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Interannual changes in recruitment of the Atlantic salmon (*Salmo salar*) population in the River Oir (Lower Normandy, France): relationships with spawners and in-stream habitat

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Since 1985, the dynamics of the Atlantic salmon (*Salmo salar*) population in the River Oir, a spawning tributary of the River Sélune (Lower Normandy, France), have been studied from a data set of parr density and the number and the age structure of migrating fish (smolts and adults). Parr densities (1.5–17.4 per 100 m^2) and smolt production (0.25–9.2 per 100 m^2) varied considerably from year to year. Migrating juveniles were mainly 1 year old. Abundance of parr and smolts was strongly correlated with 0+ densities. Egg-to-smolt survival rates were highly variable year on year (0.044–1.07%). During the juvenile freshwater phase, mortality was highest between the egg and the 0+ stage (97.5–99.9%). The fluctuations in abundance of juvenile salmon appear to be linked to the number and distribution of spawners within the stream during spawning, and also to the amount of silt deposition on the spawning beds. As a result, mortality was highest during the under-gravel phase, and the mean survival rate from egg to smolt was much lower than in rivers less impacted by human activities. Therefore, during the study period, the low production of smolts during some years might lead to a low renewal rate of the salmon population.

Keywords: abundance, anthropogenic impact, Atlantic salmon, silt deposition, survival.

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Introduction

Owing to its local geological and hydro-climatic characteristics, the Armorican Massif (Brittany and Lower Normandy) is the area of France with the most salmon rivers. Atlantic salmon (*Salmo salar*) are found in 25 main rivers ranging in length from 30 to 75 km (Fontenelle *et al.*, 1980), and about 80% of the annual French rod-and-line salmon catches are made in the area. The rivers have specific physical and chemical characteristics (relatively moderate slope, good water quality, suitable water temperature for salmonids), a low stream order, a high heterogeneity, and a weak resilience to any perturbation. Their fish assemblages are among the most studied of all the biotic compartments, and are relatively well known (Baglinière, 1979; Baglinière and Arribe-Moutounet, 1985). The diversity of fish species is low, and includes two salmonids: Atlantic salmon and brown trout (*Salmo trutta*).

The ecosystems are sensitive to anthropogenic pressures on the drainage basin, some of which are long established (hydraulic and hydroelectric energy), whereas others are more recent (agriculture). The modifications of the physical and agronomic structure of the drainage basin result in strong perturbations of the various biotic compartments. They exert both direct (toxicity) and indirect (in-stream habitat alterations) effects that strongly influence the abundance of fish populations.

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Since 1984, a research programme on salmonid population dynamics has been carried out on the River Oir, a tributary of the Sélune in Lower Normandy. A long series of data (20 years) has been collected on ecological characteristics, as well as on the distribution and abundance of salmon within the river. Previous papers utilizing these data focused on analysing the stock-recruitment relationship, and showed that average recruitment and smolt production in the River Oir was relatively low compared with northern European and Canadian rivers (Prévost *et al.*, 1996; Rivot *et al.*, 2001, 2004). Moreover, the research facilitated the development of tools for decision analysis related to the sustainable management of salmon fisheries at a regional level (Prévost and Porcher, 1996; Rivot *et al.*, 2001). Here, we analyse the data series with two main objectives: (i) to evaluate the river's salmon production and the status of the population; (ii) to analyse the evolution of the parameters of Atlantic salmon population dynamics in a stream in relation to variance in the environment, including especially the impact of anthropogenic activities in the drainage basin.

The study area and resources

Geographical, physical, and chemical characteristics of the River Oir drainage basin

The River Oir is a tributary of the River Sélune, which flows into the English Channel in the Bay of Mont Saint-Michel and shares a common estuary with the River Sée. Its confluence is located in the estuarine part of the Sélune, just 8 km upstream from the mouth (Figure 1). The River Oir is 19.5 km long and has an average slope of 11‰. Its 87 km^2 drainage basin is made up of schists with a few enclaves of granite, and is situated in an area with an oceanic climate (Baglinière *et al.*, 1988). Mean annual water temperature fluctuates between 3°C and 19°C, daily water temperature rarely exceeding 20°C.

