Comparison of two methods of estimating atlantic salmon (Salmo salar) wild smolt production

Jean-Luc J.-L. Baglinière, Gérard Maisse, A. Nihouarn

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Jean Luc Baglinière and Gérard Maisse

Station de Physiologie et d'Ecologie des Poissons - INRA
65 route de St-Brieuc - 35042 Rennes Cédex - France

and Alix Nihouarn

Délégation Régionale de Bretagne-Basse Normandie - CSP
84 rue de Rennes - 35510 Cesson Sévigné - France

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Two methods to estimate wild smolt production of Atlantic salmon, *Salmo salar* L., were compared in the River Oir, a tributary of the River Sélune in Lower Normandy, France over 5 years. The first estimated smolt number by analysing the characteristics of the habitat and those of the juvenile salmon population in autumn. The second method estimated smolt number from trapping downstream migrants.

The study showed that 1+ smolts came mainly from the upper modal growth group of the 0+ autumnal population and the over winter survival rate depended on winter conditions, age-class, size and state of maturity. The comparison between the two methods showed that the 1+ and 2+ smolt number estimations could differ according to year and age-class. The two methods were in best agreement for the youngest age class (1+), the most abundant one in this study.

Different aspects are discussed to assess the reliability of the habitat method and to improve agreement between the two methods used.

Deux méthodes d'estimation de la production naturelle en saumoneaux de saumon atlantique (*Salmo salar* L.) sont comparées sur la rivière Oir, affluent de la Sélune (Basse-Normandie, France) durant 5 ans. La première estime le nombre de saumoneaux à partir des caractéristiques automnales de l'habitat et de la population de jeunes saumons. La seconde méthode évalue le nombre de saumoneaux à partir des captures faites par piégeage durant la dévalaison.

L'étude montre que les saumoneaux 1+ proviennent essentiellement du mode haut de la bimodalité observée en automne dans la population de 0+ et que le taux de survie hivernale dépend des conditions climatiques, de l'âge et de l'état de maturité. La comparaison entre les deux méthodes montre que les estimations du nombre de saumoneaux 1+ et 2+ peuvent différer selon l'année et l'âge. Les résultats obtenus apparaissent beaucoup plus proches pour la plus jeune classe d'âge (1+) qui est la plus abondante dans l'étude.

Différents aspects sont discutés pour connaître la fiabilité de la méthode à partir des caractéristiques automnaux de l'habitat et de la population de juvéniles et pour améliorer l'agrément entre les deux méthodes utilisées.

Introduction

A knowledge of smolt production is useful for the management of an Atlantic salmon (*Salmo salar* L.) population. There are two methods for estimating this production in French rivers, characterized by the presence of 1+ and 2+ age-classes in the smolt population (Prévost 1987). One is the trapping of juvenile salmon during downstream migration to the sea. It requires data on trapping efficiency in relation to water discharge conditions. The other method has been perfected by Baglinière and Champigneulle (1986). It is based on the characterization of the parr autumnal population in relation to habitat characteristics. The two methods have not previously been compared.

The establishment of an Atlantic salmon study program using a trap in the River Oir (a tributary of the River Sélune, Lower Normandy), has enabled comparison of these two methods for a 2-yr period (Baglinière et al. 1988). Analysis of these results showed a relatively good reliability of the method which used autumnal population characteristics. But it also demonstrated the need of further work in order to confirm certain hypotheses and to improve the precision of some parameters used in this method. Thus, after analysis of the characteristics of standing and migrating juvenile salmon populations in the River Oir, smolt numbers were estimated by both habitat and trapping methods and were compared over a 5-yr period.

Materials and Methods

Study Area (Fig. 1)

The study was carried out on the River Oir, a right bank tributary of the downstream part of the River Sélune in the Armorican Massif (Lower Normandy), from 1985 to 1990. The characteristics of the environment have been described by Baglinière et al. (1988). Briefly the River Sélune is 75 km long with a drainage area of 1010 km^2 and a mean slope of 1.9 ‰. It flows into The Channel in a common estuary with the River Sée. The Atlantic salmon production area is limited to the main river downstream of La Roche qui boit an impassable dam at 16 km from the sea, and two tributaries, the Rivers Beuvron and Oir. This last tributary is 19.5 km long with a drainage area of 85 km^2. The salmon production area is distributed over 12.3 km of the main-stem river and some tributaries, for example, Pont Levesque (5.4 km) and La Roche brook (3.4 km), between the trapping site and Buat watermill (impassable dam). The upstream and downstream traps are located at Cerisel Mill, 2.3 km before the confluence with the River Sélune (Fig. 2). Downstream trapping is not total except in conditions of low water discharge.

Characteristics o Habitat and Juvenile Populations

Habitats in the main-stem river were classified into four categories (Table 1) in July 1985, using the parameters proposed by Baglinière and Champigneulle (1986), namely, depth, velocity and substrate. The stretch was partitioned into four zones because of the non-uniform distribution of habitats categories in the main river (Z_1, Z_2, Z_3) and the necessity of taking La Roche brook into account (Z_4). Over the 2.25 km of the downstream water course of this tributary colonized by salmon, there is a fast run-riffles sequence with a rough substrate. Production surface area (riffle and runs of the river and La Roche Brook) was estimated at 44.982 m^2 (96.8% of the water surface area). This value may have decreased to 10% for the dry years of 1988 and 1989 .

