background information of the migratory behaviour of adult salmon needed for setting up a monitoring system and creating the theoretical basis for species recognition from the hydroacoustic data.

Many people have been involved with the compilation of the data. The river data were compiled with the help of Kauko Vaara. Bothnian Bay data were provided by Alpo Tervo and Alpo Tuikkala and organised by, among others, Marja-Liisa Liedes. We would like thank all of you.

## 2. MATERIAL

### 2.1 Catch data on the River Tornionjoki

Data on salmon caught in the River Tornionjoki were collected in 1933-1957. Most of the salmon were caught at Kiviranta weir and at other sites near the mouth of the river (Fig. 1, Tables 1 and 2).



Figure 1. The location of the study area, fishing sites and data on hydrological conditions.



The size of the annual reported catch varied from 56 to 7885 fish (Fig. 2). The catch data consisted of information on the individual weight (rounded to the nearest kilogram) of the fish, the fishing date and the site where salmon were caught. Salmon were classified by weight into three size classes for analysis (Table 2). Caught salmon were not aged, but it can reasonably be assumed that salmon weighing 1 or 2 kg were mainly one-sea-winter (1SW) salmon called also as grilse and salmon weighing 3 kg or more were mainly multi-sea-winter (MSW) salmon.

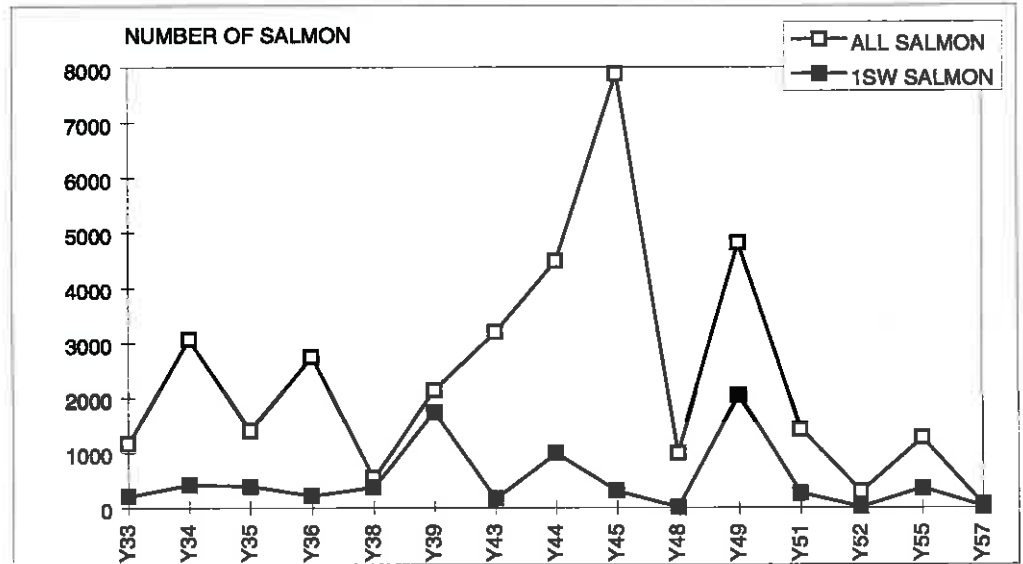


Figure 2. Total annual catches (number) in the Tornionjoki in 1932-1957. Total catches of salmon (MSW and 1SW salmon pooled) and of grilse (1SW) are shown separately. Y33= year 1933 and so on.

Table 1. Fishing sites in the Tornionjoki and distance from the sea along the river.

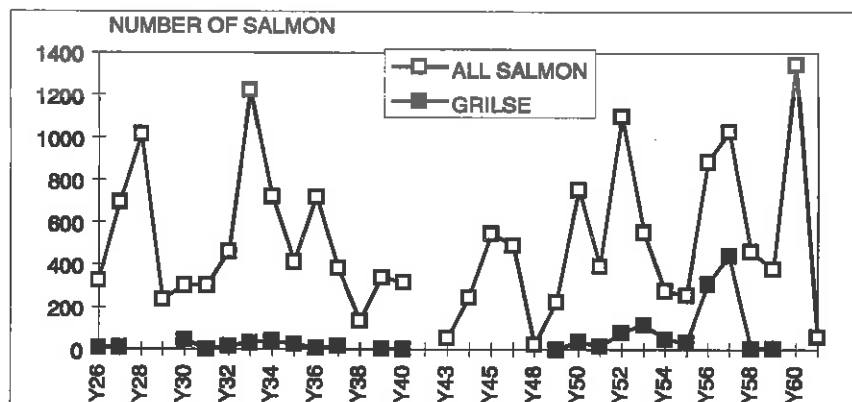
No.	Site	Village	Gear	Distance (km)
1	Kiviranta	Kiviranta	weir	6
2	Sumisaari	Alavojakkala	weir	10
7	Paasin pato	Kukkola weir	weir	18
8	Niskapato	Kukkola	weir	20
3	Lake Karunki	Karunki	drifting nets	25
23	Mustasaari	Karunki	drifting nets	30
9	Selkäsaari	Korpikylä	net weir	40
10	Maasaari	Korpikylä	net weir	40
11	Vonkaniska	Korpikylä	dipnet	40
22	Kallioisen niemi	Korpikylä	dipnet	40
4	Marjosaari-Palosaari	Kaulinranta	weir	80

**Table 2. Number of salmon caught at different sites in the Tornionjoki. Size classes are shown separately. MSW salmon = multi-sea-winter salmon. 1SW = one-sea-winter salmon (grilse).**

Fishing site	Size classes of salmon			TOTAL
	> 6 kg (Large MSW)	3-6 kg (Small MSW)	< 3 kg (1SW)	
Kiviranta	8261	9551	7039	24851
Sumisaari	239	145	203	587
Paasin pato	41	28	-	69
Niskapato	8	13	-	21
Lake Karunki	1636	2629	89	4354
Mustasaari	1674	793	36	2503
Selkäsaari	3	1	-	4
Maasaari	2	-	-	2
Vonkaniska	4	3	-	7
Kallioisen niemi	1	-	-	1
Marjosaari-Palosaari	1390	1511	121	3022
<b>TOTAL</b>	<b>13259</b>	<b>14674</b>	<b>7488</b>	<b>35421</b>

## 2.2 Data on fish wholesaler in Bothnian Bay

Catch data collected from the receipts of a fish wholesaler consisted of information on daily purchases made in 1926-1961 (Fig. 3). In the receipts, number of fish and weight of catch were pre-divided into three size classes. The class limits seemed to be similar to those chosen for the Tornionjoki data. Therefore salmon in the smallest size class were called as 1SW salmon (grilse) and the two larger size classes were assumed to consist of MSW (small and large) salmon. However, no data was available on the individual weight of fish. Majority of the salmon were caught by trapnets in Bothnian Bay, at the R. Iijoki estuary (Fig. 1).

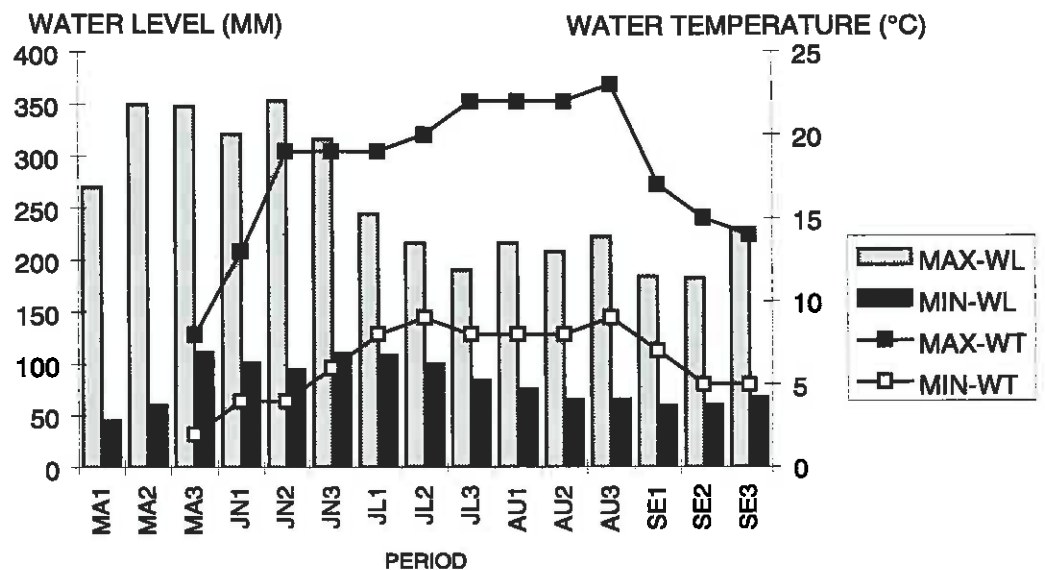


**Figure 3. Total annual catches (number) in Bothnian Bay. Data on fish wholesaler in 1926 - 1961. Total landing (MSW and 1SW spawners) and landing of grilse (1SW) are shown separately. Y26= year 1926 and so on.**

The catch likely consisted of a mixture of the R. Iijoki salmon and salmon from the other rivers in the northern Bothnian Bay (Romakkaniemi et al. 1995). There may be a lag of about a day between the fishing time and the date of the contract of purchase.

## 2.3 Data on hydrological conditions

The salmon run was analysed in relation to the water level in the river and the temperature of the sea surface water (Fig. 4). In addition, the seasonal run of salmon was analysed in relation to the breakup date of ice on Bothnian Bay coast (Leppäranta and Seinä 1985). Water level was reported daily at Kukkolankoski, 18 km upstream from the mouth of the river. The temperature of sea water was reported daily during the ice-free season in the open sea in Bothnian Bay (Plevna) (Fig. 1).



**Figure 4. Range of water level at Kukkolankoski and sea surface temperature in Bothnian Bay (Plevna) during May-September in 1933-1957. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.**

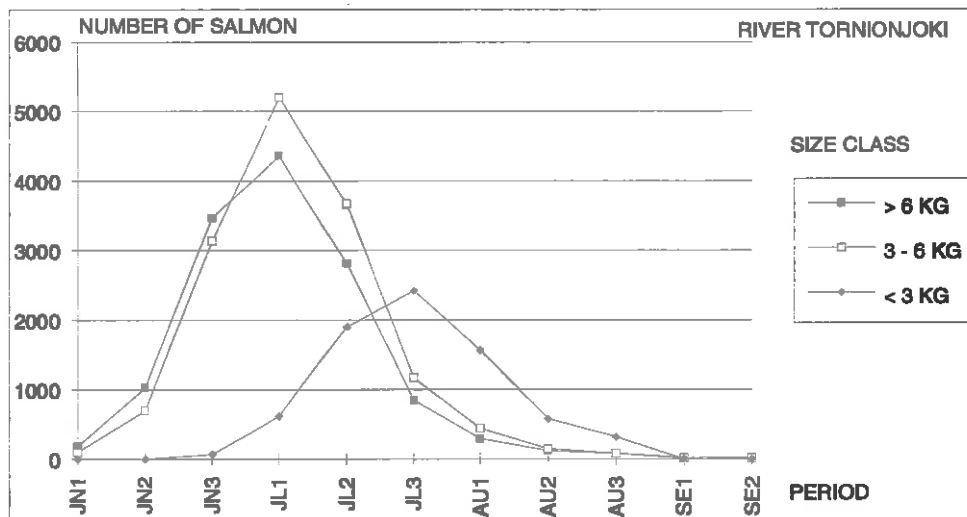
## 2.4 Methods

River and sea data were analysed separately, because they were collected and documented in different ways and because the salmon catches consisted of salmon of partly different origin. The data used in the analysis were classified into size classes. The mean catch date (mean time of a catch at a fishing site) was calculated from the sum data by taking a weighted mean. Otherwise weighting was not used.

### 3. RESULTS

#### 3.1 Seasonal timing of spawning migration

Salmon were caught in the Tornionjoki mainly during the summer months, that is, June, July and August. The catch of multi-sea-winter (MSW) salmon peaked during the period July 1-10 (Fig. 5), one month after the first catches. The frequency of one-sea-winter (1SW) salmon was greatest in July 21-31.



**Figure 5. Salmon catches (number of spawners) periodically during the spawning run in the Tornionjoki in 1933-1957. Size classes, large MSW salmon (> 6 kg), small MSW salmon (3-6 kg), and grilse or 1SW salmon (< 3 kg), are shown separately. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.**

The frequencies of MSW salmon ( $\geq 3$  kg) were greatest in July 1-10 at the fishing sites 6, 30 and 80 km upstream from the estuary in 1933-1957 (Fig. 6). The value of comparison is, however, impaired by the fact that salmon were partly caught in different years in the different places. In 1933, the peak of MSW salmon was during June 20-30 at the lowest site (Kiviranta), but during July 1-10 at the uppermost site (Marjosaari-Palosaari at Kaulinranta). Also in 1935 the catch peaked earlier at

Kiviranta than at Kaulinranta. In 1934 and in 1936 the highest frequency of MSW salmon at Kiviranta was in the same or in later period as at Kaulinranta (Fig. 7).

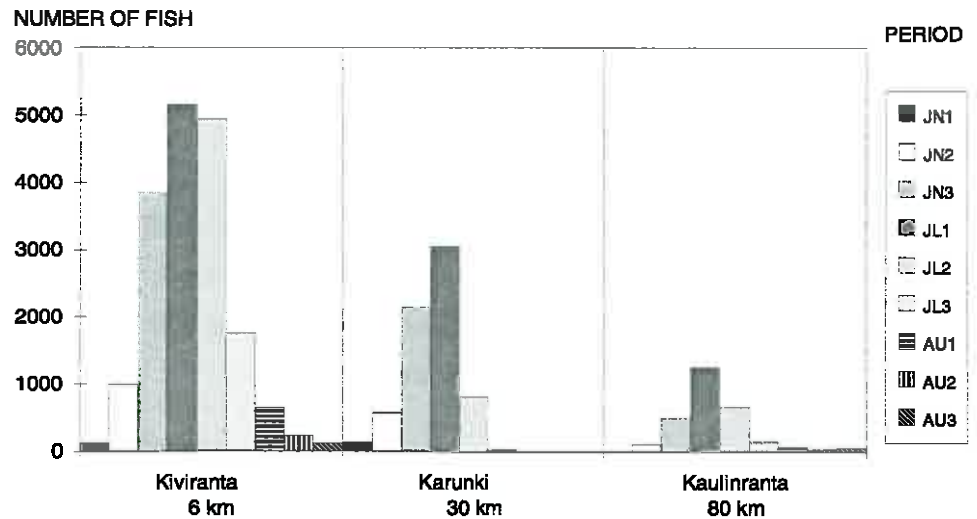
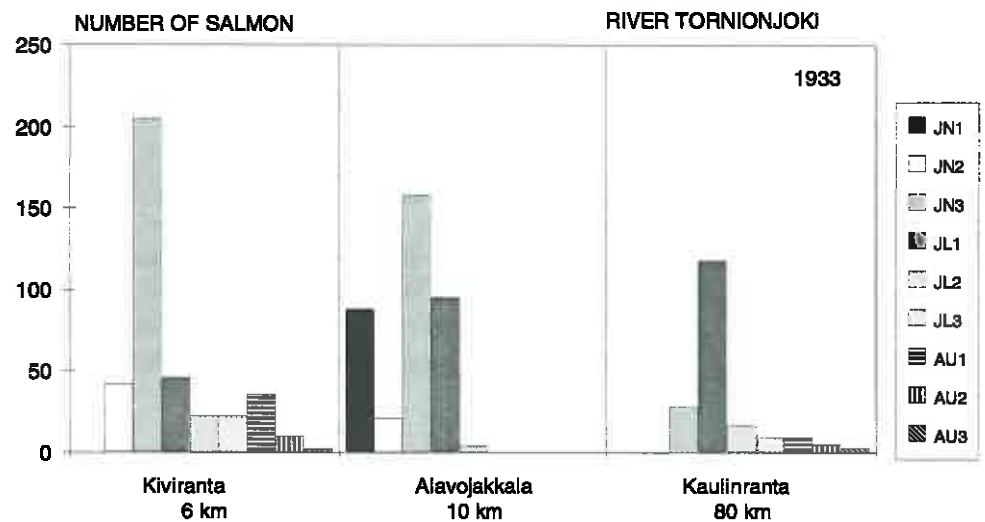


Figure 6. Number of MSW salmon ( $\geq 3$ kg) periodically at three fishing sites along the Tornionjoki in 1933-1957. Salmon were partly caught at different sites in different years. Distances upstream from the sea are shown. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.