The study area is located between the two mills of Cerisel and Buat (Figure 1). The mill at Buat, 12.5 km upstream from Cerisel, can be a serious obstacle to migration of adult salmon, because it can be crossed only during periods of high discharge (Baglinière *et al.*, 1988). A second dam (the Castle dam) in the middle of the study area can also prevent access of adult salmon to the upper basin and the La Roche Brook during low-flow conditions. The River Oir has several tributaries in the study area, the most important being Bois Tyrel, L'Arçonnière, Sourvallée, Moulinet, Moulin du Bois, Pont-Lévesque, and La Roche, this last being accessible to salmon in the lower 2 km only. Therefore, the study area covers the main salmon production area within the Oir Basin.

Human activities in the drainage basin are mainly agricultural (crops and livestock). Recent analysis of the physico-chemical composition of the River Oir and some of its tributaries reveals a slightly alkaline pH (7.1−7.8) and well-oxygenated water (113−130% saturation). Nitrate concentrations are high (30 $mg\,l^{-1}$; Baglinière *et al.*, 2002) as a result of anthropogenic sources of nitrogen in the river catchment, notably sewage and livestock waste. Silt deposition in the main river and its tributaries (in particular, the Moulinet and Bois Tyrel Brooks) is significant, and it results from erosion of the steep banks (deep soils in relation to the schist geological substratum), as well as cattle grazing and trampling in riparian areas.

Data on water contamination by herbicides and heavy metals are fragmentary, and depend on year and site (Baglinière *et al.*, 2002). Triazines and isoproturon, measured in spring and at the end of summer, are below the detection threshold in 85% of the samples collected. Some values of copper (7−24 $mg\,kg^{-1}$) and lead (13−20 $mg\,kg^{-1}$) measured in sediments in winter and summer exceed the class 1 threshold limit (risk of chronic effect on sensitive stage or species: 1.9 $mg\,kg^{-1}$ for copper, 4.1 $mg\,kg^{-1}$ for lead) in the quality grid of Water Authorities, and even the class 2 threshold limit (risk of chronic effect on species abundance: 19 $mg\,kg^{-1}$ for copper; Anon., 1997).

The fish community

Atlantic salmon cohabit with brown trout in both anadromous and freshwater form in the River Oir, the two morphs being impossible to distinguish at the juvenile stage (Baglinière *et al.*, 2000). Other species present include three other diadromous fish, the European eel (*Anguilla anguilla*), the sea lamprey (*Petromyzon marina*), and the river lamprey (*Lampetra fluviatilis*), and five freshwater fish, bullhead (*Cottus gobio*), stone loach (*Neimacheilus barbatula*), minnow (*Phoxinus phoxinus*), brook lamprey (*Lampetra planeri*), and gudgeon (*Gobio gobio*). Species richness of the river system has never exceeded ten, decreasing from the lower to the upper stretches, and becoming much lower in the tributaries (two to four species). However, it is artificially increased in some places by non-native species such as northern pike (*Esox lucius*), perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), and common carp (*Cyprinus carpio*), entering from man-made ponds.

In terms of salmon, the Oir is a spawning tributary of the Sélune. Adults migrate upstream in autumn shortly before spawning, essentially December. Most returning adults (average 90.6%; range 42.2−100%) are not born in the River Oir (Rivot, 2003). Rod-and-line fishing is forbidden. The adult population is mainly grilse (one sea-winter, 1SW), up to 85.5% on average from 1984 to 2003. In all years, males dominate the sex ratio (59.8% on average) of the adult population. Although the grilse include a majority (64.8% on average) of males, females dominate multi sea-winter (MSW) salmon (68.9% on average) and multiple-spawners (87.5% on average).