The standing population was recorded by an electrofishing census (De Lury's method):

— in different sectors (62 to 666 m^2) of the main river in October from 1985 to 1989.

— on the whole main-stem and in a small downstream sector (307 m^2) of the La Roche Brook in October 1986.

— in several sectors of the La Roche Brook (23 to 224 m^2) in October 1987 and on all the water course of this tributary colonized by salmon in October 1988, 1989 and May 1989.

Whichever capture (trapping and electrofishing) method was used, all fish were measured (fork length in mm) and scale samples taken from almost all juvenile salmon. Spermating males were detected by pressure on the flanks. The stage of juvenile migrating salmon (parr, presmolt, smolt) was defined according to morphology and the usual colour criteria (Johnston and Eales 1967).

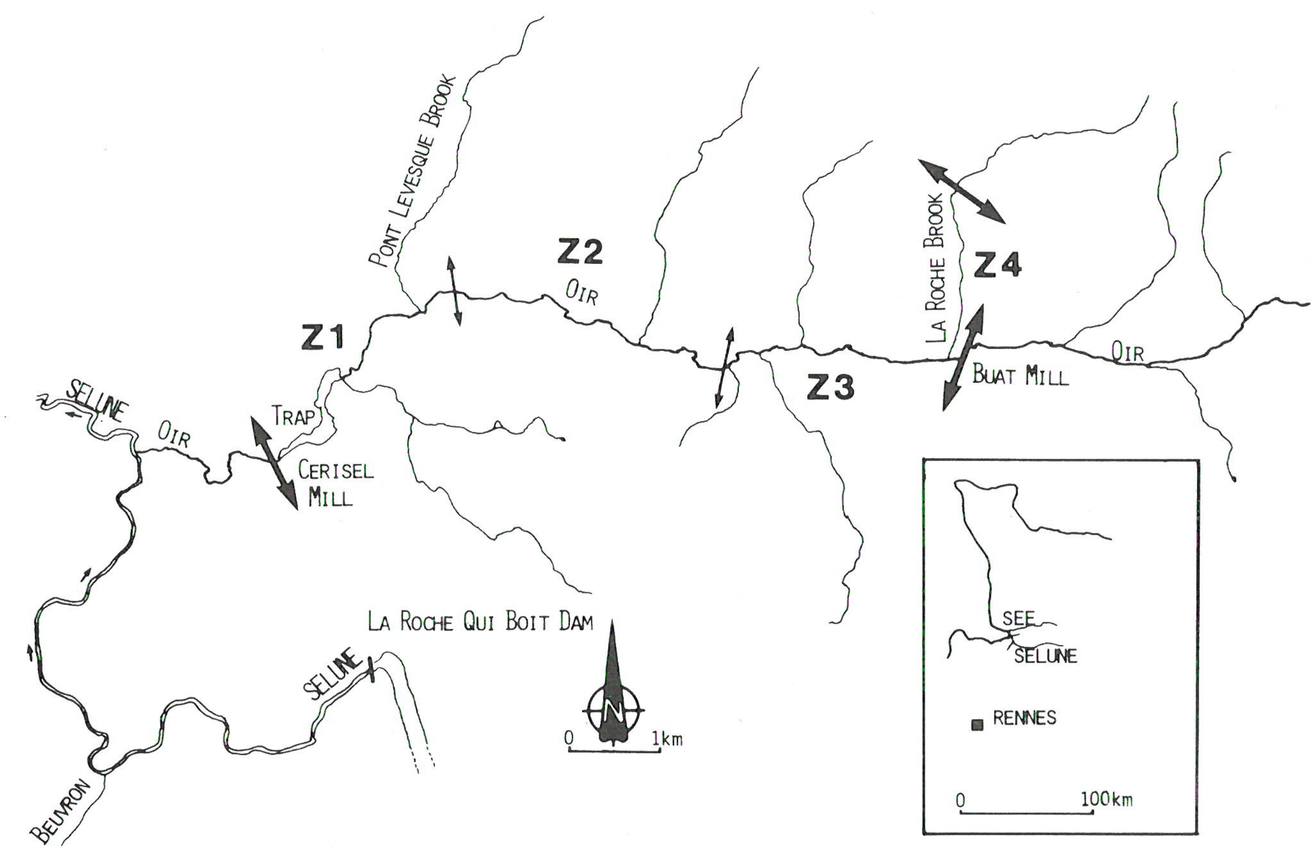

FIG. 1. The map of the River Oir and localization of four studied zones (Z_1, Z_2, Z_3 on the main river and Z_4 in La Roche Brook). ◄—► limit of study area ◄—► limit of zone

TABLE 1. Physical characteristics and water surface area of different habitat types in the R. Oir.