(Fig.7: see next page)

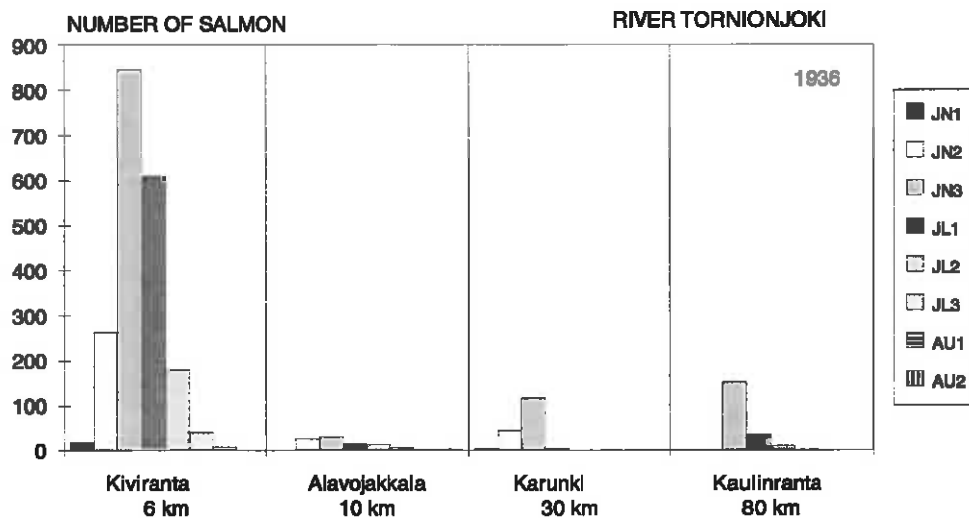
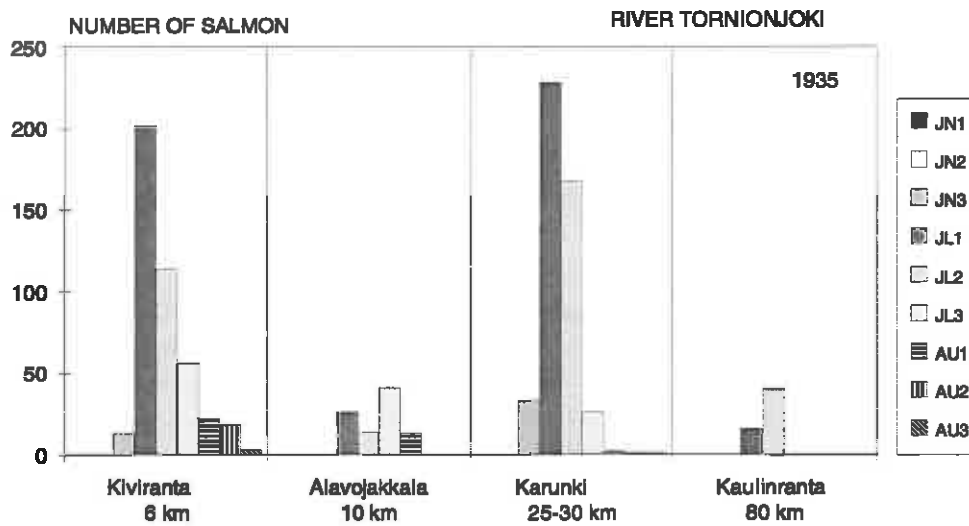
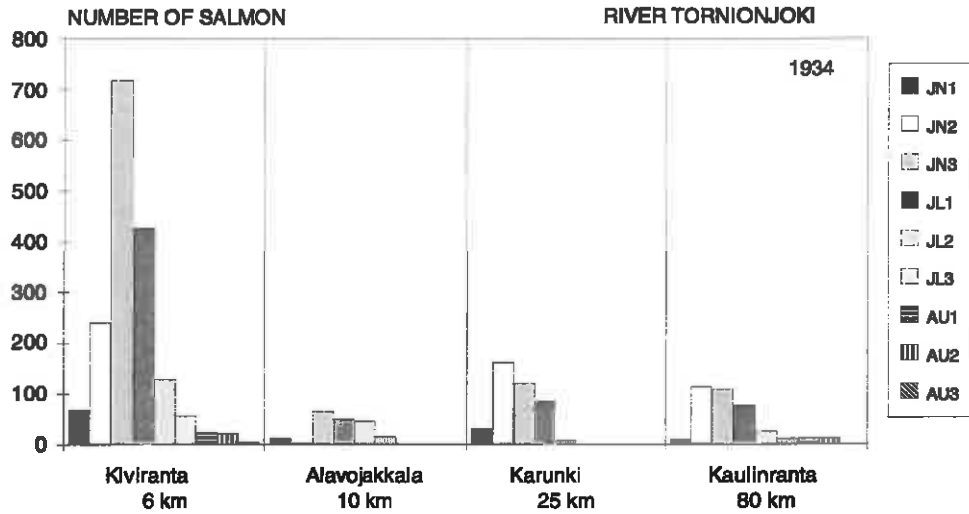
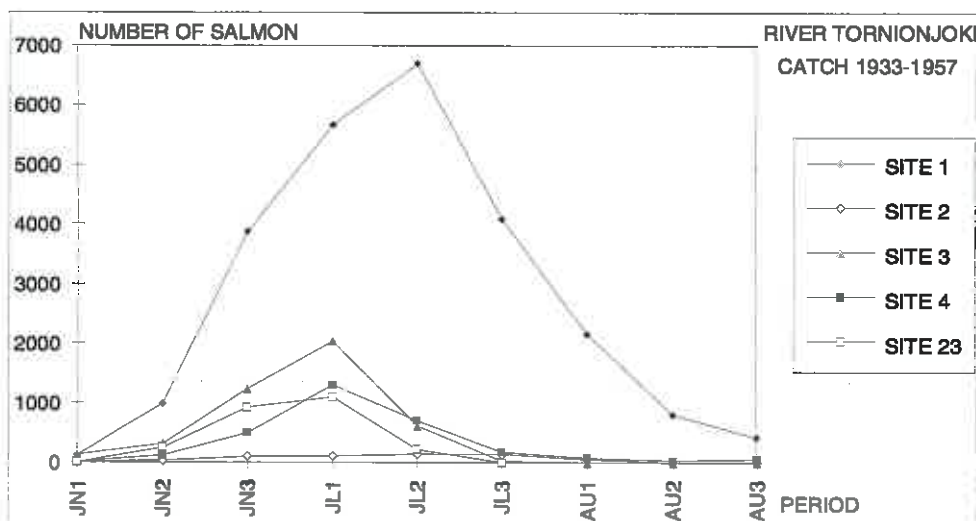
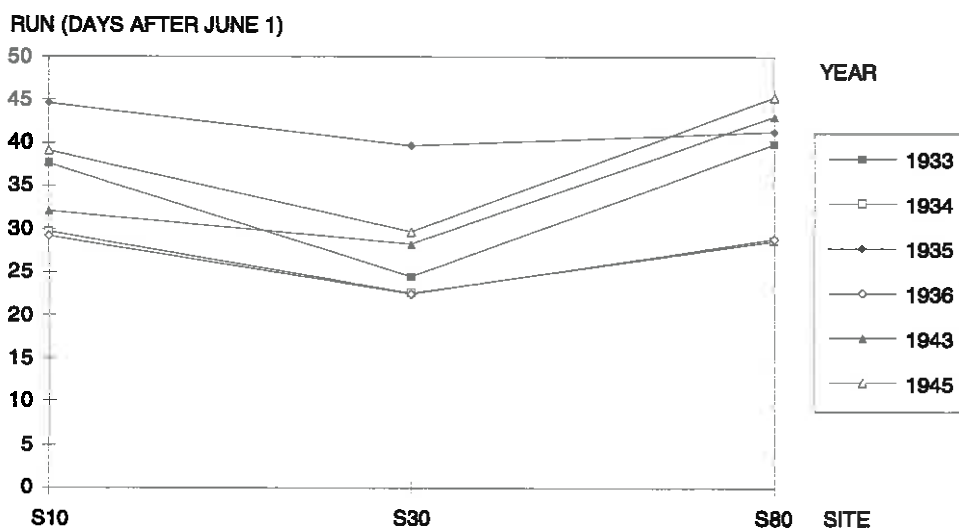


Figure 7 (see also previous page). Number of salmon (over 3kg) periodically at fishing sites along the Tornionjoki in 1933, 1934, 1935 and 1936. Distances (km) upstream from the sea are shown below the names of the sites. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.

Catches peaked at about the same time at the different fishing sites in the pooled data (Fig. 8). The mean time of the catches of small (3-6 kg) MSW salmon was not delayed by an increase in the migration distance in the river in the annual data (Fig. 9). Salmon were caught seasonally at about the same time both at Kiviranta-Alavojakkala, 6-10 km upstream from the sea, and at Kaulinranta, 80 km upstream.



**Figure 8. Number of salmon spawners (MSW and 1SW) caught at five sites along the Tornionjoki during spawning runs in 1933-1957. Sites: Kiviranta (1); Sumisaari (2); Lake Karunki (3); Marjosaari-Palosaari (Kaulinranta) (4); Mustasaari (Karunki) (23). Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.**



**Figure 9. Mean catch dates of small MSW salmon (3-6kg) along the Tornionjoki in six years. Fishing sites: S10 = Kiviranta-Alavojakkala, 6-10 km upstream from the sea; S30 = Karunki, 25-30 km; S80 = Kaulinranta, 80 km.**

The salmon catches in Bothnian Bay peaked in June in 1926-1961. Large MSW salmon (> 6 kg) were mainly caught in June and 1SW salmon in July and in August (Fig 10). The large MSW salmon were caught, on average, 10-20 days later in the Tornionjoki than in the R. Iijoki estuary in Bothnian Bay (Fig. 11).

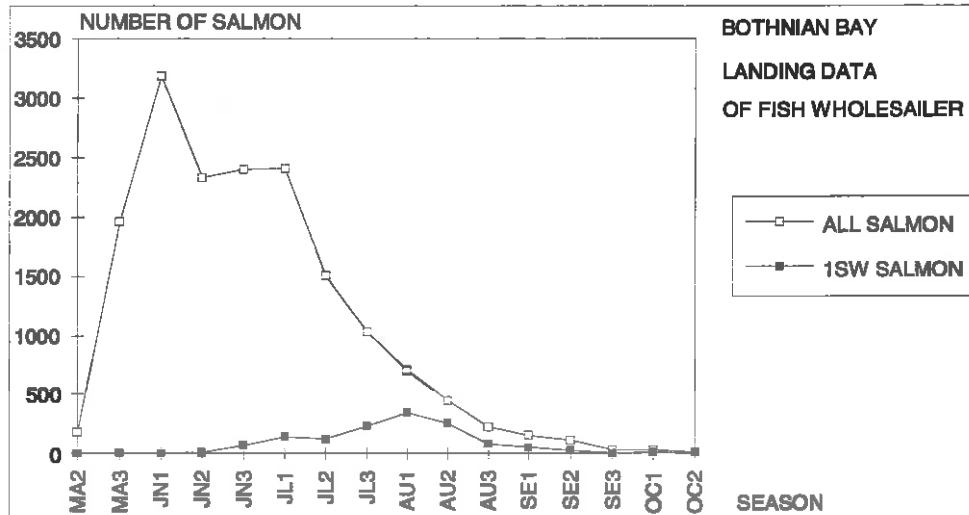


Figure 10. Total catches (number) during salmon spawning run in Bothnian Bay in 1926-1961. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.