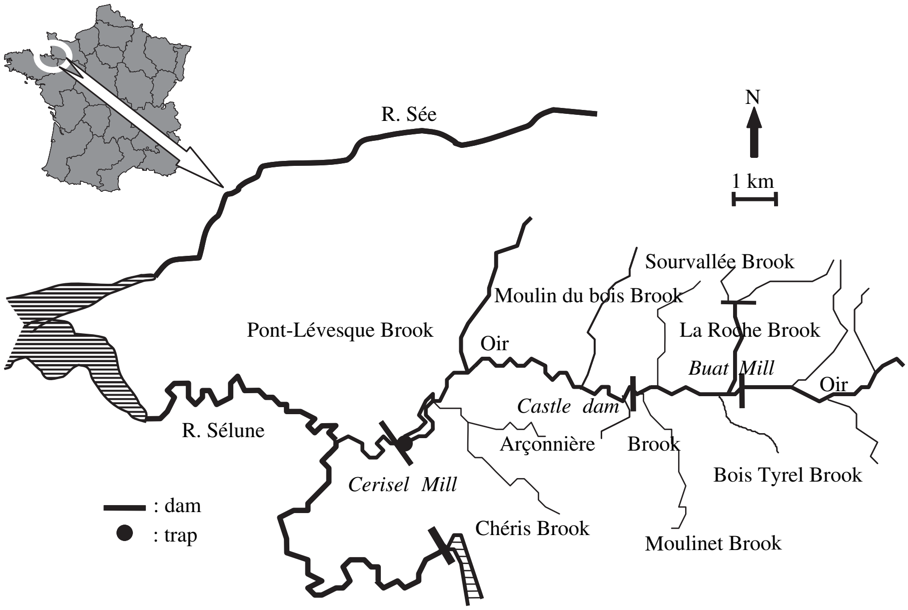

Figure 1. The River Oir drainage basin.

Juveniles are mainly distributed along the main stream. Only two brooks are regularly colonized: Pont-Lévesque, with a modest presence of juveniles, and La Roche Brook, with a high level of abundance. In some years, juveniles have also been found in the Moulin du Bois Brook (Figure 1). Juveniles migrate towards the sea in spring after 1 (on average 88.5%) or 2 years in freshwater, depending on their growth (fork length range 70–205 mm) at smolting.

Material and methods

Salmon population dynamics have been monitored since 1984 by electro-fishing resident juveniles in autumn (October), and by trapping smolts and adults at the Cerisel Mill, upstream and downstream traps operating the whole year. The electro-fished area on the Oir was $<3000\ m^2$ before 1995, but has varied between 11 874 and 22 500 m^2 since 1996, whereas the number of electro-fished tributaries has increased from one (La Roche Brook) to six (La Roche, Sourvallée, Moulinet, L'Arçonnière, Moulin du Bois, and Pont-Lévesque Brooks). There was no electro-fishing census in 1990.

Habitats have been described for the whole area accessible to salmon, and classified into four categories (riffle, fast run, slow run, pool). Whole production surface area was estimated at 44 582 m^2, the sum area of the riffle and fast- and slow-run habitat categories. Pool habitat was omitted from this calculation because juveniles are rarely found in such habitat. The 2 km below the Buat Mill has nearly half of the total riffle area in the main stem of the river, and the whole course of La Roche Brook is a suitable habitat for salmon, with both fast-run and riffle parts and a rough substratum. Silt deposition is low in the brook compared with the other parts of the Oir Basin. The good quality of the habitat there can be related to the steeper slope (36‰) and the granite substratum. The spatial and temporal organization of the salmonid population in La Roche Brook has been extensively studied (Baglinière *et al.*, 1993; Haury *et al.*, 1995; Bardonnet and Baglinière, 2000).

The standing population of juveniles is recorded by a successive removal method. Population densities were estimated by the method of Seber and Le Cren (1967) in sectors representative of the different habitats in the main stem and the brooks. The total standing density or stock of parr was estimated by taking into account the relative proportion of the different habitats in the production surface area (for more details, see Baglinière *et al.*, 1993).

