

Variability of demographic parameters and population dynamics of Atlantic salmon (*Salmo salar* L.) in a southwest French river

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Dumas, J., and Prouzet, P. 2003. Variability of demographic parameters and population dynamics of Atlantic salmon (*Salmo salar* L.) in a southwest French river. – ICES Journal of Marine Science, 60: 356–370.

The abundance of the salmon population in the Nivelle River was assessed for 11 cohorts during all the stages of their life cycle, from eggs to spawners. A stochastic life history model was used to simulate the changes in numbers at each stage over several years and to evaluate the parameters of a Ricker-type Stock and Recruitment (S–R) relationship. Parameters necessary for managing the exploitation of the species were also estimated. The results indicated that an average deposition of 611 700 eggs (values varying in a proportion of 1 to 3, depending on the year) produced 4870 0+ parr in autumn (variation from 1 to 5.6); 71.8% of which belonged to the group of future 1-year old smolts. The age 1+ parr were eight times less numerous. Survival from egg to 0+ parr was on average 0.97%, but highly variable (varying from 1 to 15). It was density-dependent and followed Ricker S–R model with an optimum of 7800 parr for a survival rate of 3%. During their second year, the survival of 1+ parr reached 53.4% and varied little. The adult runs of complete cohorts amounted to 196 maiden salmon (range, 88 to 382) and previous spawners comprised only 0.9% of adults. Grilse (1 year in the sea) constituted the majority (88.7%). The overall survival rates from 0+ parr to adult returns (6.2% on average) varied three-fold. The majority was females among the grilse (56.2%) and 2-sea-year salmon (88.6%); all 3-sea-year adults were female. Eggs deposited per female averaged 4200, 8500 and 12 750 eggs in each age group, respectively. Simulations of population abundances at various life stages were in good agreement with the observed data. The S–R relationship revealed the low productivity and the vulnerability of this stock, mainly due to the low survival rate of the young during their first year of life. The maximum yield of 12.2% of recruits could be obtained from a deposition of 1 424 000 eggs, which is twice the present average level.

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Keywords: fisheries, life history, modelling, population dynamics, salmon.

Received 7 May 2002; accepted 28 December 2002.

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Introduction

The dynamics and functioning of Atlantic salmon populations have frequently been studied and reviewed (e.g. Buck and Hay, 1984; Chaput *et al.*, 1998; Cunjak and Therrien, 1998; Elson, 1975; Hutchings and Jones, 1998; Kennedy and Crozier, 1993; Marschall *et al.*, 1998; Symons, 1979). However, few population have been examined at the southern edge of their distribution area (Gros and Prouzet, 1988; Prouzet, 1990; Prévost *et al.*, 1996; Anon., 1998). From the Portuguese border to the French Pyrenees, numerous streams exist where the population may be endangered in relation to habitat loss,

overexploitation or global climatic change. Monitoring salmon populations in southern streams may provide an early warning of the fate of more northerly populations.

The studies conducted in the Nivelle River provide information on the abundance of the different stages of this southern stock and allow to model its functioning. In the early 1970's, adult numbers had decreased to a few dozen individuals. Between 1976 and 1995, the salmon population of the Nivelle underwent restoration programmes with stocking of smolt followed by fry in the zones upstream from a dam, which was impassable to migratory salmon. Restoration was associated with a program of fish-ladder construction in order to establish a self-sustaining

population (Dumas, 1997; Dumas and Barrière, 1991). The careful monitoring of adult runs since 1984 and the juvenile stages since 1985 made it possible to follow changes in the population and to better understand their dynamics. Fry releases stopped in 1990 in most of the upstream zones. Thus, studying number fluctuations for the year classes from 1991 to 2001 allowed measurement of the variability of the demographic characteristics of the self-sustained population throughout the zone now accessible to spawners. This study provided the relevant data for the development of a Stock–Recruitment (S–R) model designed to cover all the aspects of the life cycle of this species, considered for the first time for a southern river.

Materials and methods

Study site and monitoring installations

The river

A coastal river of the Basque Country, the Nivelle has its source in Spain and flows into the Bay of Biscay at

Saint-Jean-de-Luz after travelling 39 km (Figure 1). Its watershed of 238 km², dominated by marly-calcareous formations, is essentially agro-pastoral with more than 50% of the land area in moors (Dumas and Haury, 1995). The oceanic climate, mild and wet (1700 mm year⁻¹ in St-Pée-sur-Nivelle), provides a mean annual discharge of 5.4 m³ s⁻¹ downstream from the confluence of the main tributary, the Lurgorrieta and 9 m³ s⁻¹ at the mouth. The water, neutral to slightly alkaline, is of good quality upstream from St-Pée, but deteriorates downstream.

Monitoring installations, accessibility and population management

The Nivelle River was equipped with two upstream migrant monitoring traps in the fish passes. The site at Uxondo, situated 4.7 km upstream from the limit of brackish water, has been in operation since 1984 and the site at Olha, 4.5 km further upstream, has been operating since 1992. In the fall of 1990 and 1991, before the opening of the Olha fish pass, a portion of the spawners caught at the Uxondo

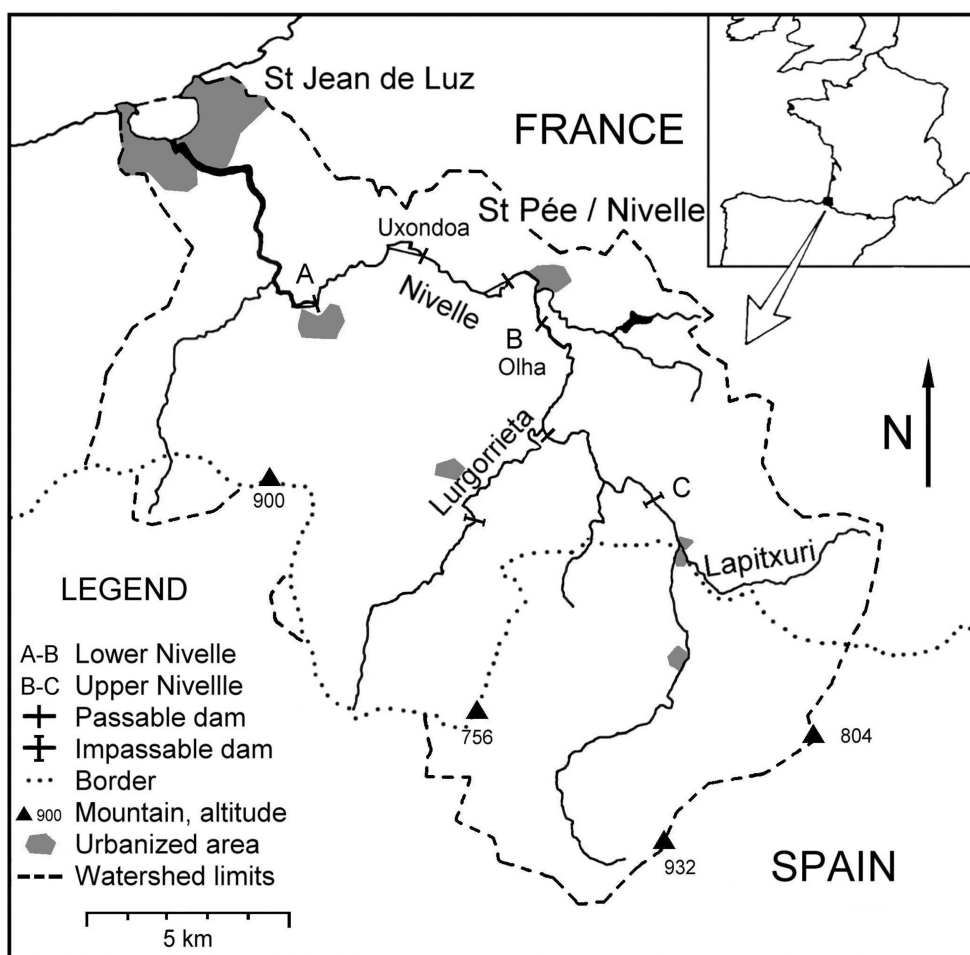


Figure 1. The Nivelle River watershed and zones occupied by salmon.

trap was transferred upstream from the Olha dam (Dumas, 1997). Since 1992, the salmon have had access to the first 18 km of the main watercourse in freshwater and to 4.7 km of the main tributary (Figure 1). The Olha site is the transition between the "Lower Nivelle" (made up of three homogenous stretches between dams) and the upper basin, which includes the "Upper Nivelle" (two stretches) and the Lurgorrieta (one stretch). This constitutes the area where salmon reproduce naturally. Fry-stocking ceased after 1990 in the Upper Nivelle and in the Lurgorrieta, while it was still carried out on a smaller scale, in 1991, 1992, 1994 and 1995, upstream from these colonised areas, in the very upper French part of the Nivelle and/or a tributary, the Lapitxuri.