Type of habitat	Depth (cm)	Current Velocity(V) (cm/s)	Nature[a] of substrate	Aquatic vegetation	Percentage by zone			Water surface area	
					Zone 1 (4.4 km)	Zone 2 (4.7 km)	Zone 3 (3.2 km)	m²	%
Riffle	< 25	> 40	Type 2 or 3	Present	24.2	20.7	52.5	13,878	32.7
Fast run	< 40	30< V <40	Type 2 or 3	Present	38.3	29.1	27.6	13,043	30.7
Slow run	> 40	20< V <30	Type 1, 2 or 3	Absent	32.0	47.2	17.1	14,061	33.1
Pool	> 60	< 20	Type 1, 2 or 3	Absent	5.5	3.0	2.8	1,483	3.5
TOTAL								42,465	100.0

[a]Nature of substrate was defined from three types: type 1 uniformly sandy; type 2: mixture of sand, gravels and pebbles (> 60% of fine materials cover the bottom surface); type 3: coarse (> 40% coarse materials (Ø > 2 cm) cover the bottom surface).

Estimation of Smolt Production

1. Baglinière and Champigneulle's Method (1986) (Habitat Method)

This method is based on three points:

a) Estimation of 0+ and 1+ parr autumnal density in sectors representative of different habitats in the main river and the brook. Pool habitat was neglected owing to the near absence of juveniles (Baglinière and Champigneulle 1982; Baglinière and Arribe-Moutounet 1985). Population densities were estimated by Seber and Le Cren's (1967) method and age structure was determined by scale reading (Baglinière 1979).

b) Analysis of autumnal size frequency distribution in 0+ parr. The existence of size bimodality was determined either using the Battacharya method (Laurent and Moreau 1973) or by direct observation of the size histogram in the field. To determine if 1+ smolts came from the upper mode as reported by Thorpe et al. (1980), 0+ salmon were marked differently according to size (1985 or 1987) or presence in one of the two modal groups.

c) Estimation of over winter survival rate in relation to size, age and state of maturity from capture-recapture experiments (tagging by either alcyan blue injection into the fin either fin-clipping or nasal microtag). Thus a mean value of the overwinter survival rate was calculated from:

— recapture of two age-classes of fish during either downstream migration (trapping) or subsequently (electrofishing census in May and October).

— value of the survival rate of 1+ parr between May and October (72.4%) in La Roche Brook in 1989.

The mean value obtained for each age-class has been increased by 5% to take into account the negative effects of handling and tagging on the survival of fish (Mears and Hatch 1976; Johnson and Ugedal 1988), tag loss (mainly with microtags) and incomplete data or recapture for certain years.

The estimated number of 1+ smolts produced by zone and by type of habitat data was expressed by the following equation (1) taking into account an overwinter survival rate in spermating fish half of that in immature fish (Myers 1984).

(1) $N = d \times A \times p \times s^{im}(1 - m/2)$ where

d = autumnal density of 0+ salmon (n/100 m²)
A = surface area of the habitat (in 100 m²)
} Parameters in relation to type of habitat

p = proportion of 0+ salmon in the upper mode
m = proportion of 0+ spermating in the upper mode
s^{im} = overwinter survival rate in immature fish
} Parameters in relation to zone

The same equation was applied to 1+ salmon for the estimation of 2+ smolts production. In this case, p was very close to 1, as the 2+ parr population recorded in autumn was very low (0 to 0.2%), and m was the proportion of spermating fish observed in the sample.

Total smolt production was estimated in three different ways:

— by adding the number of smolts produced by zone and by type of habitat (habitat cumulative method). As La Roche Brook was not electrofished in 1985, the density used in the estimation was that of the riffle habitat located in the main river near its confluence with the brook. Density in this riffle was always closest to that observed in the tributary in other years.

— by calculating the number of smolts produced in the whole main river from the mean values of the parameters and adding that estimated in La Roche Brook (whole basin method habitat).

— in using the estimation made from the total census of the River Oir and from the downstream part of the tributary in 1986 (total census).

2. Smolt Trapping Method

Trap efficiency was estimated each year from capture-recapture experiments made in different water discharge conditions. Tagged juvenile salmon were released at the same site above the trap every year (Fig. 2). The number of downstream migrants (from parr to smolt) was estimated by the following equation (2)

(2) $N = \Sigma N_i / e_i$ where

N_i = number of downstream migrants trapped during the time corresponding to the water discharge *i*

e_i = efficiency of the trap for water discharge *i*

In both methods, the smolt number was calculated in taking into account the confidence limits (95%) of density and each proportion (percentages of spermating fish and 0+ salmon in upper mode).

Data were analysed by standard statistical methods (χ^2, Student's *t*-test, analysis of variance, linear regression).

Results

Juvenile Population in Autumn

Population density varied, according to environment (brook, river), habitat, age-class and year from 0 to 39.1 n/100 m^2 (Table 2). The highest values were always observed in La Roche Brook and in the riffle habitat in the main river where 82% of the juvenile population was concentrated, on average, during the study period. Almost all the population was 0+ and 1+ year old, as 2+ fishes were present in the sample only in 1988 (0.2%) and 1989 (0.8%). In the main river, annual variation of the population density was twice-fold higher for 0+ salmon than for 1+ fish. In the tributary, this annual variation was similar for two age classes. Throughout the total study period, the 0+ population was the most abundant in the whole basin: 60 to 89% of total population in River Oir and 65 to 90% in the brook.