Runs of smolts and adults were estimated from capture–mark–recapture (CMR) analyses. The trap efficiencies were estimated from stratified CMR experiments, so accounting for temporal variations in the trapping efficiency attributable to variations in the environment and fish behaviour. On average, the efficiency of the downstream traps (smolts) and upstream traps (spawners) falls in the ranges 44.9–88.2% and 18–100%, respectively. At downstream traps, smolts from the La Roche Brook were easily identified, because all juveniles were tagged in autumn. The production of migrating juveniles can be expressed both by the number of smolts produced per

100 m² of production surface area and per 100 m² of riffle-rapid equivalent area. This last area was specified by Prévost and Porcher (1996) as the most suitable unit in which to express the surface area of smolt production, and is calculated as the sum of the area of riffle-rapids plus 20% of the area of fast- and slow-run habitats. The total surface area of riffle-rapid equivalent in the Oir river catchment, including the main course and the most important tributaries (Pont-Lévesque, Moulin du Bois, and La Roche Brooks) was estimated at 27 910 m².

Annual overwinter survival rate was estimated from capture−recapture experiments (tagging by either alcyan blue injection into the fin by fin-clipping, or nasal microtag). A mean annual value of the overwinter survival rate was calculated from the recapture of 1+ migrating (trapped) and resident (electro-fished) fish.

The annual number of eggs deposited was calculated from the mean fecundity and the annual estimates of grilse and MSW females. The fecundities of grilse and MSW salmon (the latter mainly 2SW) are 4691 (±367, 95% CL) and 7965 (± 627, 95% CL) eggs, respectively (Prévost *et al.*, 1996). Survival rates from egg-to-0+ parr and -to-smolt were computed from the annual estimates of the number of eggs, 0+ parr, and smolts.

Data analyses focused on the spatio-temporal variation in the density of resident juveniles, variation in the number of smolts and adults, the age structure of juveniles, the spawning potential, and survival rates (egg to alevin or emerging fry, egg-to-0+ parr, egg-to-smolt).

Results and discussion

Density and distribution of juveniles

Average autumnal density of juvenile salmon in the Oir Basin (6.2 0+ fish 100 m^{-2} and 1.2 1+ fish 100 m^{-2} over 20 years) was above the average observed in other rivers of similar size in the Armorican Massif during the same period (data from the Réseau Hydrobiologique et Piscicole 1985−2001 of the Conseil Supérieur de la Pêche, courtesy E. Baglinière). Annual abundance in the Oir Basin was highly variable among years, between 1.5 and 17.4 per 100 m², only exceeding 10 per 100 m² in 6 years out of 20 (Figure 2).

Juveniles were mostly in riffle habitats in the main river (Figure 3), as is the general pattern in spatial abundance in other rivers (Baglinière and Champigneulle, 1982; Heggenes *et al.*, 1999). Densities in riffles were on average five times higher than in run habitats (Figure 3), corroborating the method proposed by Prévost and Porcher (1996) for estimating smolt production in a stream.

Juvenile (0+ and 1+ fish) abundance in autumn varied along the course of the main river, usually being greater upstream, including the La Roche Brook, seemingly being related to the availability of the most suitable habitats. The average density in the 2 km immediately below Buat Mill over the 20-year period was higher (8.6 per 100 m²; range, 1.1−21.2 per 100 m²) than in the middle (5 per 100 m²; range, 0.3−12.2 per 100 m²) and downstream (3.1 per 100 m; range, 0.6−9.6 per 100 m²) parts of the river.