Collection of data

Adults

The number of fish moving past the Uxondoa dam was estimated by marking all the captured salmon at this site and then controlling marked and unmarked salmon at the Olha trap. Population estimates were obtained according to the Petersen method (Cuinat *et al.*, 1975). Length, weight, morphological characteristics for sexing and scale samples for ageing were collected. Before release upstream of the trap, the fish were tattooed with alcian blue for later identification (Johnstone, 1981). The spawners, which remained downstream of Uxondoa were assessed by counting the redds, determining the number and sea age of the females from the number and the size of the redds with the same criteria as for redd counts in the Upper Nivelle, where the number and characteristics of females were precisely known, and applying the sex ratio of the previously collected sample. Spawners from downstream of the Uxondoa represented 2.9–13.6% of the total population depending on the year. Examination of the fish caught by angling and of the fish found dead completed the data base.

The sex of the fish sampled before September (when the period of clear anatomical differentiation begins) was determined using a discriminant factorial model. This calculation, which takes into account the fork length, the length of the upper maxilla (Maisse and Baglinière, 1986; Maisse *et al.*, 1988) and the nostril-snout length, was carried out on a sample of 144 fish whose sex was checked between 1990 and 1992.

Ageing from scales allowed to establish age types *ij*, where *i* is the smolt age and *j*, the sea age.

Number of eggs deposited

Annual escapement of the spawners was estimated for each of the three colonised zones according to the number of females, which managed to reach upstream of each trap, deducting all mortalities, and then cross-validating with redd counts. The number of eggs that were deposited was estimated from the proportion of females and the fecundity

of each sea age group. Fecundity was calculated from a sample of females collected in autumn between 1977 and 1987, including wild and farmed spawners. The egg-retention rate during spawning was estimated at 1.5% (observed in an experimental spawning channel, Beall, beall@st-pee.inra.fr) and was applied to fecundity rates to provide an overall estimate of naturally spawned eggs.

Juvenile habitat

Juvenile habitats were quantified in 1985 according to a habitat survey based on water velocity, depth and characteristics of the substrate (Baglinière and Champigneulle, 1982, 1986). Parr production was observed in swift-flowing habitats (riffles and rapids) that corresponded to class A habitats as defined by Kennedy and Crozier (1993), and to a lesser extent, in the runs where densities were on average five times lower than in the former, as previously observed by Prévost and Porcher (1996). Their respective surface areas, in the colonised zones, accounted to 46 181 and 49 497 m², i.e. 56 080 m² of "riffle or rapid equivalent" as defined by Prévost and Porcher (1996), on 320 995 m² of total water surface area as used by Elson (1957).

Juvenile density estimates

Each year, between the end of September and mid-October, the juvenile population was assessed by electrofishing on 11 to 13 sections that were representative of longer and homogenous stretches. Each section included one or several habitats, i.e. swift flowing habitats, runs, and slower flowing water and pools, that ranged in size from 39 m² to 1538 m². They represented 9.4–13.2% of the surface area of the riffles and rapids, 4.2–7% of that of the runs and 0.2–0.5% of that of the slower flowing water and pools. The number of fish and their variances were estimated by age group for each habitat according to the method of Seber and Le Cren (1967). Parr estimates for the sampled habitats were extended to the total surface areas of homologous habitats for each stretch and for all the colonised area (Beall *et al.*, 1994).

Migratory and sedentary fractions in juveniles

Age 0+ autumn parr of the Nivelle River present a bimodal size distribution, as in rivers where growth is fast (Baglinière and Champigneulle, 1986; Heggnes and Metcalfe, 1991; Utrilla and Lobon-Cervia, 1999). A size frequency histogram (5 mm length classes) of the subjects caught in each sample section allowed visual separation of the two size groups. Parr in the upper modal group were assimilated to the future 1-year-old smolt and those in the lower modal group to the future sedentary individuals of the following year, as shown with farmed parr by Thorpe *et al.* (1980) and observed in a stream by Heggnes and Metcalfe (1991). Each fraction was estimated for the whole river by summation.

Estimating the runs originating from upstream stocking

Additional returns of adults originating from fry released in the “Very Upper Nivelle” and the Lapitxuri stream in 1991, 1992, 1994 and 1995 were subtracted from the estimations of the naturally colonised zone. Their numbers were calculated based on the following hypothesis that the return rates of the 0+ upper modal group or 1+ parr produced in the colonised or stocked areas were identical for the same age classes, whatsoever the zone. For each of the two production zones, adult returns were, therefore, proportional to the numbers of 0+ parr of the upper mode for fish that became 1-year-old smolts, or to the numbers of 1+ parr for those that became 2-year-old smolts. Their numbers were allotted proportionally to the estimates of each group of juveniles of both areas.

Modelling

Stochastic model of the life cycle of salmon

A stochastic model of the life cycle of salmon, developed by Dumas *et al.* (1996) and Faivre *et al.* (1997), was implemented using Mathcad[®] and simplified in order to take into account the following four stages: deposited eggs, autumn parr, adult returns and spawner escapement. It simulated the numerical evolution of the cohorts at their different stages and linked them together for several years. Passing from one stage to another was carried out using four different functions whose parameter values were stochastic (i.e. varied according to a given law of probability, with a set mean and standard deviation). Those functions were survival rates between life stages, proportion of separation (distributing the 0+ parr into upper and lower modes), exploitation rates (taking into account angling to calculate escapement) and egg deposition (converting the number of spawners of each age class into number of females according to proportions, and into deposited eggs according to fecundity). After calibration with the Nivelle data, the calculation for each stage and each year was randomised 500 times, over a long enough period of 35 years to allow the simulation to stabilise.

Identifying mechanisms and the model regulating the abundance of the early stages based on the production data of the parr observed

The descriptive laws of population growth have been described by an equation known as the “Verhulst–Pearl logistics curve” (Pearl, 1925; Verhulst, 1884). The equation (1) is defined in the following way:

$$X(t) = \frac{X_{\max}}{1 + ae^{-rt}} \tag{1}$$

with X(t), the abundance at time (t), X_{max}, the maximum limit of the population, a, higher than zero and r, the population maximum growth rate. This means that the

growth rate of the population defined by $dX/Xdt = r[1 - (X/X_{\max})]$ tends towards zero when the population tends towards the level X_{max}. This equation makes it possible to explore as to how the population growth is constrained by regulatory mechanisms known as “compensatory mechanisms”, which prevent the population from changing in a monotonous manner.

It is commonly acknowledged (Prouzet, 1994) that salmon populations are regulated to a large extent by phenomena, which depend on density during the young parr stage, i.e. during the freshwater phase for a migratory species such as Atlantic salmon. Because of this, we modelled the relationships between the deposited eggs and the life stages that they generate by compensatory-type relations (Ricker, 1954) whose general formula analysed by Larkin and Hourston (1964) is:

$$Z = \omega \exp^{a(1-\omega)} \tag{2}$$

with ω being the parental stock, Z, the resulting stock and a, the shape co-efficient.

Thus, the abundances of 0+ parr generated by the stocks of deposited eggs were subjected to compensatory mechanisms, which regulated parr production depending not only on the number of eggs but also on the carrying capacity of the environment. These mechanisms were described by the Ricker model as $y = \alpha x \exp(-\beta x)$, with x, the number of deposited eggs, y, the number of 0+ parr, α and β, the equation parameters. Fitting this model to the observations allowed us to estimate the parameters of the equation and to define the relationship between the number of 0+ parr produced by each cohort (Oparr) and the number of eggs deposited (eggs) such that:

$$Oparr = \alpha \times \text{eggs} \exp(-\beta \times \text{eggs}). \tag{3}$$

The optimum of the curve is attained when the first derivative of the equation is zero, that is when $(1 - \beta x)\alpha \exp(-\beta x) = 0$. Thus, the optimum is defined by the pair of co-ordinates with values 1/β on the abscissa and α/βe, on the ordinate. It corresponds to a theoretical survival rate of eggs to 0+ parr defined by α/e. This model makes it possible to fix, in a deterministic manner, a maximum theoretical production of 0+ parr.

Estimating the size of parr territories and the maximum carrying capacity

The survival and the abundance of parr in autumn were essentially controlled by two groups of factors: the surface area of the productive habitat (sprod) and territorial competition, mainly the one exerted by older salmon parr. The outcome of the latter was expressed as a proportion of the habitat occupied by age 1+ parr (sprod1); while the remaining surface areas occupied by 0+ parr (sres) were made up of surface areas left vacant by older parr and of a fraction of the territories of the latter. Symons and Héland (1978) observed in an artificial stream that the number of 0+ parr decreased between 20 and 50%, depending on their

size, when habitats were previously occupied by 1+ parr. This suggests a proportionality relationship between 0+ parr number and the overlapping fraction of older parr territories. The value of this fraction, estimated on average at 35%, defines an overlapping rate (Tc). Thus,

$$Sres = sprod - sprod1(1 - Tc). \quad (4)$$

In order to determine the minimal surface areas of the territories of the 0+ and 1+ parr when these habitats are fully populated, it is necessary to know the maximum number of parr of the year (N0) and the concomitant number of older parr (N1) which can be assimilated to the carrying capacity of the environment. These numbers correspond to the highest totals of the annual biomass values of each group observed in each of the large zones of the Nivelle since 1985 (B0 and B1), including the years of stocking in the upper basin. As the surface area of a territory is proportional to the individual weight of the parr (Allen, 1969; Grant and Kramer, 1990), the surface areas of production occupied by each age class were proportional to their respective biomasses (B0) and (B1). The theoretical biomass (Bt) corresponding to the surface areas necessary for both age groups was equivalent to:

$$Bt = B0 + B1(1 - Tc) \quad (5)$$

These biomasses were proportional to the surface areas occupied by the two classes of parr so that:

$$Sres = (sprod \times B0)/Bt \quad (6)$$

$$sprod1 = (sprod \times B1)/Bt \quad (7)$$

Thus, the individual surface area of a territory of 0+ parr (sterr0) in a situation of maximum habitat saturation is:

$$sterr0 = sres/N0 \quad (8)$$

Given that the weight of an older subject is Kp times that of a 0+ parr, the individual surface area of a 1+ parr is:

$$sterr1 = sterr0 \times Kp \quad (9)$$

Territory surface areas once defined, we then calculated for each year (t) the number of 0+ parr, given the number of 1+ parr (N1_t) and the production area that the latter occupy. Equation (7) becomes:

$$sprod1_t = sterr1 \times N1_t. \quad (10)$$

Thence:

$$sres_t = sprod - sprod1_t(1 - Tc) \quad (11)$$

For each year (t), the maximum number of 0+ parr corresponding to the carrying capacity (parrmx_t) is defined as:

$$parrmx_t = sres_t/sterr0 \quad (12)$$

The number of parr is regulated by the compensatory mechanisms described by a Ricker-type relationship

between the deposited eggs and the parr produced. It is based on the hypothesis that the maximum number of 0+ parr is defined by their individual territorial requirements and the production surface area unused by the older parr. Each year, the simulated number of 0+ parr (0parr_t) depends on the simulated number of deposited eggs (eggs_t), the simulated egg to parr survival rate (S1_t) and a constraint given by the maximum number of 0+ parr to be produced (parrmx_t), which corresponds to the optimum of the Ricker equation. The observed survival rate (S1) presented a distribution skewed to the left, with higher probabilities of values close to zero. Thus, the simulated survival rate (S1_t) was computed with a lognormal distribution, with a mean of $\mu = \ln[\bar{S}1/(\sigma_{S1}^2/\bar{S}1^2) + 1]$ and a standard deviation of $\sigma = 2 \ln \left[\sqrt{\sigma_{S1}^2/\bar{S}1^2} + 1 \right]$. The following relation directly deduced from the Ricker model was used:

$$0parr_t = S1_t \text{eggs}_t \exp \left(- \frac{S1_t}{e \times parrmx_t} \text{eggs}_t \right). \quad (13)$$

The S-R relationship and the estimation of the dynamic characteristics of the population

A complementary output of the model took 500 pairs of deposited egg and recruited egg data simulated at each generation to assess the parameters of the S-R relationship according to the Ricker model, previously defined in Equation (2), as well as the parameters making it possible to set biological reference points to manage the exploitation (maximum yield, optimum egg deposition) on the Nivelle salmon stock. As the parental stock, and the recruits which it generates, are expressed in the same unit, the general equation proposed by Ricker (1980) becomes:

$$R = P \exp^{a(1-P/Pr)} \quad (14)$$

with R being the number of recruits, P, the abundance of the parental stock, a, the shape parameter determining the appearance of the curve and equal to Pr/Pm, Pr being the abundance of spawners required to ensure the replacement of the stock, Pm, the abundance of spawners corresponding to the maximum recruitment level.

The model parameters were estimated by the Levenberg-Marquardt algorithm in Mathcad[®] software (More *et al.*, 1980). The maximum yield was then found analytically by calculating the co-ordinates on the curve adjusted to the point where the tangent is equal to 1. The maximum exploitation rate was then estimated as the ratio of the surplus of spawners (difference between the number produced and the number required) to the maximum yield.

Results

We present the results according to the sequence of life stages. Adult returns are complete for brood years prior to 1997. To take into account all available information on the

different stages, means and their standard deviations were calculated from the number of complete year classes, which varied from 11 for the egg stocks to six for the last adults.

Egg deposition

The number of eggs deposited annually depended on the number of females of each sea age estimated, present at the time of reproduction (Dumas, 1990–2001), as well as on their individual fecundity, corrected by the retention rate during spawning. These two latter data came from samples collected in autumn from 1977 to 1987 (Table 1). The fecundity values in these samples were considered comparable with spawners of the recent period, since their size had varied little and the 95% confidence limits for the means overlapped: lengths of females for the first and second period were respectively 632 and 636 mm for grilse (1-sea-year), 796 and 782 mm for 2-sea-year salmon, and 920 and 909 mm for 3-sea-year salmon. Individual fecundity of the females relative to their weight was slightly lower in grilse, with 1661 ova deposited per kilogram (Table 1), than that of the older ones, with 1740 ova for 2-sea-year salmon and 1752 ova for the 3-sea-year salmon.

Mean escapement for the 1990–2000 period was 122 females, among which grilse represented 80.3% (Table 2). The stock of eggs deposited in December of each year was on average 612 000 eggs (s.d. = 251 000), i.e. 1091 eggs 100 m⁻² of riffle equivalent or 191 eggs 100 m⁻² of river, whereas the median value of 528 000 eggs represented only 86.3% of the mean. It varied by a factor larger than 3 between the lowest value (375 000 eggs in 1998) and the highest value (1 208 000 eggs in 1993).

Abundance and survival of autumn juveniles

Only the groups of 0+ and 1+ parr were considered in this study (2+ parr were rare). The variability in annual estimates of numbers was small (variation coefficients from 2.7 to 5.2% for 0+ parr and from 1 to 7.2% for 1+ parr). The autumn population was on average 4867 0+ parr (s.d. = 2758) for a population density of 8.7 individuals 100 m⁻² of riffle equivalent or 1.5 parr 100 m⁻² of water surface area. The 2000-year class showed the largest abundance with 9865 individuals, a figure 5.6 times higher than the lowest, 1751 in 1995 (Table 3). The highest values were observed on the last five cohorts. The upper modal group of the size distribution that was likely to smolt in the following spring (mean, 3370 individuals) reached 71.8% on average of the annual percentages (s.d. = 7.3%; Table 4). Extreme values were relatively close, at 59 and 79.4%, in 2000 and 1994, respectively. The 1+ parr originating from the lower mode of the previous year were on average 7.8 times less numerous than the younger ones with a total number of 627 individuals (s.d. = 372).

Thus, the average survival rate between the egg and the first autumn was 0.97% (s.d. = 0.76%), with annual values

Table 1. Average fecundity and egg deposition estimates for Nivelles River salmon females. The standard deviation is shown in brackets.

Sea age (years)	Number	Ova number per female	Number of deposited egg	Number of deposited egg per kg
1	48	4258 (1150)	4194 (1133)	1661
2	34	8660 (1967)	8530 (1938)	1740
3	1	12957	12763	1752

varying by a factor of 15 (Table 4). The lowest rate (0.16%) corresponded to the greatest mass of eggs, while the highest survival rate (2.35% in 1999) corresponded to the lowest initial stock. The survival rate of 1+ parr, with reference to the numbers of the lower modal group of the previous year 0+ parr, was on average 53.4% (s.d. = 12.3%) and varied little (from 36.5 to 65.4%).

Density-dependence relationship between 0+ parr and the stocks of deposited eggs

Data from the Nivelles suggested that the probable existence of compensatory mechanisms, which regulated 0+ parr production not only depended on the number of eggs, but also on the carrying capacity of the environment (Table 3).

Fitting the Ricker model to the observations (Figure 2) made it possible to estimate the parameters of the equation and to define the relationship between the number of 0+ parr produced and the number of eggs deposited so that:

$$0\text{parr} = 8.135 \times 10^{-2} \text{eggs} \exp(-3.84 \times 10^{-6} \text{eggs})$$

with R² = 0.93

and with s.d._α = 3.76 × 10⁻² and s.d._β = 9.07 × 10⁻⁷.

Table 2. Total returns to River Nivelles with female spawning escapement and estimated egg deposition. * Including previous spawners.

Run year	Adult returns*	Female escapement			Egg deposition
		1-sea-year	Multi-sea-year	Total	
1990	291	131	23	154	745 700
1991	184	63	31	94	528 100
1992	240	92	38	130	709 400
1993	472	229	29	258	1208 300
1994	325	124	32	156	792 800
1995	224	80	13	93	446 500
1996	228	95	32	127	671 000
1997	127	72	10	82	387 400
1998	169	75	7	82	374 500
1999	167	65	24	89	477 000
2000	158	52	20	72	388 400
No. of years	11	11	11	11	11
Mean	235	98	24	122	611 736
s.d.	98	50	10	54	250 721

Table 3. Estimated numbers of different stages for year classes 1991–2001 (age type $ij = i$ th freshwater age and j th sea age). Adult numbers are indicated with one decimal place because they were allotted proportionally to juvenile estimates in colonised and stocked areas.