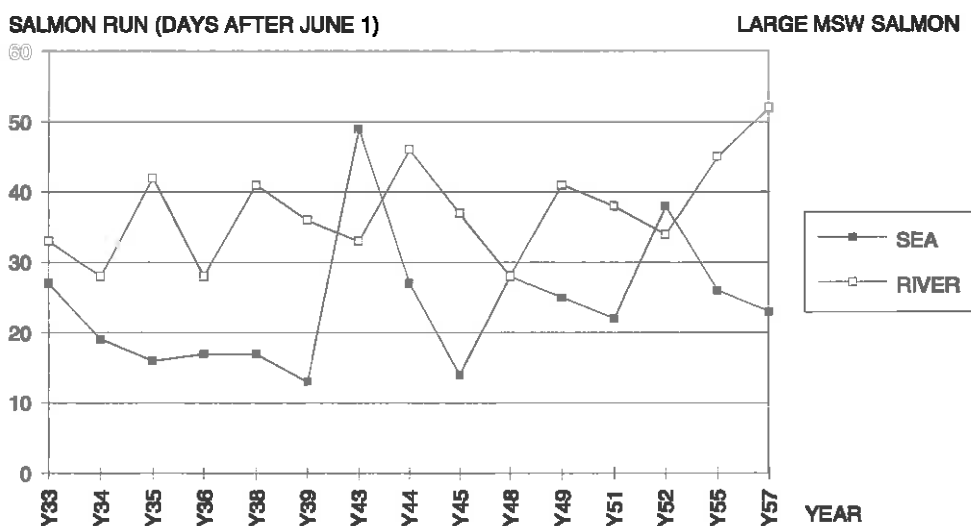


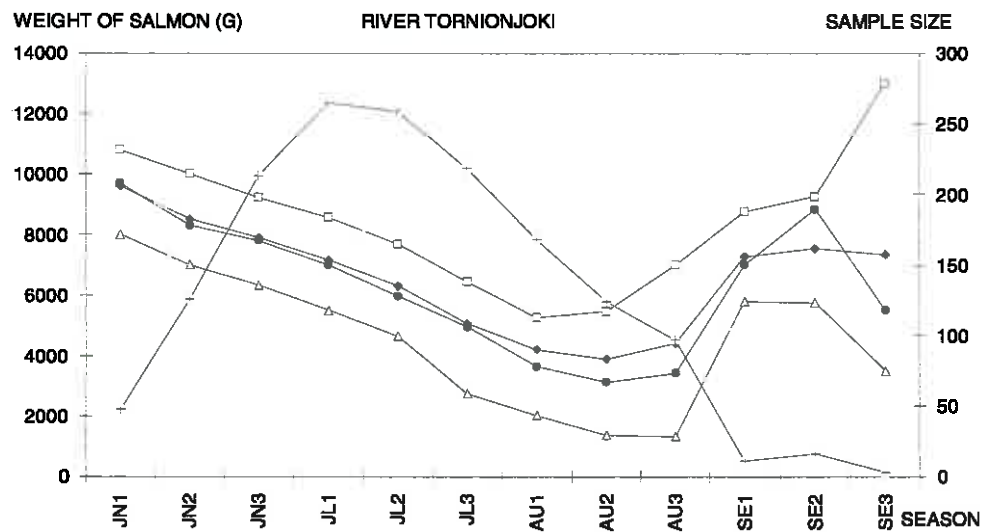
Figure 11. Mean catch dates of large MSW salmon (> 6 kg) in Bothnian Bay and in the Tornionjoki by year. Y33= year 1933 and so on.



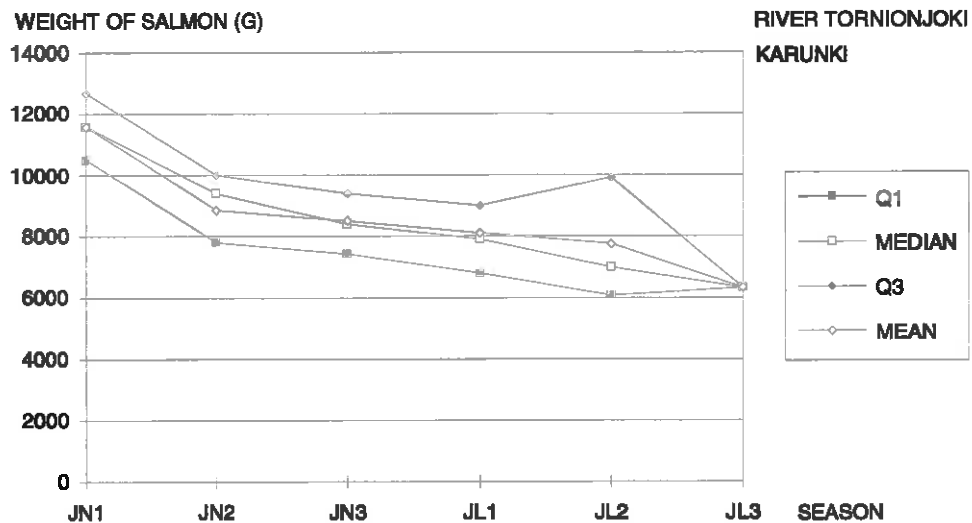
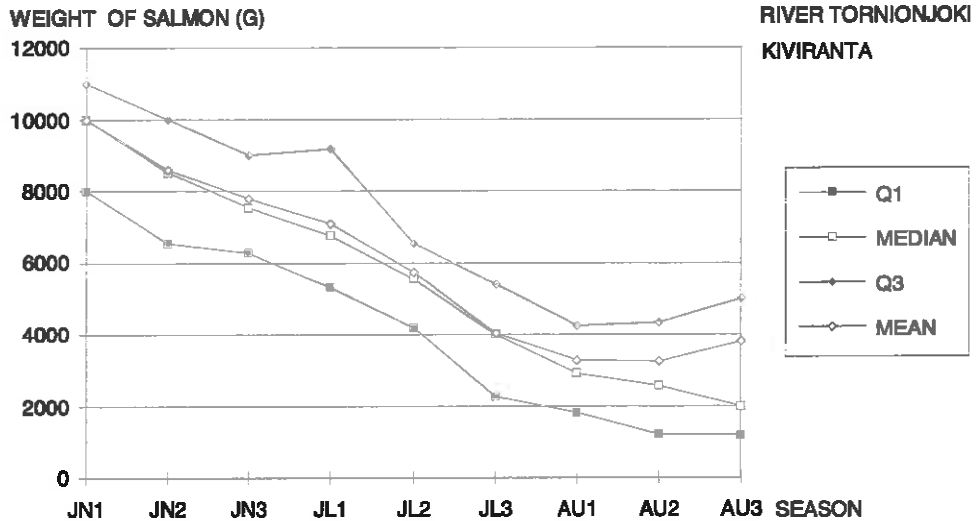
## 3.2 Timing of spawning migration and size of spawners

### 3.2.1 River Tomionjoki

Salmon caught at the beginning of the spawning migration season were larger than those caught at the end of the season (Fig. 12). The mean weight of migrants was almost 10 kg at the beginning of June but under 4 kg in August. Site specific differences in the mean size could be found. For instance, weight of salmon decreased from 10 kg to 2 kg in summer at the Kiviranta fishing site (Fig. 13) and from 11.5 kg to 6.5 kg at Karunki (Mustasaari) (Fig. 13).



**Figure 12. Weight of salmon (MSW and 1SW salmon pooled) periodically during the fishing season. Median (circle, ●), upper (square, \*) and lower (triangle, Δ) quartiles, mean (rhomb, ◆) and the number of catches (+) are shown. Total number of caught salmon is shown in the Table 2. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.**

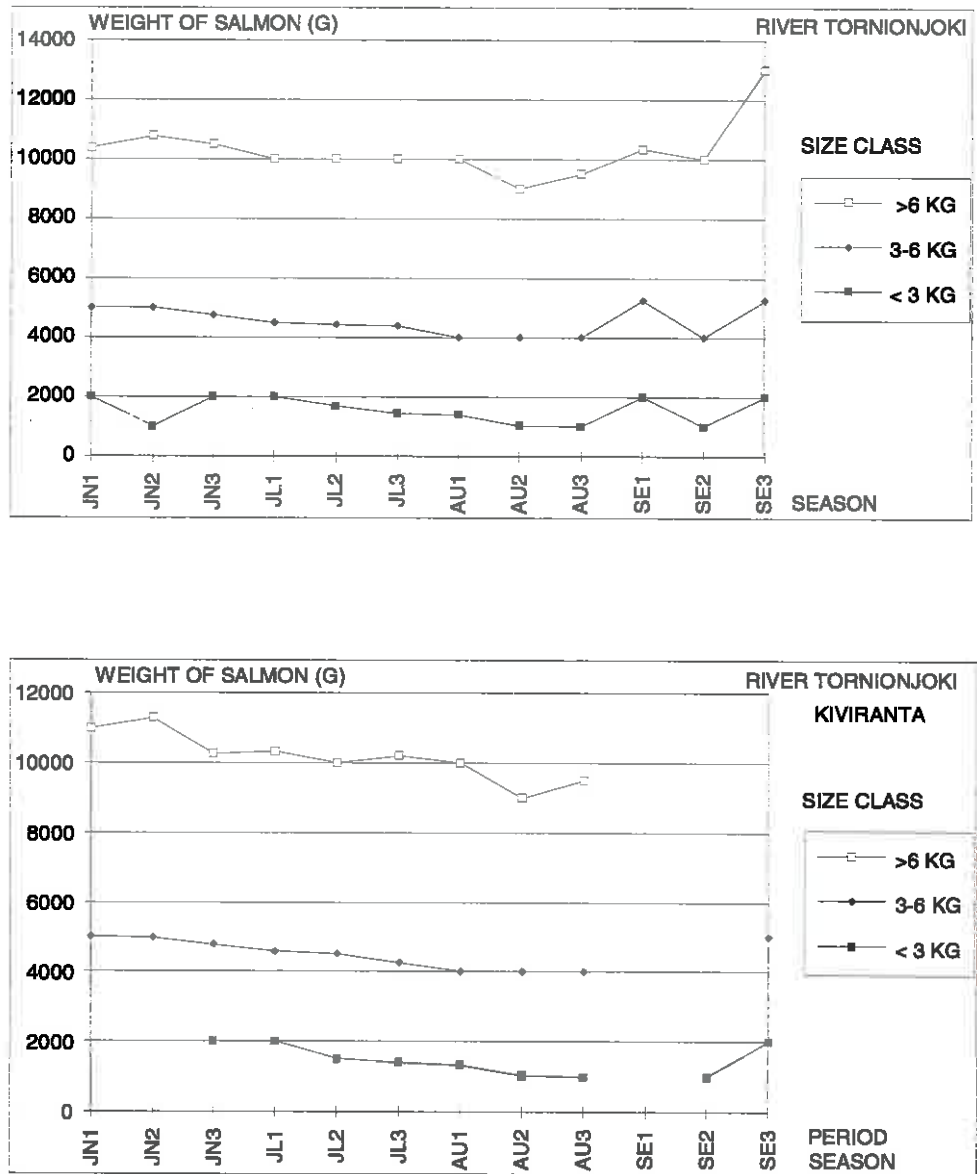


**Figure 13. Weight of salmon (MSW and 1SW salmon pooled) periodically at Kiviranta and Karunki (Mustasaari) during the fishing season. Median, upper and lower quartiles and mean are shown. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.**

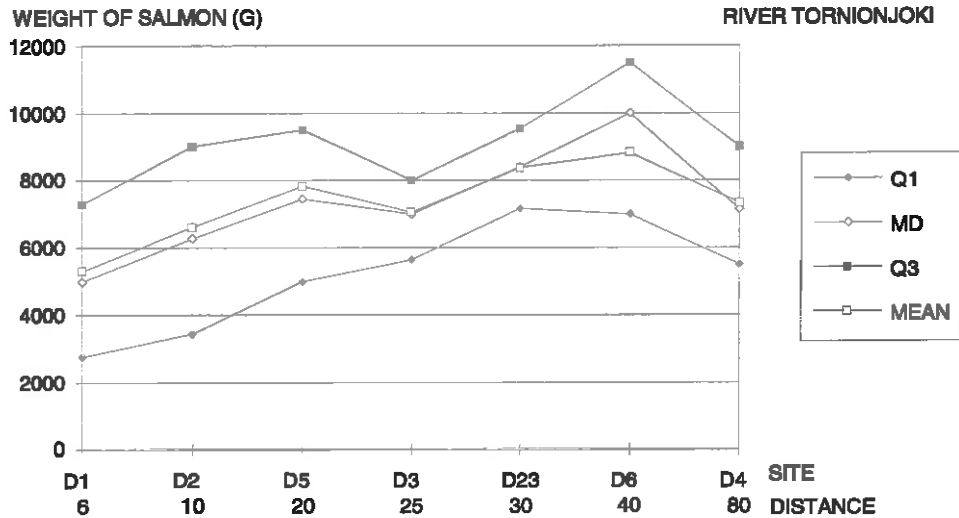
The mean weight of caught salmon decreased during the spawning run in all size classes (Fig. 14). The median weight of small MSW salmon was 5 kg in June and 4 kg in August in the catch of the whole river. The same decreasing tendency could be seen in all size classes in the catch at Kiviranta during the season ( Fig. 14).

1SW salmon (< 3kg) accounted for 28% of the catch at Kiviranta, but for only 4% at Palosaari (Table 2). The mean weight of salmon varied from place to place, with a slight tendency to increase with distance from the river mouth (Fig. 15). No grilse were caught at Kukkola or Korpikylä, 20 km and 40 km upstream from the estuary,

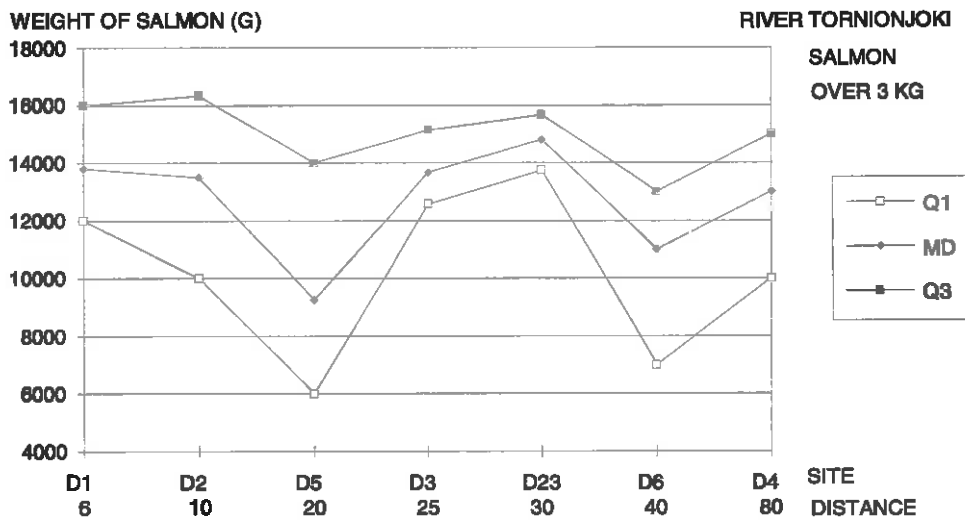
respectively (Fig. 15). On the other hand, the median weight of MSW salmon ( $\geq 3$  kg) was fairly low at these sites (Fig. 16)



**Figure 14. Median weight of large MSW salmon (> 6 kg), small MSW salmon (3-6 kg) and 1SW salmon (< 3 kg) in the Tornionjoki as a whole and at Kiviranta periodically during spawning migration. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.**



**Figure 15. Weight of salmon (MSW and 1SW salmon pooled) at fishing sites in the Tornionjoki. Medlan (MD), upper (Q3) and lower (Q1) quartiles and mean are also shown. Distances upstream from the sea are shown below the site number. D1, D2, D3, D4 and D23 refer to the site numbers given in Table 1. D1 = Kiviranta, D2 = Sumisaari, D5 = the fishing sites at the village of Kukkola pooled, D3 = Lake Karunki, D23 = Mustasaari, D6 = the fishing sites 9, 10, 11 and 22 in the village of Korpikylä are pooled.**



**Figure 16. Median weight of MSW salmon ( $\geq 3$  kg) at catch sites in the Tornionjoki. Sites have the same numbers as in Fig. 15.**

### 3.2.2 Bothnian Bay

The weight of salmon decreased throughout the fishing season (Fig. 17). Large MSW salmon (> 6 kg) weighed from 10 to 8 kg during the season (Fig. 18). The weight of small MSW salmon (3 - 6 kg) decreased from 5 kg to 3 kg and that of grilse from 3 kg to 1 kg.