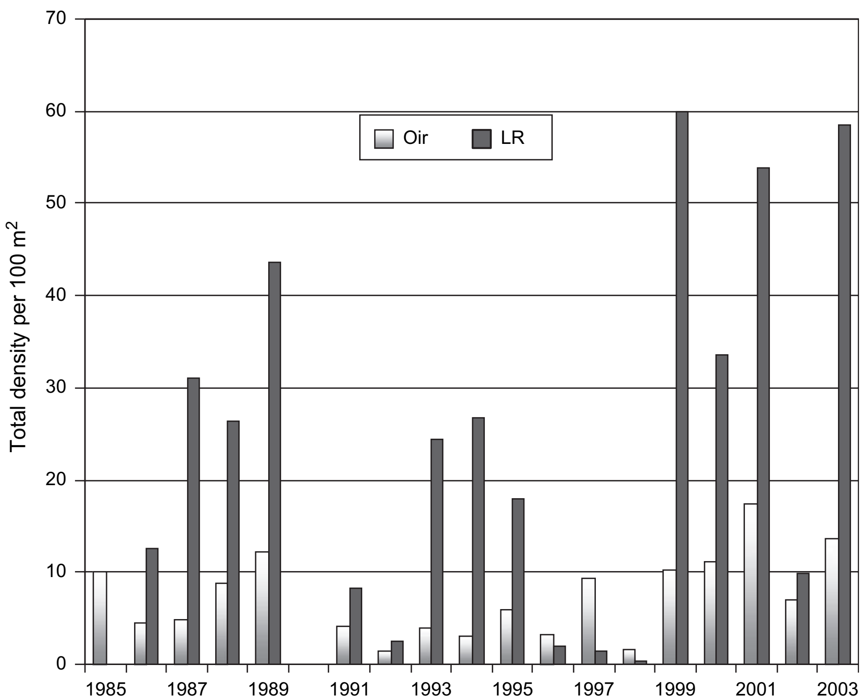

Figure 2. Total density of juvenile salmon in the River Oir and La Roche Brook (LR), 1985−2003 (no data for 1990).

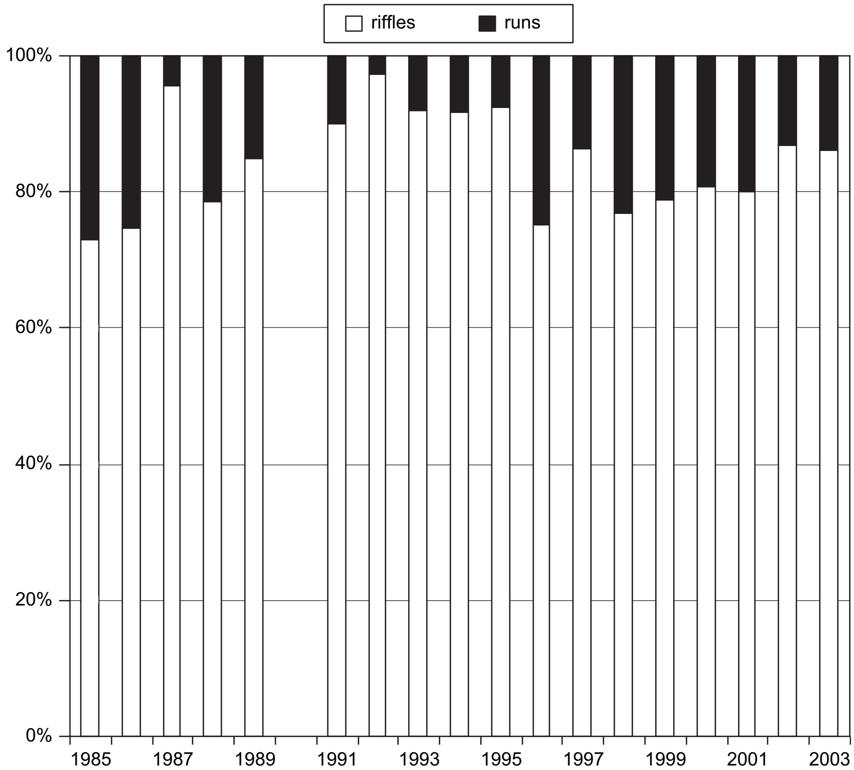

Figure 3. Distribution of Atlantic salmon juvenile density by habitat in the River Oir, 1985–2003 (no data for 1990).