Year class	Egg deposition	0+ parr		1+ parr	Adult returns (ij)						Total	
		Upper mode	Lower mode		1-sea-year		2-sea-year		3-sea-year			
					1.1	2.1	1.2	2.2	1.3	2.3		
1991	745 700	4206	940	3266	604	312.1	33.2	33.0	4.1	0.0	0.0	382.4
1992	528 100	3105	881	2224	340	214.8	18.2	29.5	4.5	1.0	0.0	267.9
1993	709 400	2640	871	1769	540	130.0	22.0	35.0	2.0	0.0	1.0	190.0
1994	1 208 300	1956	403	1553	263	70.5	3.8	4.3	0.3	0.0	0.0	78.9
1995	792 800	1751	392	1359	143	77.7	4.5	4.3	1.0	0.0	0.0	87.5
1996	446 500	5068	1192	3876	648	129.0	20.0	19.0	4.0	0.0	0.0	172.0
1997	671 000	5888	1411	4477	790	116.0	13.0	23.0				
1998	387 400	5392	1498	3894	979	111.0						
1999	374 500	8797	3476	5321	1334							
2000	477 000	9865	3904	5961								
2001	388 400											
No. of years	11	10	10	10	9	8	7	7	6	6	6	6
Mean	611 736	4867	1497	3370	627	145.1	16.38	21.14	2.67	0.158	0.167	196.4
s.d.	250 721	2758	1216	1616	372	80.5	10.33	12.78	1.80	0.388	0.408	114.9

Thus, for the Nivelle, the optimum production of 0+ parr would be obtained with a minimum number of eggs deposited, 261 000 units, i.e. 464 eggs 100 m^{-2} of the riffle equivalent or 81 eggs 100 m^{-2} of watercourse, generating a maximum of 7794 parr. This corresponded to a theoretical survival rate of the egg to 0+ parr of 2.99%.

This model allowed to fix, in a deterministic way, a maximum theoretical production of 0+ parr and to solve the problem of the constraint, which prevents the model from simulating unrealistic levels of abundance.

Establishing the regulation model of the young stages and territorial constraint

The deterministic model previously described did not take into account the entire variability observed, and seemed to restrict 0+ parr production too strongly. Observations showed that it was possible to obtain young salmon productions higher than the calculated optimum for at least 2 years (Figure 2).

Our approach was further developed by using a Ricker-type compensatory regulation mechanism, which took into account not only deposited eggs and survival rate, but also the maximum possible number of 0+ parr, defined from the production surface area and from the average size of the individual territory, and also the varying abundance of older parr. This approach gave a better fit to the observed data. In conditions of fully populated habitats, minimal individual territory sizes calculated for 0+ and 1+ parr were, respectively, 4.16 and 14.1 m^2 (Table 5).

Figure 3 shows the numbers of 0+ parr constrained by various values of the survival rate $S1_t$ [Equation (13)]. It demonstrates clearly the variability of the shape of the constraint depending on the variation in population

productivity (number of parr produced per unit of eggs deposited).

Abundance of adults and return rate

The annual runs, which generated the 11-year classes accounted for an average of 235 salmon, including all the ages (range, 127 to 472 individuals; Table 2). Previous spawners represented only 0.9% of the stock.

The average number of adults originating from the 6-year classes in which all the age groups had completely returned amounted to 196 salmon (s.d. = 115) or 0.35 salmon 100 m^{-2} of riffle equivalent. Adult returns varied by a factor of 5 (Table 3), the 1991 class generating the largest number, 382 salmon, including 312 grilse (of age type 1.1), which greatly contributed to the large run of 1993.

On average, 6.2% of the 0+ parr of these 6-year classes came back from the ocean (s.d. = 2.4%), but the annual return rates varied three-fold (from 3.4 to 9.1%, Table 4). The detail of age-type expressed by two figures, i.e. smolt age and sea age, where smolt age 1 corresponds to 0+ parr of the upper mode, and smolt age 2 refers to the number of 1+ parr, gave more variable rates (Table 4). The mean value obtained for large 0+ parr amounted to 6.5% (5.7% for the 1.1 age type, 0.84% for the 1.2 type and 0.007% for the 1.3 type). It was lower for 1+ parr, 4.1% (3.46, 0.64 and 0.031%, respectively, for 2.1, 2.2 and 2.3 types). Among the eight complete year classes with 1.1 adult returns, the last three classes generated lower adult return rates.

Proportions of age types and females

Returning adults for fully recruited year classes were 88.7% grilse (s.d. = 5.4%; Table 6). Those originating from

Table 4. Proportions of 0+ size groups and survival of observed stages for year classes, 1991–2000 (LMG, lower modal group; UMG, upper modal group; age type ij, ith freshwater age and jth sea age; ret., adult returns).

Year class	Proportion of 0+ of UMG (%)	Survival rate of parr (%)		Survival rate of parr to adult (%)										Total		
		Egg to 0+ parr	0+ LMG to 1+parr	1-sea-year		2-sea-year		3-sea-year		1-sea-year		2-sea-year			3-sea-year	
				0+ UMG to 1.1 ret.	0+ UMG to 1.2 ret.	0+ UMG to 1.1 ret.	0+ UMG to 1.2 ret.	0+ UMG to 1.3 ret.	1+parr to 2.1 ret.	1+parr to 2.2 ret.	1+parr to 2.3 ret.	1+parr to 2.1 ret.	1+parr to 2.2 ret.		1+parr to 2.3 ret.	
1991	77.65	0.56	64.26	9.56	1.01	0.00	0.00	0.00	5.49	0.69	0.00	0.00	0.00	0.00	9.1	
1992	71.63	0.59	38.59	9.66	1.32	0.04	0.00	0.00	5.35	1.34	0.00	0.00	0.00	0.00	8.6	
1993	67.01	0.37	62.00	7.35	1.98	0.00	0.00	0.00	4.07	0.37	0.19	0.19	0.19	0.19	7.2	
1994	79.40	0.16	65.26	4.54	0.27	0.00	0.00	0.00	1.44	0.12	0.00	0.00	0.00	0.00	4.0	
1995	77.61	0.22	36.48	5.72	0.31	0.00	0.00	0.00	3.17	0.69	0.00	0.00	0.00	0.00	5.0	
1996	76.48	1.14	54.36	3.33	0.49	0.00	0.00	0.00	3.09	0.62	0.00	0.00	0.00	0.00	3.4	
1997	76.04	0.88	55.99	2.59	0.51				1.65							
1998	72.22	1.39	65.35	2.85												
1999	60.49	2.35	38.38													
2000	59.03	2.07														
No. of years	10	10	9	8	7	6	6	6	7	6	6	6	6	6	6	
Mean	71.75	0.97	53.41	5.70	0.84	0.007	0.007	0.007	3.46	0.64	0.031	0.031	0.031	0.031	6.22	
s.d.	7.30	0.76	12.32	2.88	0.63	0.017	0.017	0.017	1.62	0.41	0.076	0.076	0.076	0.076	2.42	

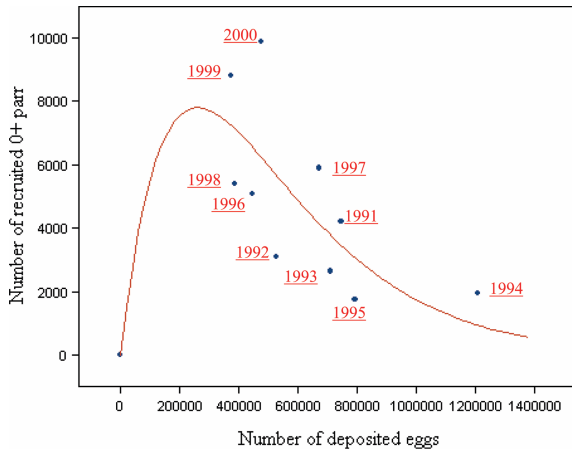


Figure 2. The Ricker model fit to juvenile recruitment data of the Nivelles River (year classes, 1991–2000).

1-year-old smolt represented 80.6% of all the adult returns. Only 11.2% of the salmon returned after two winters at sea, including 9.9% originating from young smolt. Three-sea-winter salmon were few (0.15%).

Females represented 59.9% of salmon returns for the 6-year classes (Table 7). Females comprised 56.2% (s.d.=6.4%) of the grilse, 88.6% (s.d. = 4.2%) of 2-sea-year subjects, and the two 3-sea-year fish.

Mean weight of females

The weight of female grilse was on average 2528 g (s.d. = 116 g), and was independent of smolt age (2525 and 2532 g, respectively, for those of 1 and 2 years). The average weight of 2-sea-year salmon was 4884 g (s.d. = 296 g), i.e. 4879 and 4990 for 1- and 2-year smolts, respectively. Three-sea-year salmon weighed 7278 g (s.d. = 548 g).

Angling catches

In the Nivelles, professional net fishing is forbidden both in the estuary and in the river (Dumas and Haury, 1995). Only angling is authorised, but declaration of catches is compulsory. The angling catches, from one to seven salmon a year, were very small and during the 1983–

2000 period, represented only 3.6% of the runs of 2- and 3-sea-year salmon and 0.9% of grilse runs. Beginning in 1996, the angling season was stretched to mid-October to take advantage of the late runs of grilse, which constitute the majority of the stock. The extended season has tended to increase the exploitation rate of grilse, which rose to 1.6%.

Summary of the life-cycle parameters

The parameters used in the life-cycle modelling exercises belonged to the four groups: survival rate, separation rate, exploitation rate and egg deposition (Table 8). Their values or their distributions, depending on the type of parameter, were incorporated into the model.