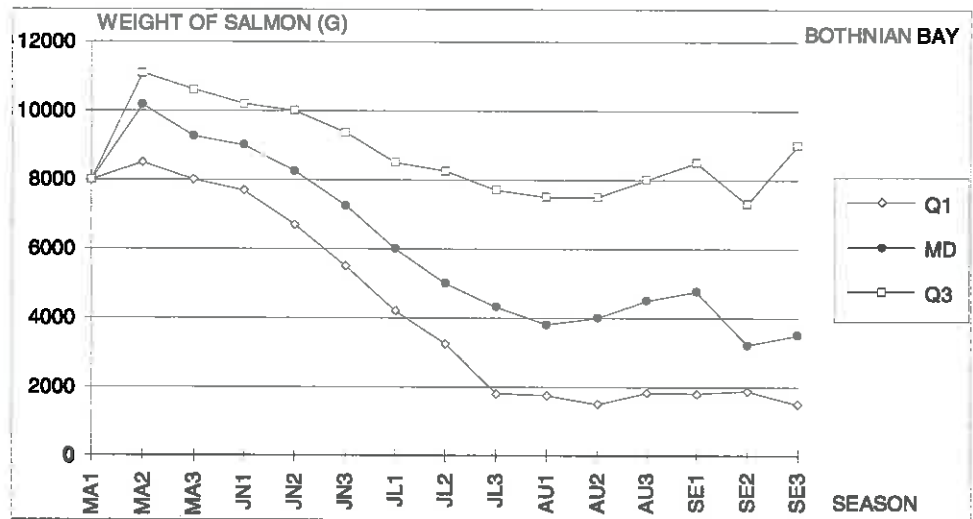


Figure 17. Median weight of salmon periodically during the spawning season in Bothnian Bay catch. All the years are pooled. Number of salmon is shown in Fig. 5. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.

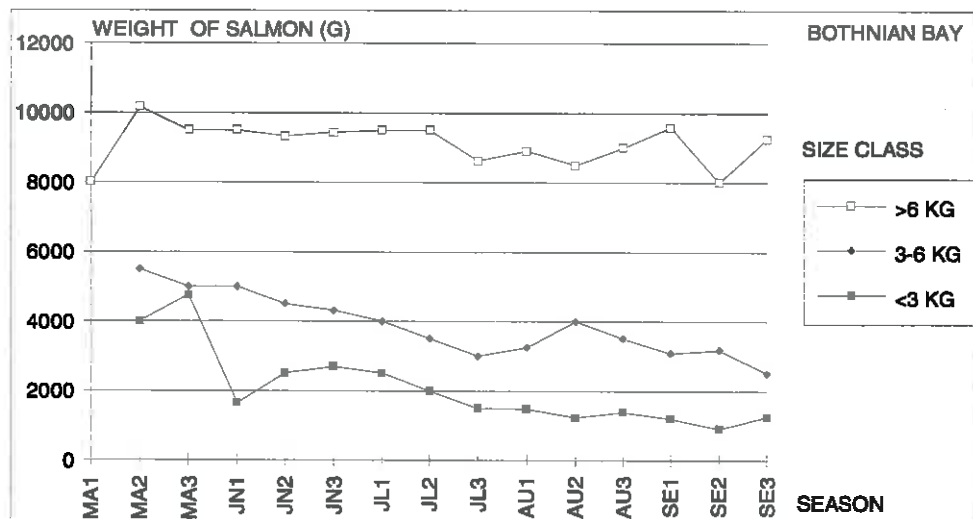
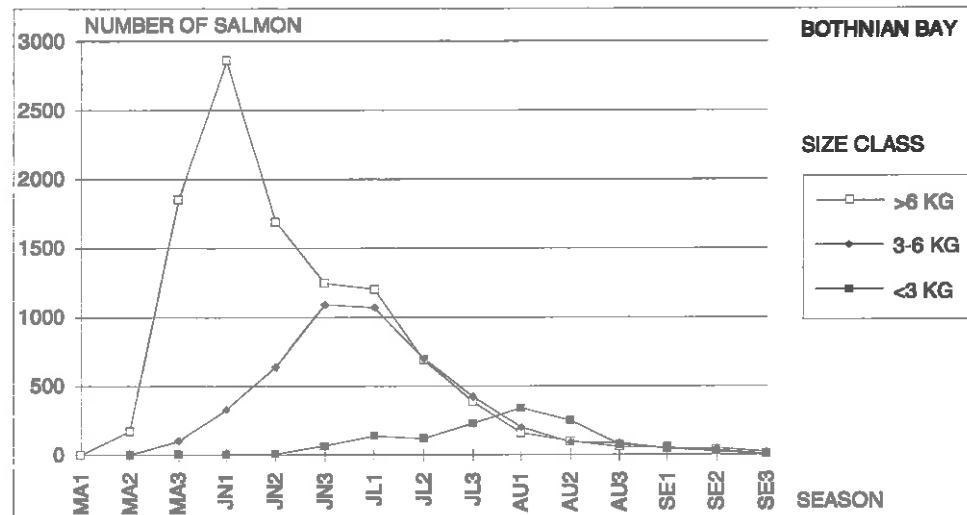


Figure 18. Median weight of the large (> 6 kg) and small MSW (3-6 kg) salmon and 1SW salmon (< 3 kg) during the season. Years 1926-1961 pooled. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.

Most large MSW salmon (> 6 kg) were caught during the period June 1-10 (Fig. 19). Small MSW salmon (3-6 kg) were mainly caught during June 20-30 and July 1-10 and grilse during August 1-10.



**Figure 19. Number of large and small MSW salmon and grilse during the fishing season in Bothnian Bay. All the years are pooled. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.**

### 3.3 Speed of spawning migration in the river

The mean annual catch dates between the different fishing sites indicate that the speed of spawning migration of MSW salmon ( $\geq 3$  kg) varied greatly. (Table 3). According to the mean catch dates, the speed of spawning migration from the lowest site, Kiviranta, to the uppermost site, Kaulinranta, was 14.8 km/day in 1933 and 18.5 km/day in 1945. In 1934-1936 the mean catch date at Kiviranta was the same or even later than the mean catch date at Kaulinranta. Also the peak catches were observed later at Kiviranta than at Kaulinranta in some years (see chapter 3.1). This indicates that catches were not unbiased estimates of the intensity of upstream migration. From Karunki to Kaulinranta, a distance of 50 km distance, the migration speed of MSW salmon ranged from 3.3 to 25.0 km/day. The mean catch date was always earlier at Karunki than at Kaulinranta.

**Table 3. Annual timing of spawning migration (mean catch date) of MSW salmon ( $\geq 3$  kg) at three fishing sites, 6, 30 and 80 km upstream from the river mouth, and speed of spawning migration (km/day) calculated from differences in mean catch dates and distance between the sites. Catches from Lake Karunki and Karunki (Mustasaari) were pooled.**

Year	Kiviranta/ 6 mean date	Karunki/ 30 mean date	Kaulinranta/ 80 mean date	Difference and (speed), days and (km/d)	
				Kiviranta- Kaulinranta	Karunki- Kaulinranta
1933	July 4	June 24	July 9	+5 (14.8)	+15 (3.3)
1934	June 29	June 23	June 29	0	+6 (8.3)
1935	July 15	July 9	July 11	-4	+2 (25.0)
1936	June 30	June 23	June 29	-1	+6 (8.3)
1945	July 8	July 1	July 12	+4 (18.5)	+11 (4.5)

The speed of spawning migration seemed to be about the same in all size classes between Karunki and Kaulinranta (Table 4). The speed of large MSW salmon ( $> 6$  kg) was 3.3-10 km/day as calculated from the differences between mean run dates. The speed of small MSW salmon was 4.5-12.5 km/day of 1SW salmon 2.6-12.5 km/day.

**Table 4. Speed of upstream migration of salmon between Karunki and Kaulinranta fishing sites annually. Distance between Lake Karunki and Kaulinranta is 55 km and between Karunki (Mustasaari) and Kaulinranta 50 km.**

Year	Size class	Karunki, 25 km	Karunki, 30 km	Kaulinranta, 80 km	Speed. Km/day
1935	large		July 6	July 11	10.0
1936	large		June 23	June 29	8.3
1943	large		June 28	July 13	3.3
1944	large		July 5	July 18	3.8
1935	small		July 5	July 11	8.3
1936	small		June 24	June 28	12.5
1943	small		June 29	July 10	4.5
1944	small		July 7	July 14	7.1
1933	1SW	July 4		July 25	2.6
1934	1SW	July 12		July 17	11.0
1943	1SW		July 4	July 16	4.1
1944	1SW		July 9	July 13	12.5
1945	1SW	July 4		July 22	3.0

### 3.4 Annual variation in timing of spawning migration

#### 3.4.1 River Tornionjoki

The annual mean time of the spawning migration of MSW salmon seemed to vary within 2-3 weeks in the Tornionjoki. The earliest mean catch date of MSW salmon ( $\geq 3$  kg) was June 29 and the latest date July 18 (48 days after June 1) (Fig. 20). The earliest mean catch date of grilse ( $< 3$  kg) was July 8 in 1952 and the latest date August 2 in 1949. At Kiviranta, MSW salmon ( $\geq 3$  kg) were caught most frequently during the period June 20 - July 20 in 1933-1955 (Fig. 21). The annual mean catch date was between June 29 - July 30. In Lake Karunki the largest number of spawners was caught during the period July 1-10, varying from June 10-20 to July 1-10 (Fig. 21). The annual mean catch time was between June 23 and July 19. At Marjosaari-Palosaari the peak catch of MSW salmon ( $\geq 3$  kg) was in July 1-10, varying from June 10-20 to July 10-20 (Fig. 21). The annual mean catch date was between June 29 and July 8.

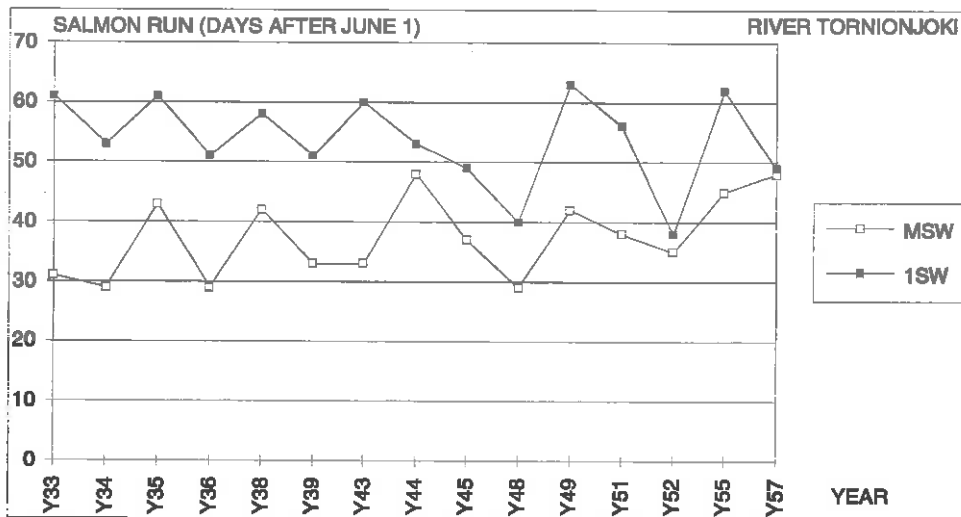


Figure 20. Timing (mean catch date, days after June 1) of the spawning migration of MSW salmon ( $\geq 3$  kg) and grilse ( $< 3$  kg) annually in the Tornionjoki. Annual number of salmon is shown in Fig. 1. Y33= year 1933 and so on.