Likewise, average density in the La Roche Brook over the 20-year period was 24.3 per 100 m^2 (range, 0.3–60 per 100 m^2; Figure 2), marking this brook as the best spawning habitat and the most productive area (per 100 m^2) in the Oir Basin.

Most of the spatio-temporal variability in abundance was due to the young-of-the-year, which was the dominant age class (80.4%). 0+ density depends on the abundance of breeding stock in the previous year. The linear regression between 0+ salmon density (D_{0+}) and egg density the year before (D_{egg}), both measured per 100 m^2, was significant ($D_{0+} = 0.0045$, $D_{egg} + 2.6398$; $r^2 = 0.5815$, $p < 0.05$; Figure 4). However, the significance of the regression was mainly influenced by the 2001 and the 2003 data points, years when the potential spawning was particularly high.

Egg deposition rates depended on adult abundance and sea-age composition, which varied during the study period (Figure 5), seemingly depending on four factors that may be synergetic.

Rod-and-line exploitation rate

Angling is not allowed in the River Oir, but a rod-and-line fishery takes place along the lower course of the River Sélune. Exploitation rate could therefore be close to 50% of the whole stock and may represent as much as 75% of the spring salmon component (MSW fish). Moreover, the Sélune is one of the two rivers in the Armorican Massif with the highest consumption rate of Total Allowable

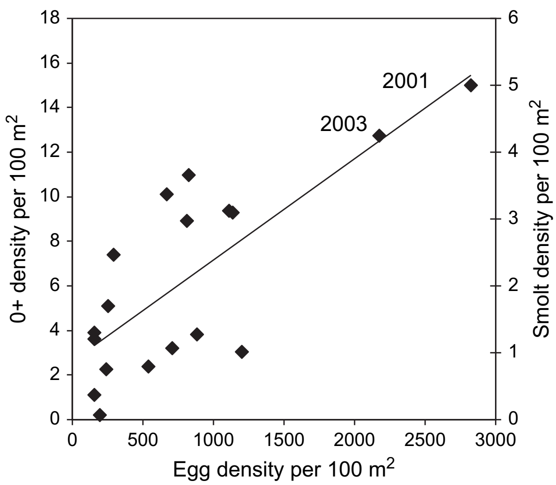

Figure 4. Relationships between egg density and 0+ salmon and smolt density in the River Oir, 1985–2003. The line is the linear regression.

Catch (TAC; see Prévost and Porcher, 1996). Catches have been very close to or have even exceeded the maximum TAC authorized in certain years (Porcher, 1999, pers. comm.).

Potential exchanges of fish between the rivers Sée and Sélune

Current studies carried out to model the population dynamics of salmon in the River Oir suggest that most adults returning to spawn were native to the Sée rather than to the Oir. Indeed, available data suggest that the Sée has a far larger smolt production than the Sélune. Moreover, straying rate may be more important in certain years, leading to many adults native to the Sée attempting to spawn in the Oir (Rivot, 2003; Rivot *et al.*, 2004). It is therefore necessary to consider the rate of exploitation of the salmon in the Sée when addressing management and conservation of the salmon populations in the Oir and the Sélune.

Decline of the spring salmon component

The spring salmon component is particularly vulnerable, given its strong decline in the Northeast Atlantic generally and in France specifically (ICES, 2001; Baglinière *et al.*, 2004). Although this apparent vulnerability can be seen for the River Oir, it is less pronounced there because the MSW salmon component only accounted for some 14.5% of the stock on average during the study period (Figure 5). Nevertheless, the proportion of MSW fish did decrease to just 6.6% of the stock on average during the period 1991−1999. Subsequently (1999−2003), the contribution by this component did increase slightly, but their overall proportion of the whole run was still lower (11.5%) than during the mid-1980s (24.6%), because of the simultaneous increase in the grilse component. MSW salmon were larger and mainly female, whereas grilse were mainly males. As a consequence, there was a decrease in the spawning potential in this drainage basin during the 1990s. Given the sex ratios and the fecundity of these two components in the River Oir, to offset the loss of eggs from spring salmon would require the number of grilse to increase by a factor of 4.36.