Simulation results

The abundance values for certain levels of data dispersion after 35 years of simulation are shown in Table 9. The large difference between the mean and the median showed the asymmetry of the probability of abundance of the population for a given year. We note that the probability of obtaining an abundance lower than a couple of spawners is about 25% of the number of simulations at the present level of fishing exploitation.

The median of the population indicates that there is a 50% chance of having a simulated value, at least equal to 143 fish. This constitutes the present level of population observed in the Nivelles, while the simulated mean (262 salmon) is higher than that was observed during the past 11 years (196 salmon of the six complete cohorts).

The S–R relationship and dynamic characteristics of the population

The parameters of the Ricker equation were estimated by non-linear resolution [(Equation 14)] and allowed us to propose the following model (Figure 4):

$$\begin{aligned} \text{Eggs produced} &= \text{eggs deposited} \\ &\times \exp^{(0.290(1-\text{eggs deposited}/2.546 \times 10^6))} \\ &\times (R^2 = 0.971) \end{aligned}$$

Table 5. Maximum carrying capacity observed for 0+ parr and minimal territory surfaces at each age.

Age	Biomass				Mean weight (g)	Weight ratio	Number	Utilised area (m ²)	Shared area (m ²)	Territory size (m ²)
	Lower Nivelles 1987	Upper Nivelles 1999	Lurgorrieta 1988	Total						
0+	60.5	63.1	17.6	141.2	12.4		11 366	47 330	4711	4.16
1+	4.3	31.1	4.8	40.2	41.9	3.37	958	13 461	4711	14.05
Total	64.8	94.2	22.4	181.4				60 791		

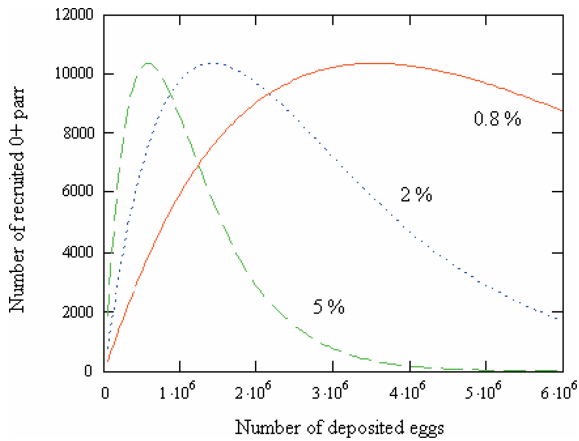


Figure 3. Representation of the population constraint according to three values (0.8, 2 and 5%) of the survival rate from egg deposition to first autumn parr.

The shape parameter of the curve *a*, equal to 0.290 and generally between 0 and 3, indicated that the population had low productivity. Parameters *Pr* and *Pm* were estimated respectively at 2.546×10^6 and 8.789×10^6 eggs. The maximum yield was 198 600 eggs for 1.424×10^6 eggs deposited, i.e. the maximum exploitation rate of 12.2% of the recruited eggs.

Discussion

In order to better understand and interpret the functioning of the salmon population of the Nivelle River, it is useful to compare its life history traits and its demographic characteristics with that of other stocks studied in different regions of the species distribution.

The relative fecundity of females of this river, between 1660 and $1750 \text{ eggs kg}^{-1}$, was comparable with that of other populations, e.g., respectively, 1758 and 1475

eggs kg^{-1} for the Miramichi and the Restigouche Rivers in New Brunswick (Randall, 1989) and $1685 \text{ eggs kg}^{-1}$ for the Elorn River in Brittany (Prouzet and Gaignon, 1982a).

In the Nivelle, the average egg deposition of $1091 \text{ eggs } 100 \text{ m}^{-2}$ of riffle equivalent, which corresponds to class A habitats as defined by Kennedy and Crozier (1993), was lower than the $1380 \text{ eggs } 100 \text{ m}^{-2}$ observed in the Oir in Lower Normandy by Prévost *et al.* (1996). When related to the total surface area of water, the value of $191 \text{ eggs } 100 \text{ m}^{-2}$ was low compared with the densities from 240 to $650 \text{ eggs } 100 \text{ m}^{-2}$ of watercourse widely recommended for maintaining salmon stocks (Egglishaw *et al.*, 1984; Elson, 1957; Kennedy, 1988).

The fluctuation of abundance of 0+ parr depended mainly on the density of deposited eggs according to a Ricker S–R overcompensation model, with larger mortality rates beyond the optimum density of deposited eggs or emerging fry, as in more northern salmon populations (Gardiner and Shackley, 1991; Gee *et al.*, 1978) and trout populations (Elliott, 1987, 1993). The simulation of parr production in Canadian rivers under the hypothesis of climatic changes followed a model of this type (Power and Power, 1994). The egg density, which maximises parr production, $464 \text{ eggs } 100 \text{ m}^{-2}$ of riffle equivalent, less than half the average egg deposition, was lower than that optimising older parr or smolt numbers observed in Lower Normandy (Prévost *et al.*, 1996), Scotland (Gardiner and Shackley, 1991) or Ireland (Kennedy and Crozier, 1993), which ranged between 700 and $1000 \text{ eggs } 100 \text{ m}^{-2}$ in the best-quality juvenile habitat.

Survival during the first year at the rate of 0.97% of eggs on average may have been partly due to poor survival in the redd substrate (12 to 31% of emerging fry depending on the year; Dumas and Darolles, 1999; Dumas, unpublished). It was similar to the 1.5% survival rate observed in a tributary of the Scorff in Brittany (Baglinière and Maise, 1989). It remained below those of the rivers of Great Britain and North America, commonly 2 to 4% (Bley and Moring,

Table 6. Proportion of adult age categories for year classes, 1991–1996 (*ij* = *i*th freshwater age and *j*th sea age).

Year class	Percentages of age groups (<i>ij</i>)									All ages
	1-sea-year			2-sea-year			3-sea-year			
	1.1	2.1	Total	1.2	2.2	Total	1.3	2.3	Total	
1991	81.6	8.7	90.3	8.6	1.1	9.7	0.0	0.0	0.0	100.0
1992	80.2	6.8	87.0	11.0	1.7	12.7	0.4	0.0	0.4	100.0
1993	68.4	11.6	80.0	18.4	1.1	19.5	0.0	0.5	0.5	100.0
1994	89.4	4.8	94.2	5.4	0.4	5.8	0.0	0.0	0.0	100.0
1995	88.8	5.2	94.0	4.9	1.1	6.0	0.0	0.0	0.0	100.0
1996	75.0	11.6	86.6	11.0	2.3	13.4	0.0	0.0	0.0	100.0
No. of years	6	6	6	6	6	6	6	6	6	6
Mean	80.57	8.11	88.68	9.90	1.28	11.18	0.06	0.09	0.15	100.00
s.d.	8.07	3.03	5.36	4.94	0.66	5.17	0.14	0.21	0.23	0.00

Table 7. Proportion of females by age category for year classes, 1991–1996 (ij = ith freshwater age and jth sea age).

Year class	Percentages of females (ij)									All ages
	1-sea-year			2-sea-year			3-sea-year			
	1.1	2.1	Total	1.2	2.2	Total	1.3	2.3	Total	
1991	58.1	76.7	59.9	92.0	80.0	90.7				62.9
1992	48.6	70.0	50.3	88.5	80.0	87.4	100.0		100.0	55.2
1993	54.2	73.7	57.0	86.2	100.0	86.9		100.0	100.0	63.1
1994	57.6	52.4	57.3	87.5	100.0	88.4				59.1
1995	65.8	55.0	65.2	100.0	75.0	95.3				67.0
1996	48.6	41.2	47.6	93.3	33.3	82.9				52.3
No. of years	6	6	6	6	6	6	1	1	2	6
Mean	55.48	61.50	56.22	91.25	78.05	88.58	100.00	100.00	100.00	59.93
s.d.	6.54	14.07	6.41	5.07	24.43	4.16			0.00	5.48

1988) or more (Cunjak and Therrien, 1998). Consequently, parr numbers were low in the first autumn, 8.7 individuals 100 m^{-2} of riffle equivalent. However, such a density was very similar to that observed in the Oir of 1.1 to 15 0+ parr (Baglinière *et al.*, 1993) or in the Scorff of 3.9 to 5.8 individuals 100 m^{-2} (Baglinière and Champigneulle, 1982). Egg-to-smolt survival, the index of comparison used by numerous authors, could be deduced from observations of the winter survival of parr carried out over 4 years (60% of 0+ parr and 36.8% of 1+ parr; Dumas, unpublished). The survival rate from egg to smolt was estimated at 0.45%, close to that observed for the Oir at

0.36% (Prévost *et al.*, 1996) or for the Bresle in Normandy (0.4 to 1.2%, Fournel *et al.*, 1987). This low survival rate, specific to southern European rivers, compared with that of rivers of other regions, is one of the lowest in the world (Hutchings and Jones, 1998; Prévost *et al.*, 1996). It resulted in a density of smolts of all ages of four individuals per 100 m^2 of riffle equivalent comparable with the carrying capacity of some rivers of the Armorican Massif in Brittany, which is 3 smolts 100 m^{-2} (Prévost and Porcher, 1996).