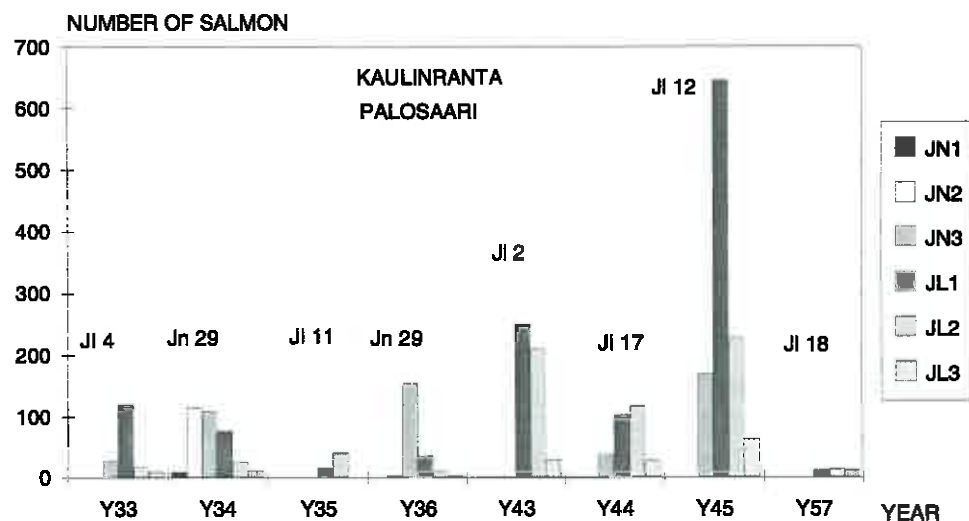
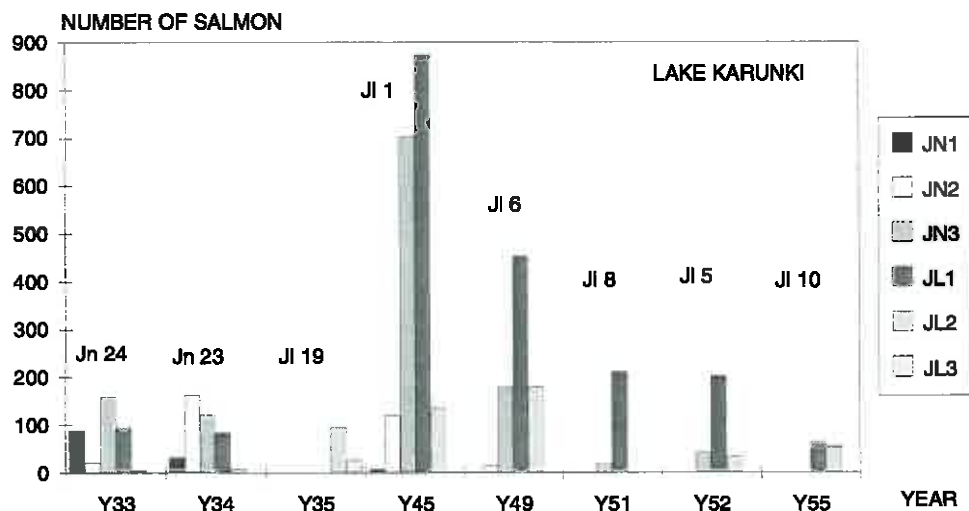
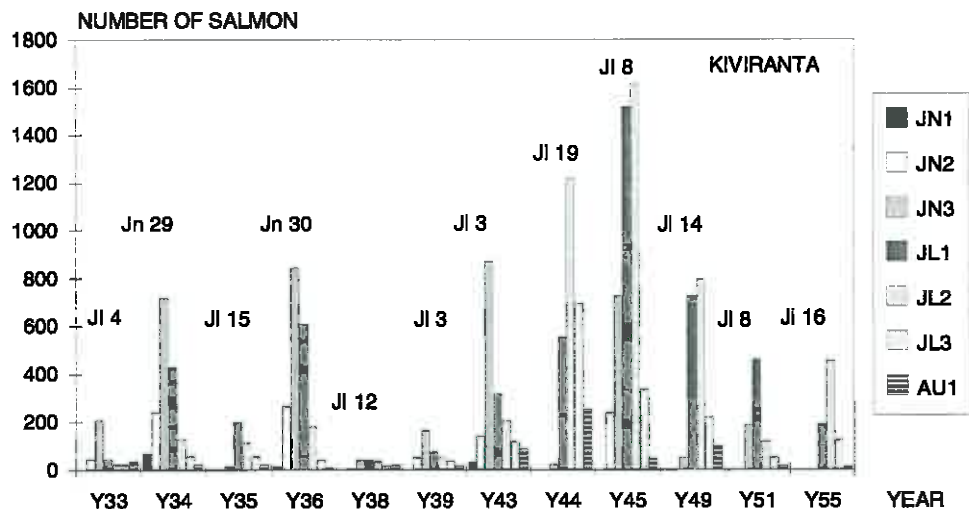
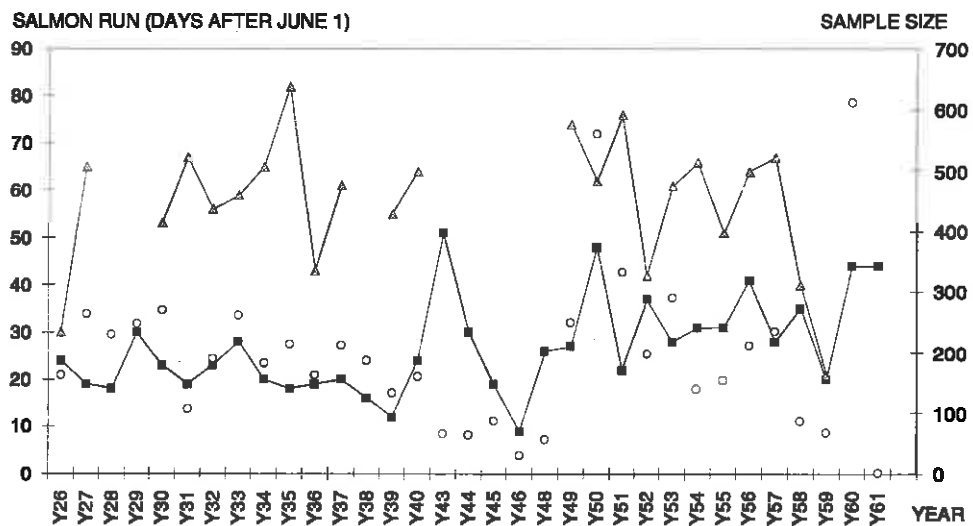


Figure 21. Number of MSW salmon ( $\geq 3$  kg) periodically and annually at Kiviranta, Karunki and Kaulinranta. The annual mean catch dates are also shown. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on. Y33= year 1933 and so on.

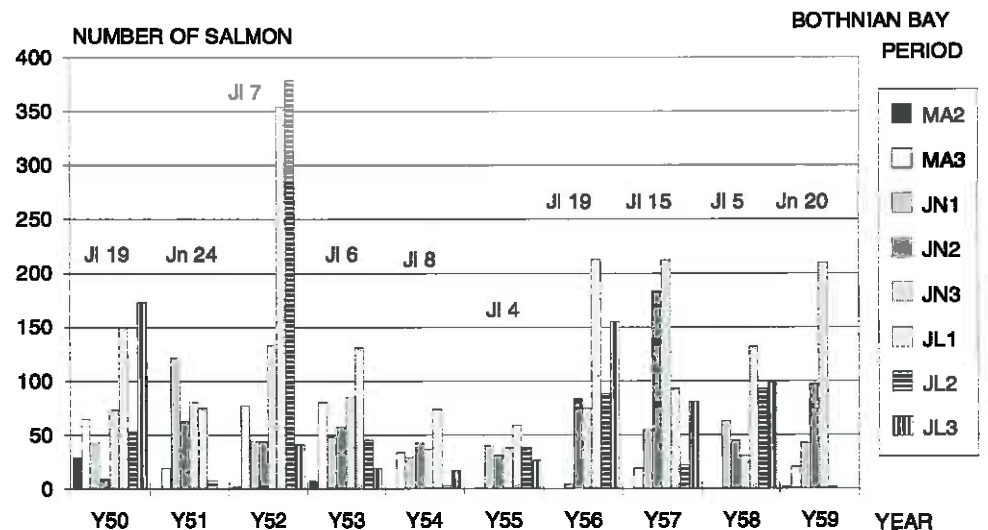
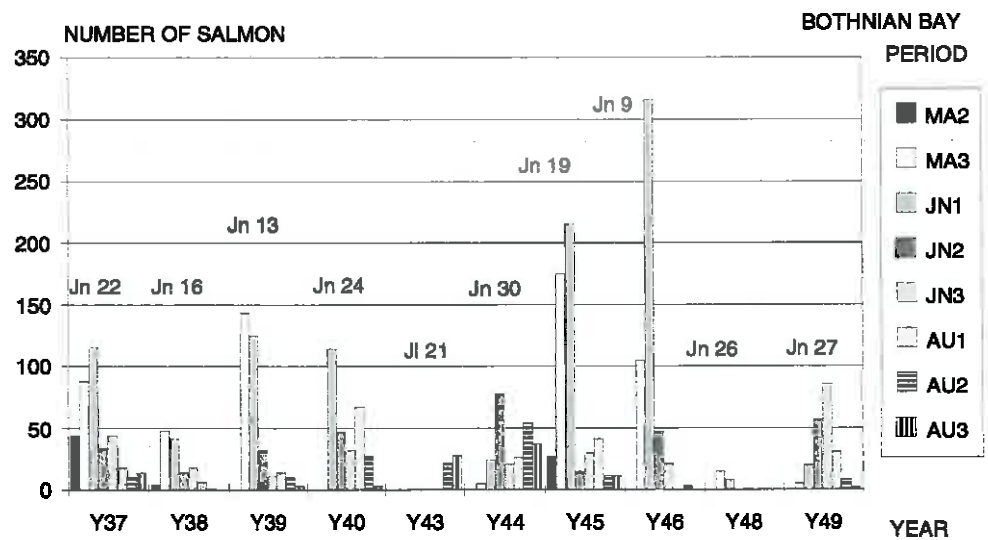
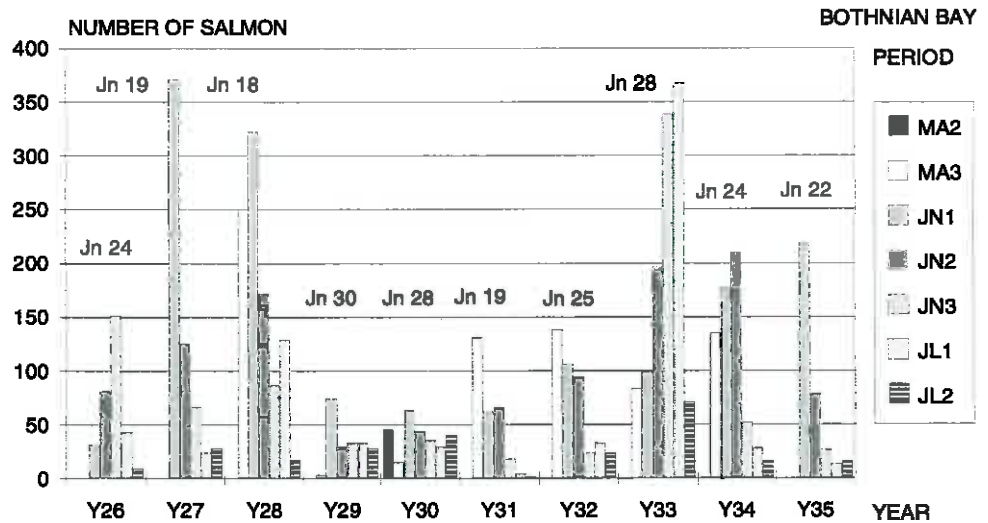
### 3.4.2 Bothnian Bay

The annual mean catch date varied within 6 weeks in 1926-1961. However, the mean catch date varied mostly only within 3 weeks. The earliest mean catch date of MSW salmon ( $\geq 3$  kg) was June 9 in 1946 ( $n = 30$ ) and the latest July 21 in 1943 ( $n = 56$ ) (Fig. 22). The mean catch date of the run was in June in 1926-1940, but in July in 1952-1958 (Fig. 23). Most MSW salmon ( $\geq 3$  kg) were caught in June in 1920 - 1949, but in July in the 1950s and 1SW salmon in July (8 cases) or August (13 cases) in 1926 - 1961 (Fig. 22).



**Figure 22. Annual timing of spawning migration (mean catch date) of MSW salmon ( $\geq 3$  kg) (square) and 1SW salmon ( $< 3$  kg) (triangle) in Bothnian Bay in 1926-1961. Y26= year 1926 and so on. Sample size (circle) = number of catches.**

Peak catches occurred most frequently during the period June 1-10 in 1926-1959 (in 10 out of 30 years) (Fig. 23). The annual peak catches occurred sometimes also during May 20-30 and June 10-July 20.



**Figure 23. Number of salmon periodically and annually in Bothnian Bay. The mean catch dates are also shown. Periods: MA2 = May 11-20, MA3 = May 21-31, and so on. Y26= year 1926 and so on.**

### 3.5 Long-term changes in size of salmon and timing of run

The mean weight of salmon decreased in the Tornionjoki from 1933 to 1957. (Fig. 24). The average weight of migrants was 7 kg in the 1930s and 5 kg in the 1940s and 1950s. The weight of migrants caught in Bothnian Bay also decreased from 1926 to 1960 (Fig. 25). The median weight of salmon was usually about 8-10 kg in the 1920s and 1930s and 6-8 kg in the 1940s and 1950s. The decrease in weight was most marked for MSW salmon ( $\geq 3$  kg) (Fig. 26). Also the proportion of MSW salmon in the catch declined (Fig. 27).

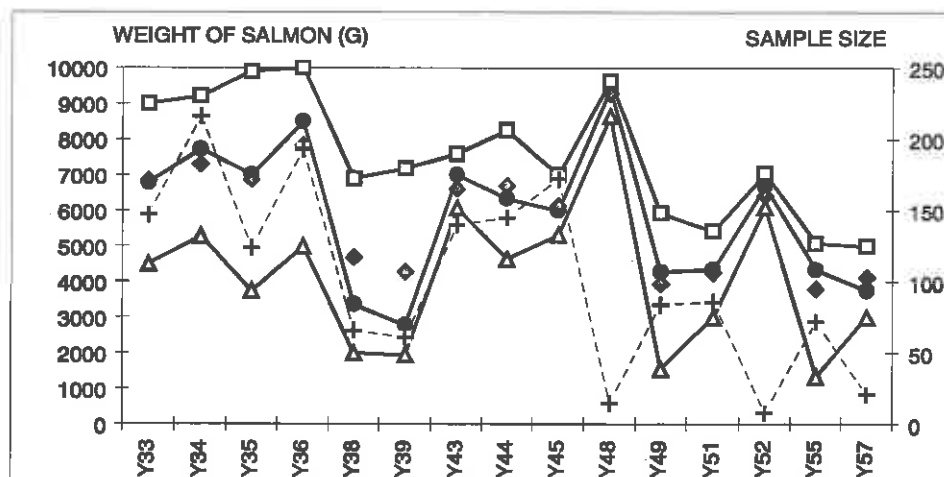


Figure 24. Annual weight of salmon in the Tornionjoki catch in 1933-1957. Median (circle) and upper (square) and lower (triangle) quartiles and mean (rhomb), and the number of catches (plus sign) are shown. Number of fish is shown in Fig. 1. Y33= year 1933 and so on.

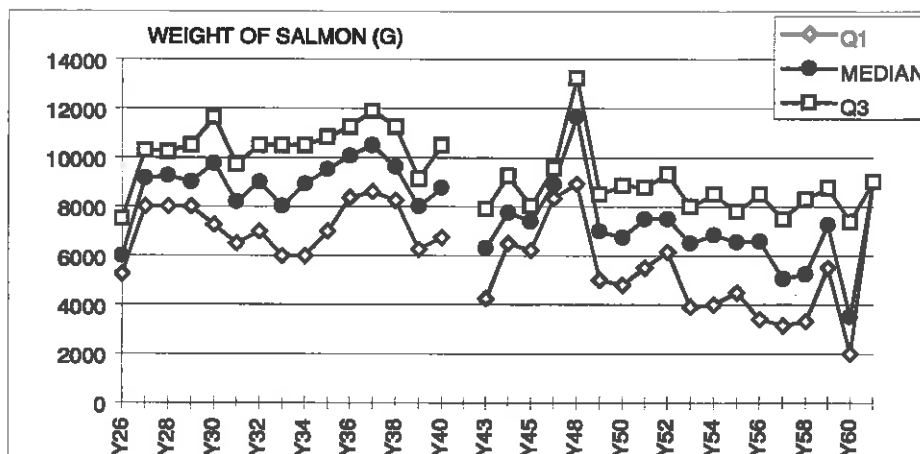


Figure 25. Median weight of salmon annually in Bothnian Bay. Number of fish is shown in Fig. 4. Y26= year 1926 and so on.