Mean fish size for the two age-classes depended strongly on zone (p<0.01, Table 3). It was largest in the downstream part of the main river (Z_1), and lowest in the tributary (Z_4) and similar in the two other zones. Annual variations, within zones, were smaller as significant differences were observed only in zones 3 and 4 for 0+ (p<0.01) and in zone 2 for 1+ (p<0.02). Nevertheless, for the total sample in the main river, the mean size of the two age-classes was higher in 1985 and 1988 (0+: p<0.01; 1+: p<0.05; Table 3).

Generally the 0+ salmon population showed a size bimodality in each zone of the main river but not in La Roche Brook (Z_4) from 1987 to 1989 (Table 3). The percentage of 0+ individuals in the upper mode and the difference between modal length changed according to zone and annual growth conditions. There was a significant correlation (r=0.727, p<0.01) between the percentage of upper mode individuals (p) and the mean fork length (Lf) of the 0+ population. A linear regression was calculated between those two parameters (3) $P = -0.9515 + 0.0157\ Lf$ (n = 17).

The proportion of 1+ spermating fish was high and generally greater than 50% (Table 4). On the other hand, the proportion of spermating 0+ salmon was much lower and varied greatly according to the year. Spermating fish of this age-class were always distributed in both modal growth groups.

Annual distribution of spermating fish changed according to zone (0+: p<0.01; 1+: p<0.05).

Migrating Juvenile Population (Table 5)

The number of salmon trapped over the entire study period ranged from 282 in 1987 to 888 in 1986. There was a balanced annual distribution of the two age-classes (1+ and 2+) in 1987 but a majority of 1+ fish in the other years. Mean size of 1+ salmon differed according to year (p<0.01) while mean 2+ fish size was higher only in 1986 (p<0.01).

Downstream migration took place between November 10th and May 15th, depending on the year,

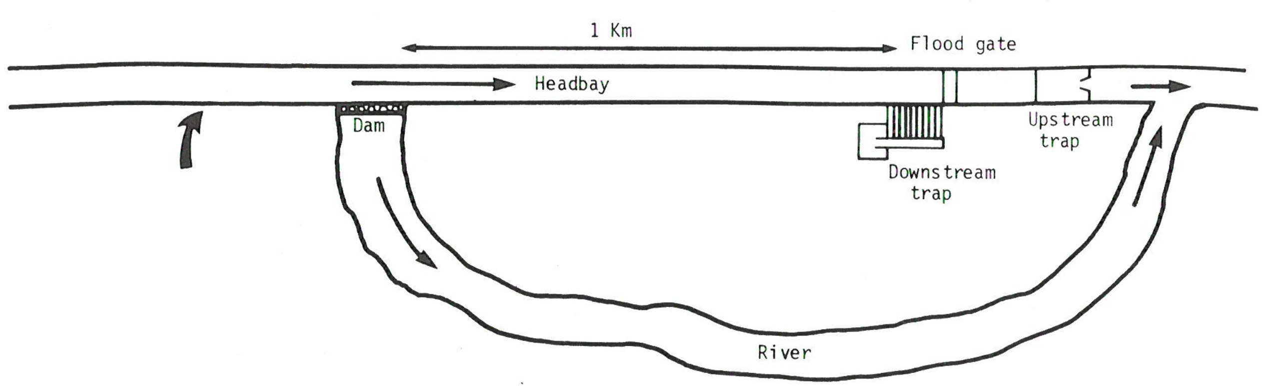

FIG. 2. Localization and scheme of the downstream trap. Release site of tagged juvenile salmon.

TABLE 2. Juvenile salmon density (n/100 m^2 ±95% confidence limits) for each habitat type in the four zones of the River Oir.

			Density (n/100 m^2)									
			1985		1986		1987		1988		1989	
		Habitat	0+	1+	0+	1+	0+	1+	0+	1+	0+	1+
RIVER	Z_1	riffle	2.2(±0.0)	2.9(±0.0)	2.3(±0.0)	2.3(±0.0)	0.9(±0.0)	1.6(±0.0)	7.8(±1.3)	0.3(±0.0)	5.9(±0.2)	0.6(±0.0)
		run[a]	0.3(±0.0)	1.0(±0.0)	0.0(±0.0)	0.0(±0.0)	0.3(±0.0)	0.0(±0.0)	0.0(±0.0)	0.3(±0.0)	1.3(±0.0)	0.0(±0.0)
	Z_2	riffle	22.7(±0.5)	3.4(±0.0)	7.9(±0.8)	4.0(±0.0)	1.4(±0.0)	3.7(±0.0)	16.7(±0.2)	0.6(±0.0)	16.1(±0.4)	3.7(±0.2)
		run	8.4(±0.7)	0.1(±0.0)	2.6(±0.8)	1.4(±0.0)	0.0(±0.0)	0.0(±0.0)	6.2(±0.2)	0.0(±0.0)	5.6(±0.3)	0.7(±0.2)
	Z_3	riffle	12.3(±0.3)	0.5(±0.0)	2.8(±0.5)	1.9(±0.0)	6.8(±0.6)	1.7(±0.0)	11.7(±0.2)	2.4(±0.0)	23.8(±0.7)	1.9(±0.0)
		run	4.0(±0.4)	0.0(±0.0)	0.3(±0.0)	0.3(±0.0)	0.9(±0.0)	0.0(±0.0)	1.3(±0.0)	0.1(±0.0)	0.6(±0.0)	0.0(±0.0)
	Mean	riffle	12.3(±0.3)	1.6(±0.0)	3.8(±0.5)	2.4(±0.0)	3.1(±0.2)	2.3(±0.1)	12.1(±0.6)	1.1(±0.0)	15.1(±0.4)	2.1(±0.0)
		run	3.6(±0.4)	0.3(±0.0)	1.0(±0.3)	0.6(±0.0)	0.5(±0.0)	0.1(±0.0)	2.6(±0.1)	0.4(±0.0)	3.2(±0.1)	0.3(±0.0)
LA ROCHE BROOK		Z_4	23.5(±0.9)[b]	1.4(±0.0)[b]	10.4(±1.6)	5.0(±0.0)	27.3(±2.3)	2.6(±0.0)	18.5(±0.3)	7.9(±0.0)	39.1(±0.8)	4.8(±0.2)