The low egg-to-smolt survival rates seemed to be partly compensated for by one of the highest growth rates for the

Table 8. Model parameters for the portion of the Nivelle River populated by salmon (LMG, lower modal group; UMG, upper modal group). *See text.

Parameter	Life stage							Distribution
	Egg to 0+ parr		0+ LMG of parr to 1+ parr		0+ UMG of parr			
	Mean	s.d.	Mean	s.d.	Mean	s.d.		
Freshwater survival rate (%)	0.97	0.76					Lognormal*	
Freshwater survival rate (%)			53.4	12.3			Normal	
Size group proportion (%)					71.8	7.3	Normal	
	1-sea-year returns		2-sea-year returns		3-sea-year returns			
	Mean	s.d.	Mean	s.d.	Mean	s.d.		
	Survival rate (%) of 0+ UMG	5.7	2.88	0.84	0.63	0.007		0.017
Survival rate (%) of 1+ parr	3.46	1.62	0.64	0.41	0.031	0.076	Normal	
Adult freshwater survival rate (%)	98		95		95		Constant	
Angling exploitation rate (%)	2		4		4		Constant	
Proportion of spawning females (%)	56.2	6.4	88.6	4.2	88.6	4.2	Constant	
Egg number per female	4200	1133	8500	1938	12 750	3000	Constant	
Mean weight of females (g)	2528	116	4884	296	7278	548	Constant	
Relative fecundity (eggs kg^{-1})	1661		1740		1752		Constant	

Table 9. Abundance probability values for different characteristic levels of distribution.

Distribution level	Egg number	Spawner number
1st quartile	4914	1.6
Median	494 000	143
Mean	803 000	262
3rd quartile	1 500 000	493
Maximum	3 200 000	1065

species (Héland and Dumas, 1994) and a growth strategy, which involves shortening the time spent by juveniles in freshwater, as shown by the proportion of future 1+ smolt, nearly 72% on average. The method of separating size groups of 0+ parr in autumn (Thorpe *et al.*, 1980) may generate biased estimates of the percentage of future 1+ smolt since a few 1+ smolt may be issued from the largest 0+ parr of the lower modal group (Baglinière *et al.*, 1993). Not taking this fact into account may underestimate the number of future 1+ smolt. On the other hand, in the upper modal group, a fraction of the 0+ precocious males may remain for one more year in freshwater, as indicated by marking experiments with Pit-tags in autumn (Dumas, unpublished). Ignoring this could overestimate the proportion of 1+ future smolt. These two migration strategies may balance and minor the error on the estimate of this proportion. The high proportion of future 1-year smolts issued from the upper modal group is characteristic of rivers in the southern part of the distribution area, such as the Oir in Lower Normandy (36 to 82%), the Scorff in Brittany (60%) and the Esva in Spain (48%) (Baglinière and Champigneulle, 1986; Baglinière *et al.*, 1993; Utrilla and Lobon-Cervia, 1999). It was also observed in a

Norwegian stream stocked with fry where the growth of 0+ parr was fast due to the lack of competition. The upper modal group amounted to 58% and during the next spring 1+ smolt belonged exclusively to this group (Heggnes and Metcalfe, 1991).

The returns generated by the first 6-year classes, 196 salmon on average or 0.35 adult 100 m⁻² of riffle equivalent, were small. They varied by a factor of 4.9 according to the cohort, and of 4.4 for similar egg depositions (year classes 1991 and 1995), which made the stock more vulnerable. Such variations are not exceptional since Kennedy and Crozier (1995, in Prévost and Porcher, 1996) observed fluctuations from one to seven for identical egg depositions in the Bush River in Northern Ireland. The large variability is due to the expression of density-independent ecological factors.

The adult returns to River Nivelle were mainly grilse (88.7%) as observed in most French rivers with comparable discharge and length, i.e. 82 to 88.4% in the Oir, Elorn and Scorff rivers (Prévost and Porcher, 1996; Prévost, 2000; Prévost *et al.*, 1996). The high percentage of grilse is comparable with that of Irish and Newfoundland rivers, which are among the highest for the species (Hutchings and Jones, 1998). The grilse and 2-sea-year salmon were 56.2 and 88.6% female, respectively. The proportion of females in the grilse age group was among the highest for French rivers (28 to 47%), which themselves had greater proportion of females than that of the rivers of more northern countries, and only Newfoundland rivers present higher proportions, 67% on average (Hutchings and Jones, 1998). A large proportion of females in 2-sea-year subjects, as observed in the Nivelle, is generally more frequent in salmon populations. It should be noted that the biased sex ratio, 59.9% for females of the anadromous population, suggested that for males, the survival rate was lower by about one-third, although the sex ratio was still balanced at the 0+ parr stage, since 53.9% of a fall sample of 466 0+ euthanised parr was found to be male during the period 1985–1988 (not significantly different from 1/1). Such a difference was probably due to the early maturation of males, observed for 18.1% of the 0+ parr population and for 65.3% of the 1+ parr for the 1991–2000-year classes (Dumas, unpublished).

The survival rate from 0+ parr to adult returns of 6.2% on average could vary by a factor of 3 depending on the cohort. It was practically identical to that observed by Prouzet and Gaignon (1982b) among the marked 0+ parr on a tributary of the Elorn in Brittany, originating from eggs of Irish strains and which was 5.8%. It corresponded to a mean return rate of smolt of all ages, essentially as grilse, of 12.6%, a value estimated from the survival rates from 0+ and 1+ autumn parr to the pre-smolt stage in the following early spring, averaged over 4 years. It was the same as that of smolts from the Bresle (14.2% according to Euzenat, Fournel and Fagard, cited by Prévost and Porcher, 1996) or from the Canadian Maritime Provinces (13%; Hutchings

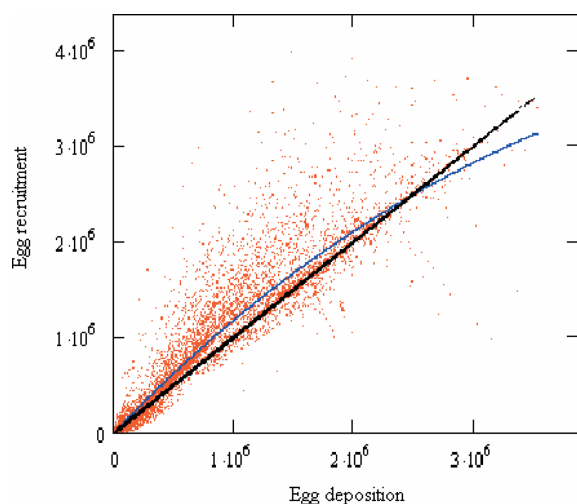


Figure 4. The S-R relationship for the Nivelle River salmon population. Estimates of characteristics of population dynamics.

and Jones, 1998), but much lower than that of the returns in coastal zones of grilse of the Bush River (31.3%; Crozier and Kennedy, 1999). Generally, this rate was higher than the mean return rates of smolt as grilse observed in most rivers (7.4%; Hutchings and Jones, 1998).

Simulating the numbers of each of the stages allowed us to generate values that fit well with the observed data. In this study, the abundance of 0+ parr depended mainly on the density of deposited eggs and little on the density of 1+ parr, which were present at lower density. It could be more dependent on older parr if they were more in number and if the overlapping rate of territories were smaller than the 35% used in this simulation. The means of results of the stochastic model, 802 500 eggs and 262 spawners, were 31 and 33% higher than the respective observed means, while the medians represented only 81 and 73% of these same observed means. This suggests that the population of the Nivelle has not yet attained a state of equilibrium and is still in a growing phase.

The S-R relationship established from the simulated values of deposited eggs and recruits at each generation (Figure 4) was based on the Ricker model (1980), in which mortality is proportional to the number of eggs, which will maximise the number of recruits for an optimum number of eggs. Beyond this, the number of recruits decreases, which has been illustrated for specific stocks in Iceland and Labrador (Dempson, 1980; Mundy *et al.*, 1978). However, no decrease in recruits was observed in the range of egg depositions generated from our analysis, and as such, the data could then be fitted to a Beverton and Holt (1957) compensation model, where the number of recruits tends towards an asymptotic maximum value, similar to what was found for a majority of other anadromous salmon populations (Myers and Barrowman, 1996). However, another analysis of the 500 individual trajectories over 35 years showed that, under certain conditions, the choice of the Ricker model was relevant. Overall, there was no clear optimum within the observed range of variation. This was due to the small number of pairs of values generated in the lower right-hand tail of the graph. By construction, the model determined the abundance of the population mainly from the value of three parameters: the egg to 0+ parr survival rate ($S_{1,t}$), the return rate of grilse issued from 1-year-old smolt ($S_{rmt1.1,t}$) and the number of eggs deposited ($eggs_t$). For the optimum to be distinct and the pairs of values to be found in the lower right quartile, the number of parr theoretically produced must be higher than the potential maximum number ($parrmx_t$), the return rate of 1.1 age type grilse must be lower than the average and the abundance of deposited eggs higher than 1 500 000. A rapid calculation carried out on the simulator showed that the probability P of having a pair of values in the lower right hand portion of the graph representing 500 trajectories for the 27 years of simulations was equal to 0.05, i.e. $\text{Prob}(S_{rmt1.1,t} < 5 \sim 0.5) \times \text{Prob}(S_{1,t} > 0.66 = 0.542) \times \text{Prob}(\text{abundance} > 1\,500\,000 \text{ eggs } 0.197)$.