Hydrological conditions before and during the spawning event

Variability of water discharge from each river plays a role in attracting spawners to either the Oir or the Sélune. On average, the abundance of adults returning to the River Oir seemed to be related to the discharge between October and December, a finding seemingly corroborating the belief that most returning adults do not originate in the Oir. Water discharge also strongly influences upstream migration in the Oir by allowing fish to pass certain obstacles and to access the best spawning sites in the river's upper course

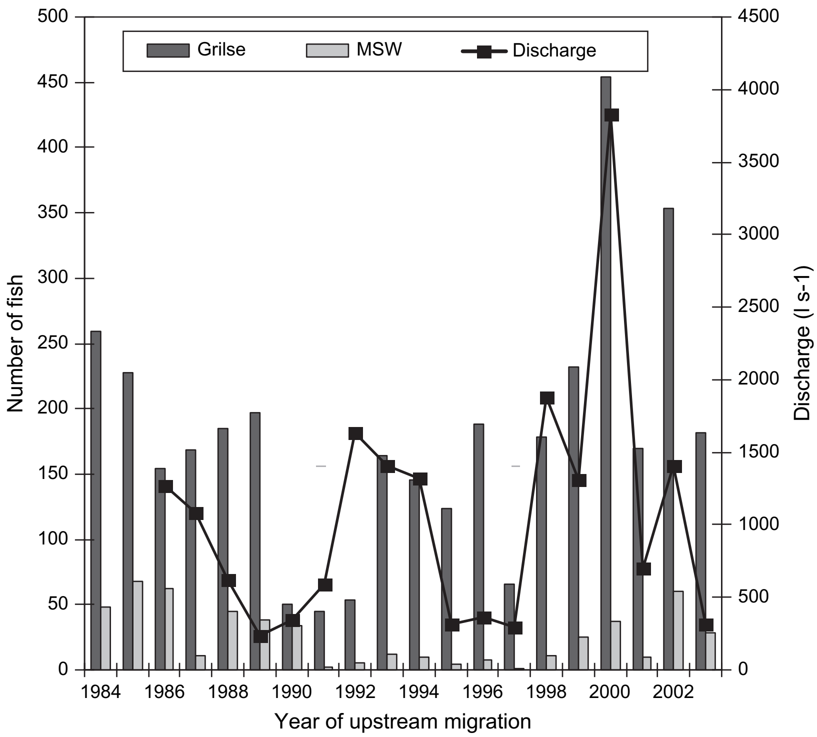

Figure 5. Estimated number of salmon returning to the River Oir (grilse and MSW salmon) just before spawning, and the average discharge during the period October−December, 1984−2003.

and in the La Roche Brook. Annual variation in juvenile abundance in the La Roche Brook can be explained largely by the annual variation in accessibility of that quality habitat part of the watershed. Further, the low production observed in some years can be related in large measure to the scarcity of spawners within the brook at peak spawning.

Smolt production

The number of smolts produced per cohort between 1984 and 2001 varied from 75 to 2563, i.e. 0.17−5.7 per 100 m^2 total water surface area (average 2.1 smolts per 100 m^2, CV 80%). Average production was influenced by four cohorts (1985, 1999, 2000, 2001; Figure 6a). The average smolt production expressed as the number of smolts produced per 100 m^2 of riffle-rapid equivalent area is 3.3 per 100 m^2, placing the Oir just above the norm established for all rivers of the Armorican Massif (3 smolts per 100 m^2: Prévost and Porcher, 1996). However, average production was equal to or exceeded the norm in just 8 out of 18 cohorts. Average density was close to but more variable (CV 82%) than that estimated for a salmon river in Brittany, the River Scorff (3.5 smolts 100 m^{-2}, CV 36%: Baglinière and Champigneulle, 1986).