[a]Run = fast run + slow run.
[b]Density observed in the riffle of the upstream part of the river near to the confluence with the brook.

TABLE 3. Mean fork lengths (Lf in mm) of juvenile salmon and the proportion of 0+ fish in the upper mode (*P* ±95% confidence limits) autumn in the River Oir from 1985 to 1989.

	ZONE	1985 Lf 0+	1985 Lf 1+	1985 *P*	1986 Lf 0+	1986 Lf 1+	1986 *P*	1987 Lf 0+	1987 Lf 1+	1987 *P*	1988 Lf 0+	1988 Lf 1+	1988 *P*	1989 Lf 0+	1989 Lf 1+	1989 *P*
RIVER	Z_1	108 (7.7)[a]	161 (23.8)	63(±34)	101 (5.4)	151 (6.5)	86(±26)	100 (20.2)	168 (8.9)	75(±42)	104 (8.2)	159 (10.6)	76(±17)	103 (10.4)	161 (10.6)	59(±21)
	Z_2	98 (10.7)	142 (7.9)	63(±10)	90 (9.0)	135 (6.4)	71(±15)	91 (8.1)	144 (9.2)	40(±43)	94 (10.9)	147 (2.8)	33(±11)	83 (8.1)	139 (7.0)	38(±11)
	Z_3	95 (13.7)	152 (14.3)	52(±08)	92 (7.8)	144 (11.4)	45(±17)	88 (8.6)	139 (8.3)	39(±18)	97 (9.4)	152 (9.9)	40(±15)	82 (11.5)	142 (8.8)	41(±11)
	MEAN	97 (12.6)	151 (10.8)	58(±06)	92 (7.8)	141 (11.1)	82(±09)	90 (6.2)	148 (13.8)	63(±16)	97 (10.1	152 (9.4)	36(±08)	85 (12.0)	141 (9.6)	40(±08)
LA ROCHE BROOK	Z_4				81 (7.2)	127 (7.4)	23(±17)	82 (8.6)	126 (6.9)	NO BIMO-DALITY 34(±09)[b]	81 (11.8)	127 (7.4)	NO BIMO-DALITY 32(±04)[c]	72 (7.1)	124 (8.6)	NO BIMO-DALITY 18(±02)[c]
TOTAL CENSUS	Z_1 to Z_4				92 (10.7)	142 (12.1)	62(±02)									

[a]standard deviation

[b]*P* was estimated from a capture–recapture experiment made in relation to the size of 0+ fish in autumn.

[c]*P* was calculated from the equation (3) (see text).

TABLE 4. Percentage (% ± 95% confidence limits) of sampled juvenile salmon wich were spermating at the beginning of October in the River Oir from 1985 to 1989.

	Zone	Age Class														
		0+										1+				
		1985		1986		1987		1988		1989		1985	1986	1987	1988	1989
		%[a]	m[b]	%	m	%	m	%	m	%	m	%[a]	%	%	%	%
RIVER	Z_1	0	0	0	0	50(±50)	67(±53)	36(±19)	47(±22)	18(±16)	15(±20)	75(±24)	57(±37)	60(±43)	100(±0)	100(±0)
	Z_2	18(±07)	24(±10)	8(±09)	7(±10)	0	0	34(±11)	33(±19)	01(±03)	00(±00)	54(±27)	39(±20)	86(±19)	0(±0)	53(±26)
	Z_3	13(±06)	14(±08)	15(±12)	19(±20)	0	0	23(±13)	18(±18)	14(±08)	06(±09)	17(±36)	60(±19)	83(±30)	27(±27)	33(±39)
	MEAN	15(±04)	18(±06)	10(±07)	11(±08)	05(±07)	13(±17)	31(±08)	35(±13)	09(±04)	09(±07)	55(±18)	51(±13)	79(±17)	33(±24)	52(±21)
LA ROCHE BROOK	Z_4	—	—	12(±13)	0	07(±05)	15(±11)	08(±02)	08(±04)[c]	03(±01)	05(±03)[c]	—	80(±21)	59(±24)	57(±06)	61(±08)
TOTAL CENSUS	Z_1 to Z_4	—	—	07(±01)	07(±01)	—							52(±01)			

[a]Proportion of spermating fish in the total population sampled by zone or on the whole main river. For 1+ individuals, this proportion corresponds to m defined in the estimation equation of the 2+ smolts number.