The shape of this curve (Figure 4) showed the low yield of this population, 1.14 recruits per spawner, although recruits per spawner values could reach high mean values of 4.3 to 5 in more northern population (Chadwick, 1987; Mundy *et al.*, 1978). Thus, for River Nivelle, the catchable portion of the population, currently at less than 12% of the 1.6 million eggs recruited at maximum yield, should be considered as very low compared with other stocks (e.g. 59% in the Ellidaar; Mundy *et al.*, 1978). Although the mean abundance observed for recruited eggs was about half that necessary for obtaining a maximum yield, this population is not endangered by exploitation in the river.

Thus, the stochastic model estimating the evolution of different stages of salmon in freshwater allowed for the first time to simulate the functioning of a population submitted to particular environmental constraints owing to latitude. It confirmed that the stock of this river had a low productivity. This was essentially linked to a low mean egg deposition, a low survival rate of eggs during the first year and a modest carrying capacity, from 14 to 17.6 0+ parr 100 m^{-2} of riffle equivalent, depending on whether we refer to the estimation by the juvenile model or to the maximum observed in 2000. Moreover, the renewal of generations as shown by the mean age of anadromous spawners during reproduction of 3.21 years, was one of the most rapid-known for this species (Hutchings and Jones, 1998). However, the runs of a single year were made up of nearly 81% of a single year class. All these facts considered together, support the idea that the salmon population of River Nivelle is fragile.

In order to partly compensate for the fragility of the stock and its vulnerability linked to the risk of occurrence of small numbers of breeders in certain years (Routledge and Irvin, 1999), the high-quality habitat in the upper part of the French and Spanish basins of the Nivelle and of the main tributary should be made accessible. This ought to allow a substantial increase in the number of juveniles that could be supported. Consequently, the critical number of adults would increase limiting the risk of extinction.

Acknowledgements

We would like to thank the Direction Régionale à l'Environnement, the Conseil Régional d'Aquitaine and the Conseil Supérieur de la Pêche for their financial support, and the fishermen organisations (MIGRADOUR, the Federation of fishermen associations of the Pyrénées Atlantiques and the Nivelle fishermen association) for their helpful contribution to trapping operations and redd surveying. We are indebted to the many people who helped in those operations, in particular Lionel Barrière, Alain Bosviel, Emmanuel Huchet, Jean-Pierre Martinet, Michel Parade et Jean-Claude Vignes. We thank Dave G. Reddin (Department of Fisheries and Oceans, St John's, Nfld, Canada) and an anonymous referee for their many helpful comments and improvements on

the manuscript. We are grateful to Edward Beall and Philippe Gaudin (Inra laboratory, St-Pée-sur-Nivelle) for the first revision of the manuscript and to Christine Young (Inra, Unité Centrale de Documentation) for the English translation of the manuscript.

References

- Allen, K. R. 1969. Limitation of production in salmonid populations in streams. *In* Symposium on Salmon and Trout in Streams, pp. 3–18. Ed. by T. G. Northcote. University of British Columbia, Vancouver.
- Anon., 1998. Définition d'une cible d'échappement et estimation des contraintes pour la pêche du saumon Atlantique sur le bassin versant de l'Adour et de la Nivelle. Document de travail pour le Comité de Gestion des Poissons Migrateurs de l'Adour et des versants côtiers. 22 pp.+annexes.
- Baglinière, J. L., and Champigneulle, A. 1982. Densités des populations de Truite commune (*Salmo trutta* L.) et des juvéniles de Saumon atlantique (*Salmo salar* L.) sur le cours principal du Scorff (Bretagne). Préféréments physiques et variations annuelles (1976–1980). *Acta Oecologica (Ecologia Applicata)*, 3: 241–256.
- Baglinière, J. L., and Champigneulle, A. 1986. Population estimates of juvenile Atlantic salmon, *Salmo salar*, as indices of smolt production in the R. Scorff, Brittany. *Journal of Fish Biology*, 29: 467–482.
- Baglinière, J. L., and Maisse, G. 1989. Dynamique de la population de juvéniles de saumon atlantique (*Salmo salar* L.) sur un petit affluent du Scorff (Morbihan). *Acta Oecologica (Ecologia Applicata)*, 10: 3–17.
- Baglinière, J. L., Maisse, G., and Nihouan, A. 1993. Comparison of two methods of estimating Atlantic salmon (*Salmo salar*) wild smolt production. *In* The Production of Juvenile Atlantic Salmon, *Salmo salar*, in Natural Waters, pp. 189–201. Ed. by R. J. Gibson, and R. E. Cutting. Canadian Special Publication of Fisheries and Aquatic Sciences, 118.
- Beall, E., Dumas, J., Claireaux, D., Barrière, L., and Marty, C. 1994. Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. *ICES Journal of Marine Science*, 51: 1–9.
- Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. *Fishery Investigations*, London, Ser. 2, 19: 1–553.
- Bley, P., and Moring, J. R. 1988. Freshwater and ocean survival of Atlantic salmon and steelhead: a synopsis. United States Fish and Wildlife Service, Biological Report, 88(9): 22 pp.
- Buck, R. J. G., and Hay, D. W. 1984. The relation between stock size and progeny of Atlantic salmon, *Salmo salar* L., in a Scottish stream. *Journal of Fish Biology*, 24: 1–11.
- Chadwick, E. M. P. 1987. Causes of variable recruitment in a small Atlantic salmon stock. *American Fisheries Society Symposium*, 1: 390–401.
- Chaput, G., Allard, J., Caron, F., Dempson, J. B., Mullins, C. C., and O'Connell, M. F. 1998. River specific-target spawning requirements for Atlantic salmon (*Salmo salar*) based on a generalized smolt production model. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 246–261.
- Crozier, W. W., and Kennedy, J. A. 1999. Relationships between marine growth and marine survival of one sea winter Atlantic salmon, *Salmo salar* L., from the River Bush, Northern Ireland. *Fisheries Management and Ecology*, 6: 89–96.
- Cuinat, R., Dumas, J., Timmermans, J. A., Arrignon, J., and Tufféry, G. 1975. Ecological diagnosis in salmonid streams. Method and example. *European Inland Fisheries Advisory Commission, Technical Paper*, 22. 122 pp.
- Cunjak, R. A., and Therrien, J. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. *Fisheries Management and Ecology*, 5: 209–223.
- Dempson, J. B. 1980. Application of a stock recruitment model to assess the Labrador Atlantic salmon fishery. *ICES, Anadromous and Catadromous Fish Committee, CM 1980/M: 28*. 15 pp.
- Dumas, J. 1990–2001. La population de saumons adultes de la Nivelle en 1989;...;2000. Annual reports, Station d'Hydrobiologie, INRA, St-Pée-sur-Nivelle.
- Dumas, J. 1997. Des exemples d'aménagement. Restauration d'un stock de saumon: le cas de la Nivelle. *In* Des activités du Grand Littoral Atlantique à l'Observatoire des pêches et des cultures marines du Golfe de Gascogne. 10^{èmes} rencontres inter-régionales de l'AGLIA, pp. 46–52, St Jean de Luz, 20–21 novembre 1997.
- Dumas, J., and Barrière, L. 1991. Contrôle des taux de recapture ou de retour des saumons de la Nivelle France, Pyrénées-Atlantiques de 1977 à 1990. *ICES, Anadromous and Catadromous Fish Committee, C.M. 1991/M: 19*. 14 pp.
- Dumas, J., and Darolles, V. 1999. Caractéristiques environnementales et survie embryolaire du Saumon atlantique, *Salmo salar* L., dans un cours d'eau du piémont pyrénéen, la Nivelle (France). *Cybium*, 23(suppl. 1): 29–44.
- Dumas, J., and Hauray, J. 1995. Une rivière du piémont pyrénéen: La Nivelle (Pays Basque). *Acta Biologica Montana*, 11: 113–146.
- Dumas, J., Faivre, R., Charron, M. H., Badia, J., Davaine, P., and Prouzet, P. 1996. Modélisation stochastique du cycle biologique du Saumon atlantique *Salmo salar* L.: bases biologiques, implémentation informatique et interprétation. *In* Méthodes d'Étude des Systèmes halieutiques et aquacoles, pp. 51–63. Ed. by J. Ferraris, D. Pelletier, and M. J. Rochet. ORSTOM Editions Bondy, Colloques et Séminaires.
- Egglishaw, H. R., Gardiner, W. R., Shackley, P. E., and Struthers, G. 1984. Principles and practice of stocking streams with salmon eggs and fry. *Scottish Fisheries Information Pamphlet*, 10. 22 pp.
- Elliott, J. M. 1987. Population regulation in contrasting populations of trout *Salmo trutta* in two Lake District streams. *Journal of Animal Ecology*, 56: 83–98.
- Elliott, J. M. 1993. A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream. *In* The Production of Juvenile Atlantic Salmon, *Salmo salar*, in Natural Waters, pp. 109–122. Ed. by R. J. Gibson, and R. E. Cutting. Canadian Special Publication of Fisheries and Aquatic Sciences, 118.
- Elson, P. F. 1957. Number of salmon needed to maintain stocks. *Canadian Journal of Fish Culturist*, 21: 18–23.
- Elson, P. F. 1975. Atlantic salmon rivers, smolt production and optimal spawning: an overview of natural production. *International Atlantic Salmon Foundation Special Publication Series*, 6: 96–119.
- Faivre, R., Dumas, J., Charron, M. H., Badia, J., and Prouzet, P. 1997. River basin management using a stochastic model of the salmon life cycle. *In* Congress on Modeling and Simulation, MODSIM'97, pp. 1536–1541. Hobart, Tasmania, Australia, December 8–11, 1997.
- Fournel, F., Euzenat, G., and Fagard, J. L. 1887. Rivières à truites de mer et saumons de Haute-Normandie. Réalités et perspectives. Le cas de la Bresle. *In* Restauration des rivières à saumons, pp. 315–325. Ed. by M. Thibault, and R. Billard. INRA, Paris.
- Gardiner, R., and Shackley, P. 1991. Stock and recruitment and inversely density-dependant growth of salmon, *Salmo salar* L., in a Scottish stream. *Journal of Fish Biology*, 38: 691–696.
- Gee, A. S., Milner, N. J., and Hemsworth, G. J. 1978. The effect of density on mortality in juvenile Atlantic salmon (*Salmo salar*). *Journal of Animal Ecology*, 47: 497–505.
- Grant, J. W., and Kramer, D. L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids

- in steams. *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 1724–1737.
- Gros, P., and Prouzet, P. 1988. Modèle stochastique prévisionnel des captures de saumons de printemps (*Salmo salar* L.) dans l'Aulne (Bretagne): éléments d'aménagement de la pêche. *Acta Ecologica (Ecologia Applicata)*, 9: 3–23.
- Guéguen, J. C., and Prouzet, P. 1994. Le saumon atlantique, pp. 330. Ed. by J. C. Guéguen, and P. Prouzet. IFREMER, Plouzané.
- Heggnes, J., and Metcalfe, N. B. 1991. Bimodal size distribution in wild juvenile Atlantic salmon populations and their relationship with age at smolt migration. *Journal of Fish Biology*, 39: 905–907.
- Héland, M., and Dumas, J. 1994. Ecologie et comportement des juvéniles. In *Le Saumon atlantique*, pp. 29–46. Ed. by J. C. Guéguen, and P. Prouzet. IFREMER, Plouzané.
- Hutchings, J. A., and Jones, M. E. B. 1998. Life history variation in growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(suppl. 1): 22–47.
- Johnstone, R. 1981. Dye marking. Colour guide to growth performance. *Fish Farmer*, 4: 24–25.
- Kennedy, G. J. A. 1988. Stock enhancement of Atlantic salmon (*Salmo salar* L.). In *Atlantic salmon. Planning for the Future*, pp. 345–372. Ed. by D. Mills, and D. Piggins. Crom Helm, London.
- Kennedy, G. J. A., and Crozier, W. W. 1993. Juvenile Atlantic salmon *Salmo salar* – production and prediction. In *Production of juvenile Atlantic salmon, Salmo salar*, in natural waters, pp. 179–187. Ed. by R. J. Gibson, and R. E. Cutting. Canadian Special Publication on Fisheries and Aquatic Sciences, 118.
- Larkin, P. A., and Hourston, A. S. 1964. A model for simulation of the population biology of Pacific Salmon. *Journal of Fisheries Research Board of Canada*, 21: 1245–1264.
- Maisse, G., and Baglinière, J. L. 1986. Le sexage morphologique du Saumon atlantique (*Salmo salar*). *Bulletin Français de Pêche et Pisciculture*, 300: 13–18.
- Maisse, G., Baglinière, J. L., Landry, G., Caron, F., and Rouleau, A. 1988. Identification externe du sexe chez le Saumon atlantique (*Salmo salar* L.). *Canadian Journal of Zoology*, 66: 2312–2315.
- Marschall, E. A., Qwinn, T. P., Roff, D. A., Hutchings, J. A., Metcalfe, N. B., Bakke, T. A., Saunders, R. L., and LeRoy Poff, N. 1998. A framework for understanding Atlantic salmon (*Salmo salar*) life history. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(suppl. 1): 48–58.
- More, J. M., Garbow, B. S., and Hillstrom, K. E. 1980. User's guide to MINPACK I. Ed. by Argonne National Laboratory ANL-80-74.
- Mundy, P. R., Alexandersdottir, M., and Eiriksdottir, G. 1978. Spawner-recruit relationship in Ellidaar. *Journal of Agricultural Research in Iceland*, 10: 47–56.
- Myers, R. A., and Barrowman, N. J. 1996. Is fish recruitment related to spawner abundance? *Fishery Bulletin United States*, 94: 707–724.
- Pearl, R. 1925. *The Biology of Population Growth*. A.A. Knopf, New York.
- Power, M., and Power, G. 1994. Modeling the dynamics of smolt production in Atlantic salmon. *Transactions of the American Fisheries Society*, 123: 535–548.
- Prévost, E. 2000. Etat du stock de saumon atlantique (*Salmo salar*) du Scorff (Bretagne sud, France) en 1999: production de smolts, retours d'adultes, échappement, taux d'exploitation et de survie. Conseil Scientifique du Moulin des Princes, CSP/INRA, Rennes. 19 pp.
- Prévost, E., and Porcher, J. P. 1996. Méthodologie d'élaboration des totaux autorisés de captures (TAC) pour le Saumon atlantique (*Salmo salar* L.) dans le Massif Armoricaïn. Propositions et recommandations scientifiques. GRISAM, Document Scientifique et Technique, 1. 15 pp.
- Prévost, E., Baglinière, J. L., Maisse, G., and Nihouarn, A. 1996. Premiers éléments d'une relation stock/recrutement chez le saumon Atlantique (*Salmo salar*) en France. *Cybiurn*, 20(suppl. 3): 7–26.
- Prouzet, P. 1990. Stock characteristics of Atlantic salmon (*Salmo salar*) in France: a review. *Aquatic Living Resources*, 3: 85–97.
- Prouzet, P. 1994. La dynamique des stocks. In *Le Saumon atlantique*, pp. 155–174. Ed. by J. C. Guéguen, and P. Prouzet. IFREMER, Plouzané.
- Prouzet, P., and Gaignon, J. L. 1982. Fécondité des Saumons Atlantiques adultes capturés sur le bassin versant de l'Elorn (rivière de Bretagne Nord) et caractéristiques de leurs pontes. *Bulletin Français de Pisciculture*, 285: 233–243.
- Prouzet, P., and Gaignon, J. L. 1982. Production de saumon atlantique (*Salmo salar* L.) juvéniles et adultes sur un ruisseau pépinière de Bretagne Nord (France) à partir d'une souche irlandaise. *Revue des Travaux de l'Institut des Pêches Maritimes*, 45: 155–174.
- Randall, R. G. 1989. Effect of sea-age on the reproductive potential of Atlantic salmon (*Salmo salar*) in eastern Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 2210–2218.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of Fisheries Research Board Canada*, 11: 559–623.
- Ricker, W. E. 1980. Calcul et interprétation des statistiques biologiques des populations de poissons. *Bulletin de l'Office des Recherches sur la Pêche du Canada*, 191F. 409 pp.
- Routledge, R. D., and Irvin, J. R. 1999. Chance fluctuations and survival of small salmon stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1512–1519.
- Seber, G. A. F., and Le Cren, E. D. 1967. Estimating population parameters from catches large relative to the population. *Journal of Animal Ecology*, 36: 631–643.
- Symons, P. E. K. 1979. Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity. *Journal of Fisheries Research Board of Canada*, 36: 132–140.
- Symons, P. E. K., and Héland, M. 1978. Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon (*Salmo salar*). *Journal of Fisheries Research Board of Canada*, 35: 175–183.
- Thorpe, J. E., Morgan, R. I. G., Ottaway, E. M., and Miles, M. S. 1980. Time of divergence of growth groups between potential 1+ and 2+ smolts among sibling Atlantic salmon. *Journal of Fish Biology*, 17: 13–21.
- Utrilla, C. G., and Lobon-Cervia, J. 1999. Life-history patterns in southern population of Atlantic salmon. *Journal of Fish Biology*, 55: 68–83.
- Verhulst, E. F. 1884. *Mémoires de l'Académie Royale*, Bruxelles, 18. 1 pp.

Errata

ICES Journal of Marine Science, 60: 356–370. 2003.☆

Variability of demographic parameters and population dynamics of Atlantic salmon (*Salmo salar* L.) in a southwest French river

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When this article was originally published there were a number of corrections which were not made, as listed below:

p. 362. In Table 3, the heading of column three should be “Total”.

p. 364. The correct model in the section “The S–R relationship and dynamic characteristics of the population” should be:

$$\text{Eggs produced} = \text{eggs deposited} \times \exp^{(0.290(1 - \text{eggs deposited}/2.546 \times 10^6))} \text{ with } R^2 = 0.971$$

p. 365. The first sentence should read: “The shape parameter of the curve α , equal to 0.290 and generally between 0 and 3, indicated that the population had low productivity”.

We regret these errors.

☆ doi of original article 10.1016/S1054-3139(03)00003-1