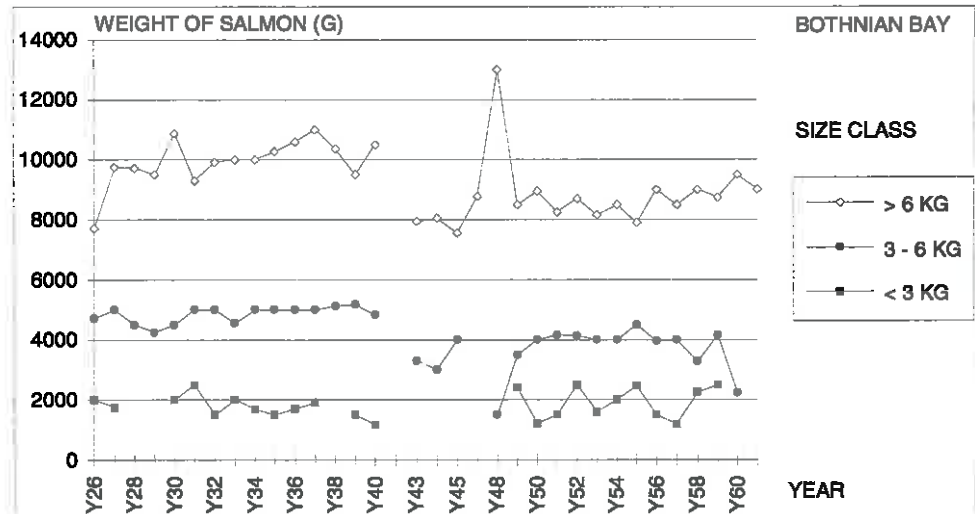


Figure 26. Median weight of large MSW (> 6 kg) and small MSW (3-6 kg) salmon and 1SW (< 3 kg) salmon annually in Bothnian Bay. Number of fish is shown in Fig. 27. Y26= year 1926 and so on.

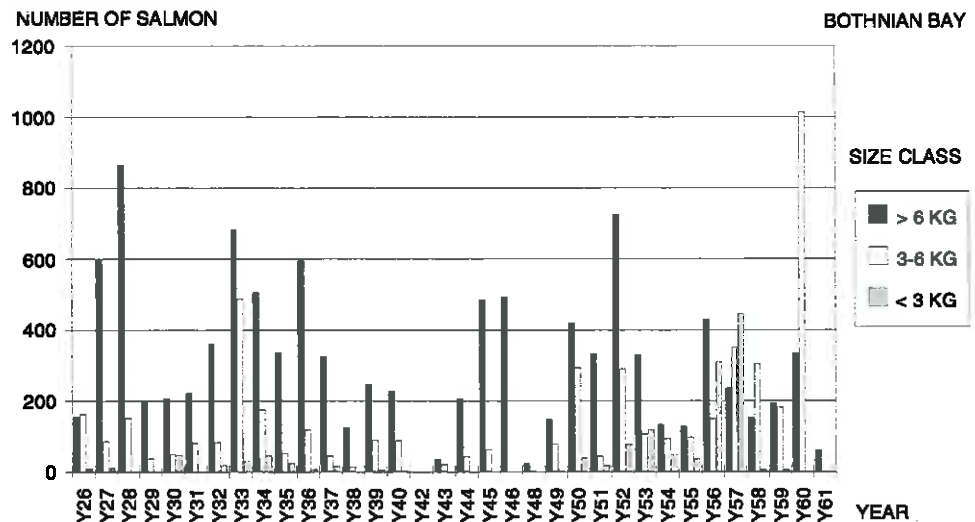
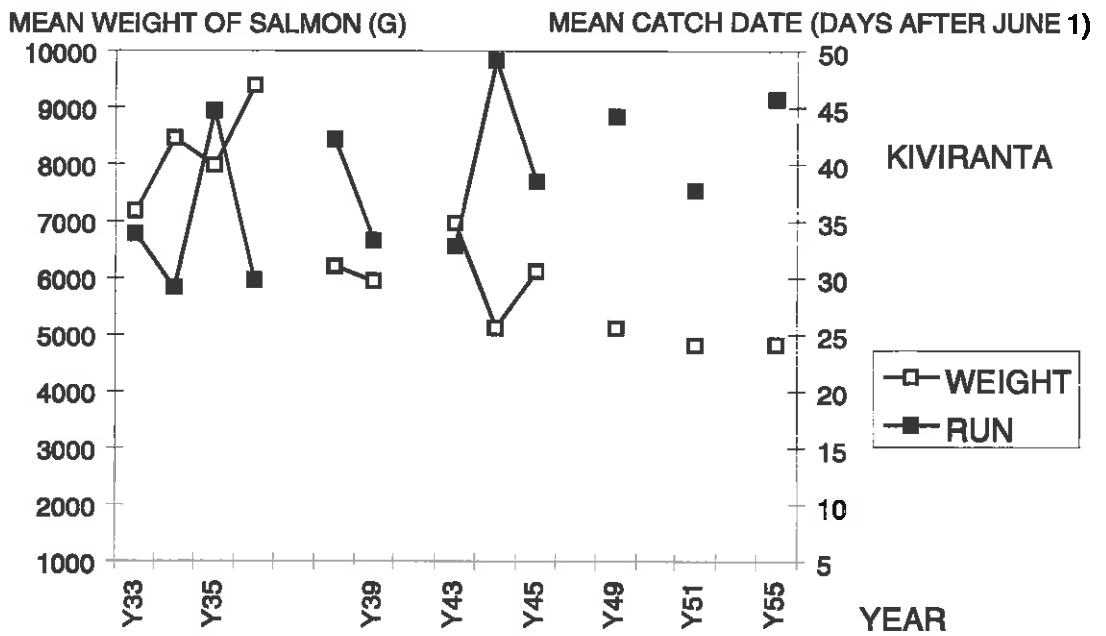
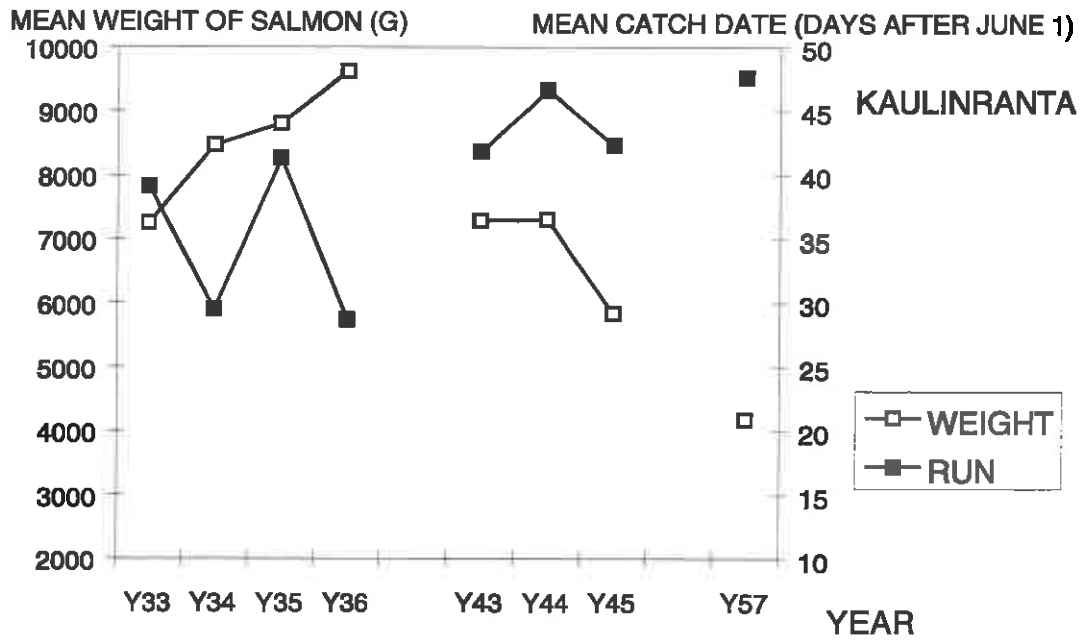
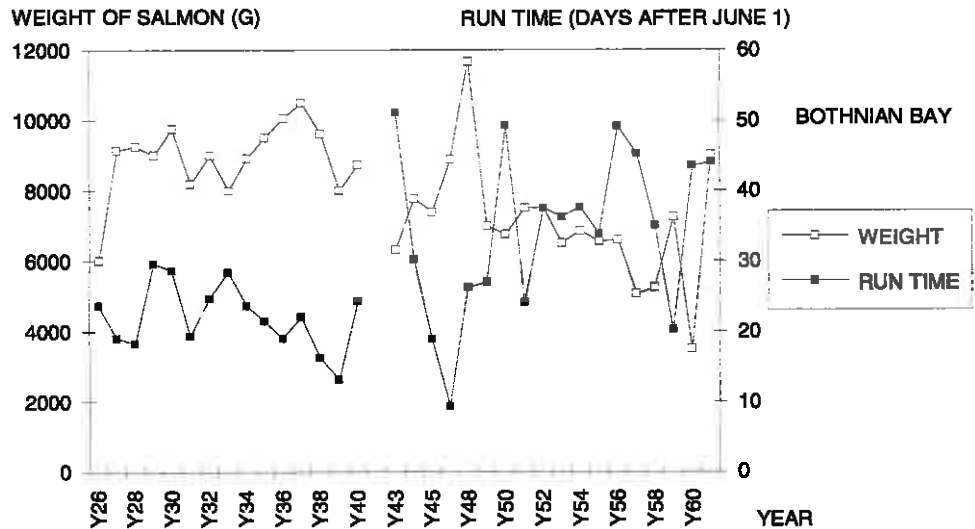


Figure 27. Number of large MSW (> 6 kg), small MSW (3-6 kg) and 1SW (< 3 kg) salmon in Bothnian Bay catch in 1926-1961. Y26= year 1926 and so on.

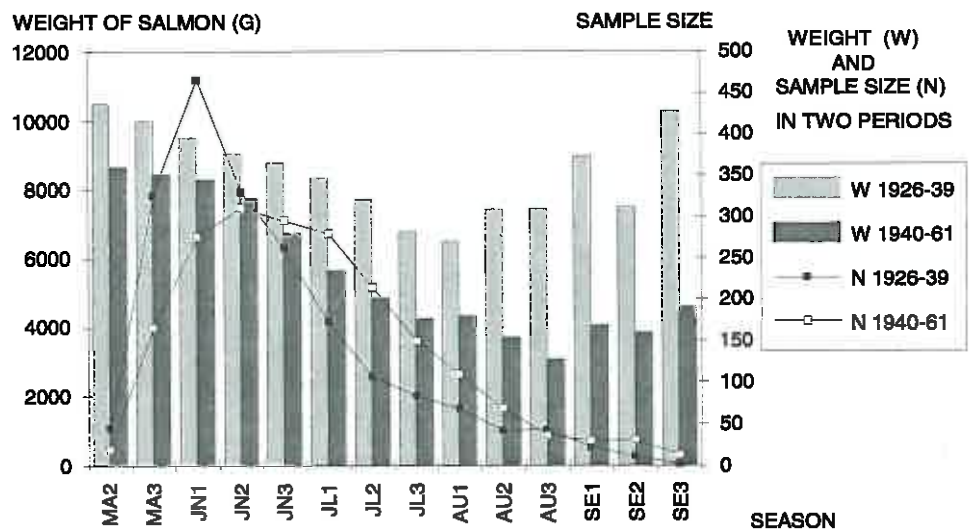
MSW salmon seemed to enter the Tornionjoki later in the 1950s than the 1930s (Fig. 20). The decrease in salmon size together with the delay in the run can also be seen at Kiviranta and Kaulinranta salmon catches (Fig. 28). The run was also delayed in Bothnian Bay with a decrease in the weight of salmon in 1926-1961 (Fig. 29). The mean weight of salmon was 2-3 kg lower in 1940-1961 than in 1926-1939 in all periods of the season in Bothnian Bay (Fig. 30).



**Figure 28. Weight and run timing (mean catch date) of MSW salmon ( $\geq 3$  kg) at Kiviranta and Kaulinranta annually. Number of fish is shown in Fig. 21. Y33= year 1933 and so on.**



**Figure 29. Weight (median) and mean catch date of MSW salmon ( $\geq 3$  kg) in Bothnian Bay in 1926-1961. Number of fish is shown in Fig. 27. Y26= year 1926 and so on.**



**Figure 30. Mean weight of salmon in 1926-1939 and 1940-1961 periodically during the season in Bothnian Bay together with number catches. Number of caught salmon are shown in Fig. 3 and Fig. 10. Periods: MA2 = May 11-20, MA3 = May 21-31, and so on.**

## 3.6 Timing of spawning migration and seasonal hydrological conditions

### 3.6.1 Sea surface temperature

The annual sea water temperature in Bothnian Bay (Plevna) during the period June 10-20 correlated negatively with the timing of catches of small and large MSW salmon ( $r = -0.683$ ,  $p = 0.042$ ,  $n = 9$  and  $r = -0.796$ ,  $p = 0.010$ ,  $n = 9$ , respectively) (Fig. 31). The timing of catches of grilse ( $< 3$  kg) in the Tornionjoki did not correlate with the sea water temperature ( $r = -0.093$ ,  $p = 0.773$ ,  $n = 12$ ).

The sea surface temperature invariably exceeded 10 °C (10.8 - 18.7 °C) during the periods, when the largest number of fish ( $\geq 3$  kg) were caught at Kiviranta (Table 4). The sea water temperature also exceeded 10 °C (10.3 - 15.5) during the periods (June 20-30, July 1-10, July 10-20) of mean catch dates (Table 5) in 1933-1955.