[b]Proportion of 0+ spermating salmon in the upper mode.

[c]Calculated factor after to have estimated the proportion (p) from the equation (3).

TABLE 5. Number (N) and characteristics of migrating juvenile salmon caught by trapping in the River Oir from 1986 to 1990.

Year	Period of migration	Stage (% of total)			1+ individuals				2+ individuals			
		parr	presmolt	smolt	median date of migration [a]	N	%	mean length (mm)	median date of migration [a]	N	%	mean length (mm)
1986	3/01–15/05	42.8	15.4	41.8	21/04	849	95.9	130(08.9)[b]	28/03	39	4.1	161(10.3)
1987	14/02–30/04	5.0	31.8	63.2	15/04	148	52.5	126(09.6)	6/04	134	47.5	154(11.2)
1988	10/11–05/05	3.4	53.6	43.0	12/04	280	91.2	130(10.6)	29/03	27	8.8	154(15.7)
1989	21/11–08/05	2.3	54.2	43.5	13/04	492	89.1	134(15.8)	29/03	60	10.9	152(10.5)
1990	27/01–08/05	0.6	46.5	52.9	14/04	707	94.9	132(09.8)	31/03	38	5.1	154(12.8)

[a]date corresponding to the capture of 50 % migrating juvenile for each age class.
[b]standard deviation.

but most fish (75 to 82%) migrated in April. The timing of migration was similar and earlier in the four latter years (median date between the 9th and 14th April) than in 1986 (mean date 21st April). Each year, the parr migrated first, then came the presmolts and lastly the smolts. However, the distribution of the different stages in the migrating juvenile population was different according to year (p<0.01) owing to a large proportion of smolt in 1987 and a equal number of parr and smolt in 1986. The 2+ fish always migrated, on average, before the 1+ ones.

Estimation of Smolt Production

Origin of 1+ Smolt (Table 6)

From the analysis of 0+ salmon tagged in autumn and recaptured as 1+ presmolt or smolt the next spring, we could see that:

— in each year, 1+ smolt came significatively more from the upper mode 0+ (p<0.01).

— the very high percentage of 1+ smolt coming from the upper mode 0+ autumnal population (89 to 100%) allowed the proportion of 0+ salmon in the upper mode to be taken into account (p) (direct observation, estimation by the Battacharya method or from the equation (3) when growth bimodality was not present) for estimating the 1+ smolt number.

TABLE 6. Number of 0+ salmon tagged in autumn according to size and recaptured as 1+ presmolts or smolts during downstream migration.

Year	0+ salmon		
	Caught in autumn		recaptured as 1+ presmolt or smolt
	type	number	
1985	Lf≥90	178	55
	Lf<90	78	3
1986	Upper mode	246	89
	Lower mode	151	11
1987	Lf≥80	74	24
	Lf<80	46	0

Estimation of the Overwinter Survival Rate (Table 7)

Analysis of the minimum and maximum values of the overwinter survival rates showed that:

— 0+ fish had better survivals rate than did 1+ fish.

— there were large annual variations. 0+ salmon survival was similar for the winters of 1986 and of 1987 (very cold in February and January: it means 3 weeks of very low air temperature between −10° and −20°C) but much lower than the other winters (mild conditions: it means no air temperature below −5° C) (p<0.001). 1+ parr survival was similar in the winters 1987 to 1989 but higher the winter of 1990 (p<0.01).

— survival in spermating fishes was lower than in immature ones only in winter 1989 for 0+ salmon (data for 1 year) and in winter 1990 for 1+ fish (data for 2 years).

From the data, mean overwinter survival rate of upper mode 0+ salmon could be estimated at 41% (36 + 5 (negative effect of handling)) in cold winters (1986 and 1987) and at 63% (58 + 5) in mild winters (1988 to 1989). The same value was used for the winter of 1990 very similar to the previous one. For 1+ fish, it was estimated at 32% (27 + 5) whatever the year.

Efficiency of Trapping

Efficiency of trapping varied from 40 to 100% according to water discharge conditions. It was much higher in period of low and mean water level (65 – 100%) than in period of spate (40 – 52%). No efficiency variability could be observed in relation to size and age of juvenile salmon since all the released fish were one year old with a fork length between 13 and 15 cm.

Comparison Between the Two Estimation Methods (Table 8).

There was a significant linear regression calculated between the 1+ smolt number estimated from trapping (x) and from two habitat methods (y):

habitat cumulative by zone:

(4) $y = 213.6(\pm 483.6) + 0.647(\pm 0.627)\, x$ $\quad r = 0.884$ $\quad p < 0.05$

habitat on whole basin:

(5) $y = 206.6(\pm 354.8) + 0.558(\pm 0.458)\, x$ $\quad r = 0.913$ $\quad p < 0.05$

Futhermore theses equations differed not significantly from this of type: $y = x$.

Thus, 1+ smolt numbers estimated from the habitat method were not significantly different from those obtained from trapping. Nevertheless there was a greater error associated with estimations from habitat method for 1+ fish since the relative errors ranged from 18 to 47% (they were higher for habitat method by zone (25–47%) than for whole basin habitat (18–43%)).

There was no significant correlation ($p > 0.05$) between the 2+ smolt estimates obtained from the two methods. Futhermore 2+ smolt number estimated from the habitat method were significantly ($p < 0.05$) higher than that evaluated by trapping except for 1987.

Discussion

Smolt number estimates from the two methods differed according to year and age-class with results obtained for 1+ smolts in closest agreement but those given by the trapping method were more precise.

TABLE 7. Over winter survival rate calculated from recapture data in 0+and 1+ salmon.

		Tagged fish in autumn		Over winter survival rate (%)	
Age	Winter	Type	Number	Minimum	Maximum
	1986	0+ total	256	27.5	37.3
		0+ upper mode	178	28.7	38.5
		0+ low mode	78	25.0	34.6
	1987	0+ total	397	≥ 25.4	≤ 36.7
		0+ upper mode	246	≥ 30.5	≤ 44.8
		0+ low mode	151	≥ 15.9	≤ 22.3
0+	1988	0+total	157	≥ 45.1	≤ 64.3
		0+ upper mode	90	≥ 49.3	≤ 70.0
		0+ low mode	67	≥ 38.6	≤ 54.2
	1989[a]	0+ total	559	48.1	56.7
		0+ non spermating	513	50.9	60.6
		0+ spermating	46	14.1	16.3
	1987	1+ total	379	23.0	33.3
	1988	1+ total	41	14.6	29.3
		1+ non spermating	12	16.7	33.3
		1+ spermating	29	13.8	27.6
1+	1989	1+ total	281	22.1	29.2
	1990	1+ total	148	≥ 8.8	≤ 10.1
		1+ non spermating	57	≥ 14.0	≤ 17.5
		1+ spermating	91	≥ 2.2	≤ 2.2

[a]In 1989 the tagging of 0+ salmon was made only in relation to state of maturity.

Different aspects are discussed in order to assess the reliability of the habitat method, to increase its precision and to improve its agreement with the trapping method (large confidence limits of agreement in relation to the short period of data recording (5 years).

Origin of 1+ Smolts

This study has verified the hypothesis that, in wild conditions, most upper mode 0+ salmon become smolt the following spring, corroborating results obtained in a previous study (Baglinière and al. 1988). However, the recapture during downstream migration of 1+ fish tagged when small or as lower mode 0+ salmon implies a small proportion of these fish contribute to 1+ smolt production. Nevertheless, the similar 1+ smolt estimations from the two methods enabled us to consider the proportion of 0+ salmon in the autumnal upper mode (p) as a reliable parameter for the production equation of the 1+ smolt.

Electrofished Surface Area, Representative Sectors and Number of Sampled Fish

The percentage of water surface area sampled was low (4.4. and 6.1%), but similar to that sampled in Girnock Burn in Scotland (7%: Buck and Hay 1984) and greater than that studied in the River Scorff (2.1%: Baglinière and Champigneulle 1986). Run habitats and particularly the slow runs were undersampled compared to riffles in 1985 and 1986, while its significance in the water surface area was 66% of the whole basin and 76% in Zone 2, but salmon density was always very low. During these 2 years, La Roche Brook was not well sampled as there was no electrofishing census in 1985 and only one in a small downstream sector in 1986. These considerations could explain the larger differences observed between the 1+ and 2+ smolt number estimations from both methods in 1986 and 1987.

From 1987, test sectors were more representative of the whole basin with more homogeneous recordings carried out in relation to the different habitat categories of each main river zone (notably in distinguishing overall the two run types defined in Table 1) and taking into account the total La Roche Brook area colonized by salmon. This brook produced 25% of the total smolt population in the whole basin (Charlot 1989).

As a result of the above changes, 1+ smolt number estimates from both methods were closer, while

TABLE 8. Estimation of Atlantic salmon smolt production (± 95% confidence limits) in the R. Oir from 1986 to 1990.

Year of trapping	Method		Estimated number of smolts 1+	2+	Total
1986	Habitat	Cumulative by zone	921(±235)	82(±14)	1003(±249)
		Whole basin	854(±156)	86(±11)	940(±167)
	Trapping		1270(±181)	55(± 8)	1325(±189)
1987	Habitat	Cumulative by zone	290(±111)	180(±32)	470(±143)
		Whole basin	306(±111)	157(±16)	463(±127)
	Total census		164(± 35)	129(± 7)	293(± 42)
	Trapping		199(± 37)	180(±33)	379(± 70)
1988	Habitat	Cumulative by zone	406(±192)	84(±16)	490(±208)
		Whole basin	372(±161)	100(±15)	472(±176)
	Trapping		408(± 62)	46(±10)	454(± 72)
1989	Habitat	Cumulative by zone	707(±293)	147(±13)	854(±306)
		Whole basin	588(±179)	135(±12)	723(±191)
	Trapping		761(±127)	97(±15)	858(±141)
1990	Habitat	Cumulative by zone	954(±294)	127(±22)	1081(±316)
		Whole basin	818(±196)	119(±16)	937(±212)
	Trapping		776(± 69)	41(± 4)	817(± 73)