**Table 5. Sea surface temperature during the periods when the largest number of MSW salmon ( $\geq 3$ kg) were caught at Kiviranta in 1933-1955. Mean catch dates of spawning migration at Kiviranta are also shown.**

Year	Mean catch date	Period of peak catch	Water temperature during the peak catch, C°
1933	July 4	June 20-30	11.8
1934	June 29	June 20-30	11.0
1935	July 5	July 1-10	12.6
1936	June 30	June 20-30	14.5
1938	July 12	July 1-10	12.2
1939	July 3	June 20-30	10.8
1943	July 3	June 20-30	11.5
1944	July 19	July 20-30	13.1
1945	July 8	July 20-30	18.7
1949	July 1	July 20-30	2.3
1951	July 8	July 1-10	11.5
1955	July 16	July 10-20	15.5



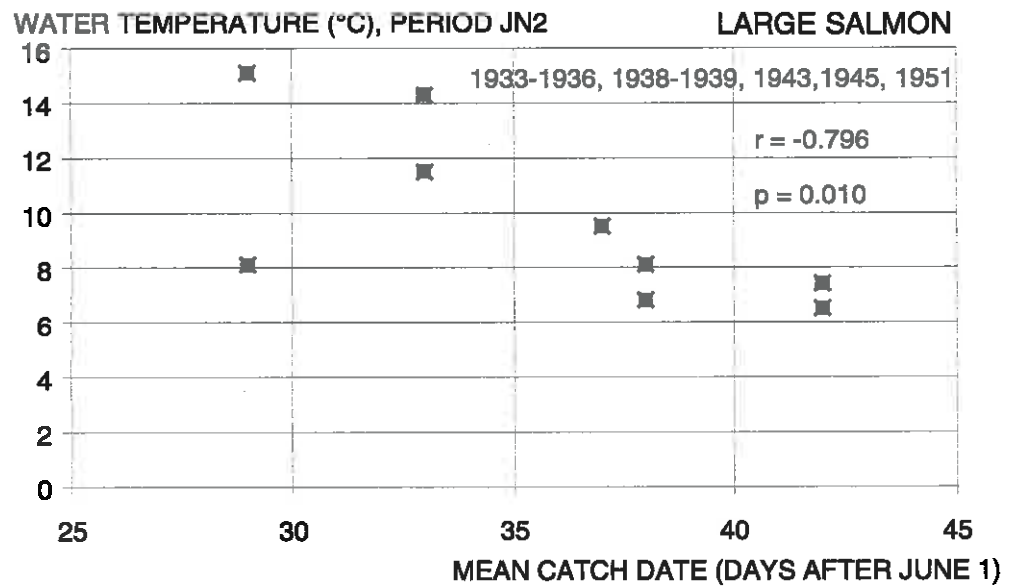
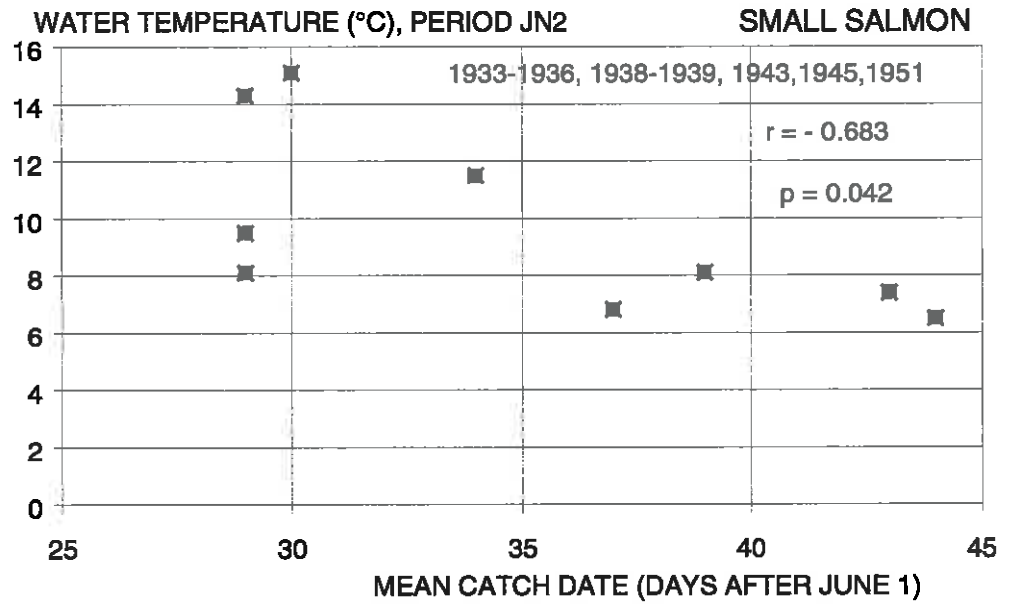
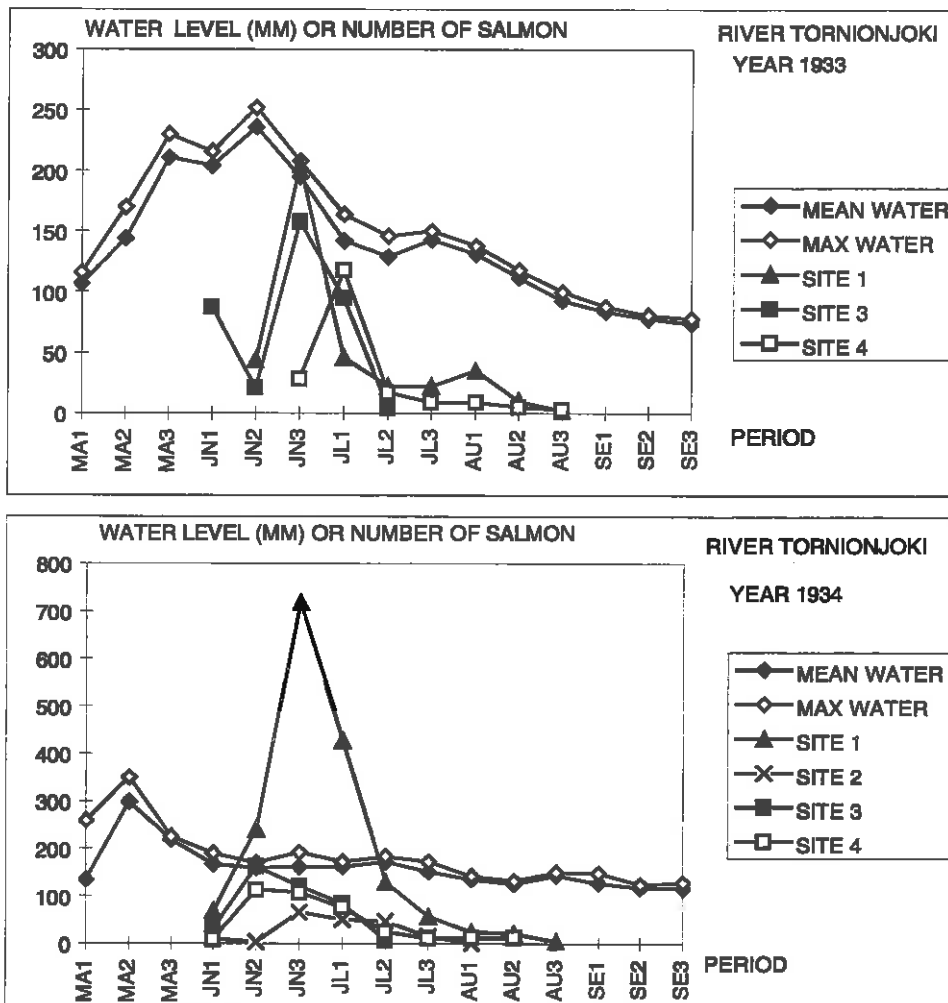


Figure 31. Surface water temperature during the period June 10-20 in Bothnian Bay (Plevna) and mean catch date of small (3-6 kg) and large (> 6 kg) MSW salmon in the Tornionjoki. Results of correlation analysis are shown covering 1933-1936, 1938-1939, 1943, 1945 and 1951.

### 3.6.2 Water level

The maximum and minimum water levels during June 10-20 or June 20-30 did not correlate with the mean catch date of large MSW salmon in 1933-1957 in the Tornionjoki (June 10-20; max. and min. water level & run:  $r = 0.33$ ,  $p = 0.221$ ,  $n = 15$  and  $r = 0.47$ ,  $p = 0.072$ ,  $n = 15$ , respectively). In 1933 the water level was highest during June 10-20 and the peak catch of salmon at Kiviranta was caught 10 days later. In 1934 the mean water level was highest during May 10-20 and the peak catch at Kiviranta was taken 40 days later, during June 20-30 (Fig. 32). The relative water level was 161-212 mm at the measuring point, when the salmon run peaked at Kiviranta ( $\geq 3$  kg) in 1933-1939 (Fig. 33)



**Figure 32.** Water level at Kukkola and timing of run of MSW salmon ( $\geq 3$  kg) periodically during the season in the Tornionjoki in 1933 and 1934. The fishing sites, Kiviranta (1), Alavojakkala (2), Karunki (3) and Kaulinranta (4), are also shown in Table 1. Periods: MA1 = May 1-10, MA2 = May 11-20, and so on.

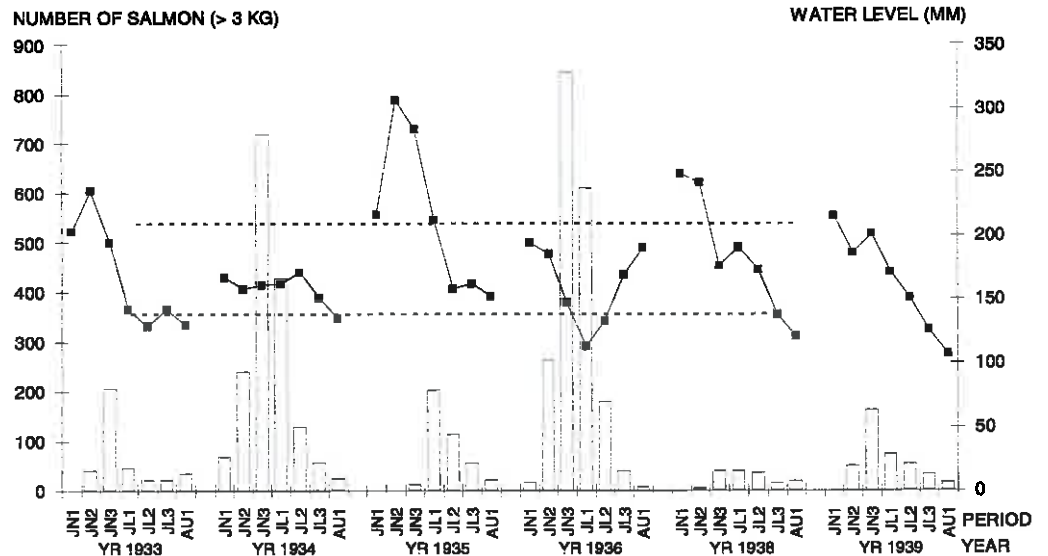


Figure 33. Number of MSW salmon ( $\geq 3$  kg) at Kiviranta and water level periodically at Kukkola in 1933-1936 and 1938-1939. Periods: JN1 = June 1-10, JN2 = June 11-20, and so on.

### 3.6.3 Ice breakup date

The ice breakup date and the mean catch date of large MSW salmon correlated positively in 1933-1957 (Fig. 34) ( $r = 0.514$ ;  $p = 0.049$ ;  $n = 15$ ). The ice breakup date did not correlate with the time of the catch of small MSW salmon ( $r = 0.329$ ;  $p = 0.230$ ;  $n = 15$ ) or 1SW salmon ( $r = 0.437$ ;  $p = 0.103$ ,  $n = 15$ ).

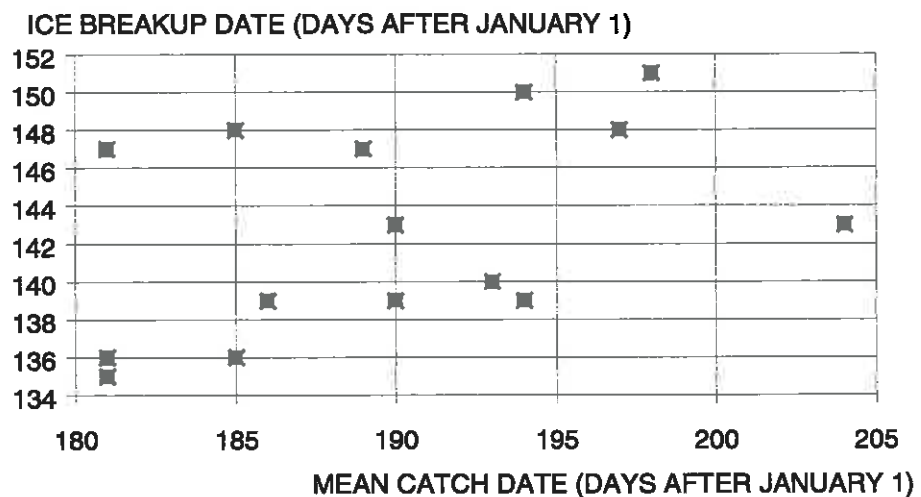


Figure 34. Ice breakup date in Bothnian Bay and mean catch date of large MSW salmon ( $> 6$  kg) in the Tornlonjoki during 15 years between 1933 and 1957.

## 4. DISCUSSION AND LITERATURE REVIEW

### 4.1 Seasonal run

#### 4.1.1 General features of homeward migration

Active return migration of anadromous salmon begins already in the sea after the active feeding migration (Quinn 1984). The homeward migration of salmon is an oriented and rapid event (Healey and Groot 1987) directed by cues acquired during emigration (Brannon 1984). The routes of the return migration to coastal waters depend on the sea surface temperature (Groot and Quinn 1987). Homing, the ability to return to the home river or release site, is usually fairly precise in wild salmon, but less so in translocated salmon, which stray more frequently (Pascual and Quinn 1994, McIsaac and Quinn 1988, Jonsson et al. 1991). Sea-ranched salmon ascend rivers later and descend sooner after spawning than wild fish (B. Jonsson et al. 1990, 1991). Wild and farmed salmon may also move differently in the rivers (Økland et al. 1995, Heggberget et al. 1996). Migration behaviour in the sea and in rivers is controlled by genes and the interannual variation in environmental factors (Saunders 1967, Bams 1976, Power et al. 1987, Groot and Quinn 1987, Pascual and Quinn 1994). Atlantic and Baltic salmon (*Salmo salar*) enter rivers in the summer and autumn months (Jensen et al. 1986, Webb and Hawkins 1989, Mckinnell et al. 1994, Hansen et al. 1995). Atlantic salmon (*Salmo salar*) show stock-specific variations in life history traits, e.g., migration behaviour and size and age at maturity (Saunders 1981). Stock differentiation is a result of adaptation to local environments, and the homing behaviour of salmon maintains reproductive isolation (Leggett 1977).

We showed here that from 1930's to 1950's, the spawning migration of salmon in the Tornionjoki lasted throughout the summer (3-4 months) and that the run seemed to peak usually in the late June - mid-July. So, the run was more intensive early than late in the season. We also found that the timing of the migration was associated with size at maturity of the spawners and also with annual hydrological conditions at the sea

near the river mouth. An interesting development in the time series was that the size at maturity decreased and the timing of the migration delayed from 1920's to 1960's.

#### 4.1.2 The effect of life history characteristics of salmon on the migratory behaviour

Large, old salmon tend to return earlier in the season than small, young ones in both the sea and rivers (Kallio & Pruuki 1987, N. Jonsson et al. 1990, Ikonen and Kallio-Nyberg 1993, McKinnell et al. 1994, Trépanier et al. 1996). Moreover, female salmon are reported to have an earlier run than males (McKinnell et al. 1994, Kallio-Nyberg 1995). Grilse can enter small rivers earlier than multi-sea-winter salmon if water flow is a limiting factor (N. Jonsson et al. 1990). Large salmon with an early run spawn in the upper parts and small salmon with a late run in the lower parts of a stream (Saunders 1967, Hawkins 1987, Summers 1995, 1996). Early running fish also tend to have spent longer in freshwater as juveniles than later running fish (Saunders 1967). A study of Kallio and Pruuki (1987) on the Tornionjoki salmon stock indicated that large female spawners that had spent four years in the river were the first to migrate upstream during the season, and the frequency of salmon spawners with two river years was higher in the lower part than in the middle or upper parts of the river.

Our study clearly supports earlier findings that the largest salmon migrate first in the sea and also enter first in the river. The decrease in the size among ascenders was constant throughout the summer except that some large salmon appeared again very late in the season. Large, very late running salmon were caught both in the sea and in the Tornionjoki. The proportion of grilse was much higher in the catch near the river mouth than in the catch further up in the river. This might indicate that grilse spawn in the lower parts of the river than MSW salmon. However, this can also be an artefact caused by differences in fishing periods and fishing methods.

#### 4.1.3 The effect of meteorological and hydrological conditions on the migratory behaviour

Timing of river entry has been associated with several characteristics, including meteorological and hydrological conditions, and the length and physical difficulty of the ascent (Saunders 1981, Hawkins 1989, N. Jonsson 1991). Water flow and water temperature are the factors most frequently cited as controlling the seasonal timing and rate of upstream migration of salmon in rivers (Banks 1969, Jensen et al. 1986,

Hawkins 1989, Jensen et al. 1989, N. Jonsson 1991, Hansen et al. 1995, Trépanier et al. 1996). An increase in water temperature and river flow is reported to have caused a significant ascent of salmon (Jensen et al. 1986). In Atlantic salmon, most fish were observed to enter freshwater during the hours of darkness (Potter 1988). The importance and level of the environmental factors in regulating the salmon run are specific to individual rivers (Jensen et al. 1986, Jonsson 1991). The salmon ascent does not usually start until the water temperature reaches the value specific for the site and water flow reduces the level specific for the stream (N. Jonsson 1991).

Here, the timing of catches of MSW salmon correlated positively with the seasonal time of the ice breakup date and negatively with the sea water temperature measured during June 10-20. These findings indicate that salmon migrate earlier during warm springs than during cold springs. In the Tornionjoki, the peak water level in springtime was over when the spawning run of MSW salmon peaked, but no other links could be found. Unfortunately, no data was available on the water temperature in the river.

The catch data in the river was based on fishing gears, which were more or less prone to fishing conditions. During the peak flood, fishing was probably less intensive and also less effective. It took also time to establish large salmon weirs in the river. This must be taken into account especially when studying the intensity of the early part of the run or effects of hydrological conditions on the run timing. The mean timing of the salmon run estimated from the catches is probably biased towards late season because of this phenomenon.

## 4.2 Speed of spawning migration

The movement of both water and fish results in a displacement. Thus, the locomotor capacity of fish, the movement of water and the directness of the movement should all be taken into account in analyses of fish migration (Quinn and Leggett 1987). The optimum speed of the return migration of sockeye salmon in the sea is calculated to be about 2 km/h, and salmon cannot sustain speeds greater than about 5 km/h (Quinn and Groot 1984). Tagging experiments in the Baltic indicate that the return migration of salmon from the southern Main Basin of the Baltic to Bothnian Bay (about 1400 km) is very fast, about 40 km/day (Carlin 1969). The ground speeds of maturing Pacific salmon studied with depth-sensing ultrasonic transmitters were 1.9-2.4 km/h (47-57 km /day) in the open sea (Ogura and Ishida 1995). In the home river estuary,

the movement of spawners may also be random and net progress slow, 10 km/day, or then movement may be more oriented, showing a net progress of approximately 25 km/day (Westerberg 1982). The average swimming speed in the river has been assumed to be about 3.3 km/day (Lapointe 1993).

On the basis of earlier findings, our rough evaluations of the speed of upstream migration in the Tornionjoki are realistic. The salmon were, however, caught with different gears and under varying conditions in the river. Thus, catches are not necessarily concomitant with the actual spawning run.

### 4.3 Long-term changes in size at maturity and timing of run

Analyses of catch data have revealed long-term fluctuations in the size of Pacific and Atlantic salmon (Järvi 1948, Ricker 1981, Larsson 1983, Healey 1986, Summers 1995). Historic information on the size and age of Pacific salmon in several stocks demonstrates that size declined between 1951 and 1975, but increased between 1975 and 1981 (Healey 1986). The decrease in size could be a consequence of genetic selection of size-selective fishery. The increase in size and failure of some stocks to demonstrate similar changes in size support the hypothesis that size changes could also be a consequence of long-term variations in the ocean environment (Healey 1986). Larsson (1983) speculated that changes in age-specific size of Baltic salmon stocks were caused by environmental rather than genetic factors. Several reasons have been given for the increase in Baltic salmon size between 1982 and 1992: a decrease in the driftnet effort; abundant prey fish stocks; and warm winters (Karlsson and Karlström 1994).

The decrease observed here in the size of spawners caught in the estuary of the R. Iijoki was not stock-specific, but the annual mean weight of spawners declined in several salmon stocks of the Gulf of Bothnia during that time (Järvi 1948, Lindroth 1965). The decrease in size of spawners was observed to be associated with a delay in the time of upstream migration. Both traits, growth and time of return are known to be inherited characteristics upon which selection may act (Hansen and Jonsson 1991). The change in time of return is probably secondary, being a consequence of changes in the sea age and size of salmon at the run. We can reasonably assume that similar changes in salmon stocks at the same time are affected by common factors in the sea, although causal influences are unexplained in the Baltic Sea and Atlantic Ocean (Summers 1995).

## References

- Bams, R. A. 1976. Survival and propensity of homing as affected by presence or absence of locally adapted genes in two transplanted population of pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33: 2716-2725.
- Banks, J. W. 1969. A review of the literature on the upstream migration of adult salmonids. J. Fish Biol. 1: 85-136.
- Brannon, E. L. 1984. Influence of Stock Origin on Salmon Migratory Behaviour. In: Mechanisms of Migration in Fishes. Edited by J. D. McCleave, G. P. Arnold, J. J. Dodson, & W. H. Neill. NATO Conference Series. Series IV: Marine Sciences. Plenum Press, N. Y., Volume 14. pp. 103-111.
- Carlin, B. 1969. The migration of salmon. Swedish Salmon Research Institute. Report 1969(3): 14-22.
- Groot, C., & Quinn T. P. 1987. Homing migration of sockeye salmon, *Oncorhynchus nerka*, to the Fraser River. Fishery Bulletin, Vol. 85, 3: 455-469.
- Hansen L. P. & Jonsson, B. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 38: 251-258.
- Hansen, L. P., Jonsson, N., & Jonsson, B. 1995. Factors affecting upstream and downstream migration in Anadromous European Salmonids and Catadromous Eel. ICES. Anacat Fish Committee. C. M. 1995/M:31.
- Hawkins, A. D. 1987. The return migration of adult Atlantic salmon to the Aberdeenshire Dee, Scotland. Am. Fish. Soc. Symp. 1: 558-559.
- Hawkins, A. D. 1989. Factors Affecting the Timing of Entry and Upstream Movement of Atlantic Salmon in the Aberdeenshire Dee. In: Proceeding of the Salmonid Migration and Distribution Symposium. Edited by E. Brannon & B. Jonsson. Seattle, WA: University of Washington, School of Fisheries. pp. 101.105.
- Healey, M. C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. In: Salmonid age at maturity. Edited by D.J. Meerburg. Can. Spec. Publ. Fish. Aquat. Sci. 89. pp. 39-52.
- Healey, M.C., & Groot, C. 1987. Marine Migration and Orientation of Ocean-Type Chinook and Sockeye Salmon. American Fisheries Society Symposium, 1: 298-312.
- Heggerberget, T. G., Økland, F., & Ugedal, O. 1996. Prespawning migratory behaviour of wild and farmed Atlantic salmon, *Salmo salar* L., in a north Norwegian river. Aquaculture Research, 27: 313-322.
- Ikonen, E. & Kallio-Nyberg, I. 1993. The origin and timing of the coastal return migration of salmon (*Salmo salar*) in the Gulf of Bothnia. International Council for the Exploration of the Sea. ICES statutory meeting. Anadromous and Catadromous Fish Committee. ICES. C.M. 1993/M:34. Ref. J.



- Jensen, A.J., Heggberget T.G., & Johnsen B.O. 1986. Upstream migration of adult Atlantic salmon, *Salmo salar* L., in the River Vefsna, northern Norway. *J. Fish. Biol.* 29: 459-465.
- Jensen, A.J., Johnsen, B.O., & Hansen, L.P. 1989. Effect of river flow and water temperature on upstream migration of adult Atlantic salmon *Salmo salar* L. in the River Vefsna, northern Norway. *In: Proceeding of the Salmonid Migration and Distribution Symposium. Edited by E. Brannon & B. Jonsson.* School of Fisheries, University of Washington, Seattle, WA, and Norwegian Institute for Nature Research, Trondheim. pp. 140-146.
- Jonsson, B., Jonsson, N., & L. P. Hansen 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? *Behav. Ecol. Sociobiol.* 26: 225-230.
- Jonsson, B., Jonsson, N., & L. P. Hansen 1991. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, 98: 69-78.
- Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. *Nordic J. Freshw. Res.* 66: 20-35.
- Jonsson, N., Jonsson B., & L. P. Hansen 1990. Partial segregation in the timing of migration of Atlantic salmon of different ages. *Anim. Behav.* 40: 313-321.
- Järvi, T. H. 1948. On the periodicity of salmon reproduction in the Northern Baltic area and its causes. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.* 119: 1-131.
- Kallio-Nyberg, I. 1995. Villit naaraat vaeltavat ensimmäisinä. *Suomen Kalastuslehti*, 7: 6-9.
- Kallio, I., & Pruuki, V. 1987. The diversity and seasonal spawning migration of salmon (*Salmo salar* L.) in the R. Tornionjoki. *In: Proc World Symp. on Selection, Hybridization, and Genetic Engineering in Aquaculture.* Edited by Tiews. Vol. 1 Berlin 1987. pp. 165-176.
- Karlsson, L., & Karlström, Ö. 1994. The Baltic salmon (*Salmo salar* L.): its history, present situation and future. *Dana*, 10: 61-85.
- Karlsson, L., Karlström, Ö., & Hasselborg, T. 1994. Timing of the Baltic salmon run in the Gulf of Bothnia - influence of environmental factors on annual variation. *ICES. Anadromous and Catadromous Fish Committee. C.M. 1994/ M:17.* 15 p.
- Lapointe, A. 1993. Suivi radiotéléométrique de ouananiches (*Salmo salar*) en montaison dans le bassin hydrographique de la rivière Mistassini en 1988 et 1989. *Ministère du Loisir, de la Chasse et de la Pêche, Direction régionale du Saguenay-Lac-St-Jean, Service de l'aménagement et de l'exploitation de la faune, Jonquière. Ref. Trépanier et al. (1996).*
- Larsson, P.-O. 1983. Growth of Baltic salmon in the sea . Some characteristics of the Baltic salmon (*Salmo salar* L.) population. Ph.D. thesis, Univ. Stockholm. 80 pp.
- Leggett, W. C. 1977. The ecology of fish migrations. *Am. Rev. Ecol. Syst.* 8: 285-308.
- Leppäranta, M. & Seinä, A. 1985. Data of freezing, maximum annual ice thickness and breakup of ice on the Finnish coast during 1830-1984. *Merentutkimuslaitos. Sisäinen raportti.* Helsinki 27.7.1985.
- Lindroth, A. 1965. The Baltic salmon stock - Its natural and artificial regulation. *Mitt. Internat. Verein. Limnol.* 13: 163-192.

- McIsaac, D. O., & Quinn, T. P. 1988. Evidence for a Hereditary Component in Homing Behaviour of Chinook Salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 45: 2201-2205.
- McKinnell, S., Lundqvist, H., & Johansson, H. 1994. Biological characteristics of the upstream migration of naturally and hatchery-reared Baltic salmon, *Salmo salar* L. *Aquaculture and Fisheries Management* 1994, 25 (Supplement 2): 45-63.
- Ogura, M. & Ishida, Y. 1995. Homing behaviour and vertical movements of four species of Pacific salmon (*Oncorhynchus spp.*) in the central Bering Sea. *Can. J. Fish. Aquat. Sci.* 52: 532-540.
- Økland, F., Heggberget, T. G., & Jonsson, B. 1995. Migratory behaviour of wild and farmed Atlantic salmon (*Salmo salar*) during spawning. *J. Fish Biol.* 46: 1-7.
- Pascual, M. A., & Quinn T. P. 1994. Geographical patterns of straying of fall chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), from Columbia River (USA) hatcheries. *Aquaculture and Fisheries Management* 25, (Supplement 2): 17-30.
- Potter, E. C. E. 1988. Movement of Atlantic salmon, *Salmo salar*, L., in an estuary in south-west England. *J. Fish Biol.* 33 (Supplement A): 153-159.
- Power, G., Power, M. V., Dumas, R., & Gordon, A. 1987. Marine Migration of Atlantic Salmon from Rivers in Ungava Bay, Quebec. *American Fisheries Symposium*, 1: 364-376.
- Quinn, T. P. 1984. An experimental approach to fish compass and map orientation. *In: Mechanisms of Migration in Fishes. Edited by J. D. McCleave, G. P. Arnold, J. J. Dodson, & W. H. Neill. NATO Conference Series. Series IV: Marine Sciences, Plenum Press, N. Y. pp. 113-123.*
- Quinn, T. P. & Groot, C. 1984. Pacific Salmon (*Oncorhynchus*) Migrations: Orientation versus Random Movement. *Can. J. Fish. Aquat. Sci.* 41: 1319-1324.
- Quinn, T. P., & Leggett, W. C. 1987. Perspectives on the Marine Migration of Diadromous Fishes. *American Fisheries Society Symposium*, 1: 377-388.
- Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 38: 1636-1656.
- Romakkaniemi, A., Pakarinen, T. & Ikonen, E. 1995. Spatial stock composition of salmon on the basis of tag returns in the northern Bothnian Bay fishery. *ICES C.M.* 1995/M:27. 11 p.
- Saunders, R. L. 1967. Seasonal pattern of return of Atlantic salmon in the Northwest Miramichi River, New Brunswick. *J. Fish. Res. Bd. Can.* 24: 21-32.
- Saunders, R. L. 1981. Atlantic salmon (*Salmo salar*) stocks and management implications in the Canadian Atlantic Provinces and New England, USA. *Can. J. Fish. Aquat. Sci.* 38: 1612-1625.
- Summers, D. W. 1995. Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers. *Fisheries management and Ecology*, 2: 147-156.
- Summers, D. W. 1996. Differences in the time of river entry of Atlantic salmon, *Salmo salar* L., spawning in different parts of the River Esk. *Fisheries Management and Ecology*, 3: 209-218.

Trépanier, S., Rodriquez, M. A., & Magnan, P. 1996. Spawning migrations in landlocked Atlantic salmon: time series modelling of river discharge and water temperature effects. *J. Fish Biol.* 48: 925-936.

Webb, J., & Hawkins A. D. 1989. The Movements and Spawning Behaviour of Adult Salmon in the Girnock Burn, a Tributary of the Aberdeenshire Dee, 1986. *Scott. Fish. Res. Rep.* 40: 1-42.

Westerberg, H. 1982. Ultrasonic tracking of Atlantic salmon (*Salmo salar* L.) I. Movement in coastal regions. *Rep. Inst. Freshwat. Res., Drottningholm* 60: 82-101.