those of 2+ smolts remained different. The small size of the River Oir did not always enable the determination of a large homogeneous habitat, owing to a mosaic distribution of habitats. This aspect involved two consequences. First it could modify, in years of very low density, the expression of habitat requirements of 0+ and 1+ salmon, on which the method of Baglinière and Champigneulle (1986) was grounded. That could explain, partly, the large differences between the estimates of 2+ smolts, as 1+ parr densities were often very low in autumn. Then this aspect implied to make electrofishing census in small sectors in order that they are representative of different habitats leading generally to the capture of a small number of juvenile salmon. Nevertheless, for increasing the precision of the habitat method, it is necessary to catch a large number of fish in order to decrease the confidence limits of the different proportions used in the equation (1). Precision of the habitat method will mainly be improve under that condition and not in increasing the surface area of electrofished sectors or the efficiency of electrofishing that always was high (70–100%).

Overwinter Survival

The overwinter survival rate of 0+ salmon seemed typical. The value estimated in mild winters (63%) was very close to that calculated by Baglinière and Champigneulle (1989) and used by Baglinière et al. (1988). The overwinter survival of 0+ salmon decreased when winter severeness increased. In such conditions mid-winter could be stressfull (Cunjak 1988). Survival of 0+ salmon also seemed to depend on the autumnal size, as mortality was higher in lower mode 0+ salmon than in upper mode fish as observed by Pickering and Pottinger (1988) under artificial conditions.

Overwinter survival of 1+ salmon appeared much less than expected and possibly underestimated. The obtained value (32%) was much lower than that estimated by Baglinière and Champigneulle (1986) (80%). Unlike 0+ salmon, apparently overwinter survival did not change according to year and climatic conditions. The lowest value observed (1990) could have resulted from tagging by multiple fin clipping leading to a decrease of survival as reported by Johnsen and Ugedal (1988). The lower overwinter survival of 1+ salmon, compared to that of 0+ fish, may be related to the influence of precocious male sexual maturity since the percentage of spermating fish was much higher in 1+ salmon than in 0+ fish and the precocious sexual maturity resulted in a large mortality rate (Osterdahl 1969; Leyzerovich 1973; Dalley and al. 1983; Myers 1984; Hansen and al. 1989). Overwinter survival was twice as high (17%) in 1+ immature fish as in mature ones (7%). The true influence of precocious sexual maturity on the overwinter survival of juvenile salmon, however, is uncertain as the censuses were made at the beginning of October, resulting in an underestimate of the number of 0+ and 1+ spermating fish (salmon usually spawn in mid-December).

Trapping Efficiency

Capture-recapture experiments were performed totally with 1+ fish during the month of April, corresponding to the migration peak of this age-class. In 1986 and 1988 no sampling was carried out between the end of March and the beginning of April during the flood period, corresponding to the migration peak of 2+ smolts always earlier than that of 1+ smolts (Baglinière 1976). From these different considerations it is probable that the 2+ smolt number trapping estimates were underestimated.

Influence of Climatic Conditions on Stage at Migration

Many fish (up to 43% in 1986) migrated as parr stage. In Girnock Burn, Buck and Hay (1984) did not observe completely smoltified salmon during the spring migration. Futhermore, tagged parr migrating in autumn were recaptured in this stream as grilse or multi sea-winter salmon (Youngson et al. 1983). The low 1+ smolt number estimate from the habitat method versus trapping in 1986 could be due to the high proportion of migrating parr. Lastly, Duston et al. (1991) showed that an increase in freshwater temperature during the period of downstream migration could accelerate the loss of smolt characteristics. In 1990, the water temperature during seaward migration (end of February–beginning of May) was between 3 to 5°C higher than for previous years, which might account for the smaller proportion of trapped 1+ smolts that year as compared to the habitat estimates.

Conclusion

This study shows that further work was necessary to improve the agreement between the two methods of estimation of smolt production and the precision of habitat method. For this one, the accuracy of the estimation depends directly on (1) the quality of the representation of the test sectors studied in each zone, (2) the density and the number of juvenile salmon sampled which must be large in order to decrease the confidence limits of the different parameters used in the equation of smolt number. Thus the habitat method would seem more difficult to use in streams with a low level of salmon population, (3) the necessity to analyse all the environmental (water temperature and discharge, habitat) and biotic factors (precocious sexual maturity, age, density) influencing the overwinter survival of fish.

In the trapping method, it is necessary to improve the efficiency of the trap in relation to water discharge and temperature, age and physiological state.

Nevertheless, this study demonstrates that the estimation method of smolt production from the autumnal characteristics of the habitat and the juvenile salmon population is an available tool and could be useful for the rational management of Atlantic salmon stocks even if there are some disadvantages (1) large confidence limits of the estimated number (up to 50%) and (2) overestimation of 2+ smolt production.

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