The productivity of the drainage basin therefore appears to be moderate and highly variable. Nevertheless, certain stretches of the river system do produce more (and more regular) production of smolts, unless spawners are absent. The La Roche Brook, for instance, produced an average of 5.2 smolts 100 m^{-2} per cohort, with an exceptional value in 1999 (20.1 smolts 100 m^{-2}). Its annual production equalled or exceeded the regional norm 10 times out of 14, implying that the brook sustains production in the drainage basin, especially when densities are very low in the Oir, by accounting for up to 50.7% of the total smolt production (Baglinière *et al.*, 2002). This raises the issue of spawning migration and access to the La Roche Brook spawning ground.

Most smolts were 1+ year old, 2 year olds accounting for just 13.4% on average (Figure 6a). There was a strong correlation (Figure 6b) between the density of smolts (D_s) produced by a cohort and 0+ juvenile density (D_{0+}), both expressed per 100 m^2 ($\log D_s = 1.064 \log D_{0+} + 0.91$; $r^2 = 0.851, p < 0.001$). This means that the smolt production of the drainage basin depends essentially on the abundance of 0+ juveniles produced there. This supports observations made by Crozier and Kennedy (1995a), who demonstrated a significant linear relationship between summer 0+ abundance and smolt numbers subsequently migrating.

No clear relationship could be found between smolt production and initial stock size (expressed as egg density per 100 m^2) in the Oir (Figure 7). Prévost *et al.* (1996) analysed the stock-recruitment relationship on the basis of the first 10 years of the data series. They showed that the initial stock size required for maximum smolt production (292 eggs per 100 m^2) was often equal to or exceeded the values usually found in the literature (Elson, 1975; Symons, 1979; Caron, 1992; Kennedy and Crozier, 1993; Crozier and Kennedy, 1995b; Chaput *et al.*, 1998), whereas smolt production in the Oir was low compared with other British and Canadian rivers (Table 1). Further, smolt densities were well below the theoretical optimum values calculated by Symons (1979; 10 and 5 smolts per 100 m^2 for 1- and 2-year groups, respectively). Otherwise, the observations in the River Oir confirm that smolt production per unit of habitat is actually higher in northern European and Canadian rivers, and with higher smolt ages (Baglinière and Champigneulle, 1986; Prévost *et al.*, 1996, 2001; Chaput *et al.*, 1998; see Table 1), unlike the findings of Symons (1979), who predicted greater production in rivers when smolts were mainly 1+ year old.

Inter-stage survival

The rate of survival from egg to smolt varied annually from 0.044% to 1.07% (Figure 8), lower than values observed in some rivers in Canada and the United Kingdom (Table 1) that are free of heavy impacts from human activities (Prévost *et al.*, 1996; Cunjak and Therrien, 1998). This supports the observations of Hutchings and Jones (1998), who showed less survival in Spanish and French salmon populations than elsewhere, by accounting for regional differences in mean smolt age. Rather than a low mean value, the main feature of egg-to-smolt survival in the River Oir was the very high interannual variability (CV 79.2%) compared with other populations, possibly related to the young age of smolts (Table 1). The absence of a clear relationship between egg-to-smolt survival rate and initial stock size (Figure 7) suggests that the variability in survival rate in the Oir depends mainly on density-independent environmental fluctuations (Rivot, 2003).

Further analysis of the rate of survival from egg to smolt shows that:

(i) Winter survival between stages 0+ and 1+ varied little, from 31% to 64.4% (CV 21.6%), but remained high on average (50.3%);
(ii) Survival from egg-to-0+ parr was very close to this observed in the R. Nivelle (France) and much more variable (0.1−2.5%, CV 72.5%; Figure 8), from low to very low (average 1.08%) compared with other brooks (Table 1).

The weak relationship between egg density and 0+ density, with highly dispersed data (Figure 4), and the great variability in the egg-to-smolt survival rate (Figure 8), together suggest a strong influence of the environment. In particular, it seems likely that highly variable rates of mortality during the under-gravel phase or during the first weeks of life, including the emergence phase, may be the most important factor regulating juvenile production (i.e. a bottleneck effect). This hypothesis has been

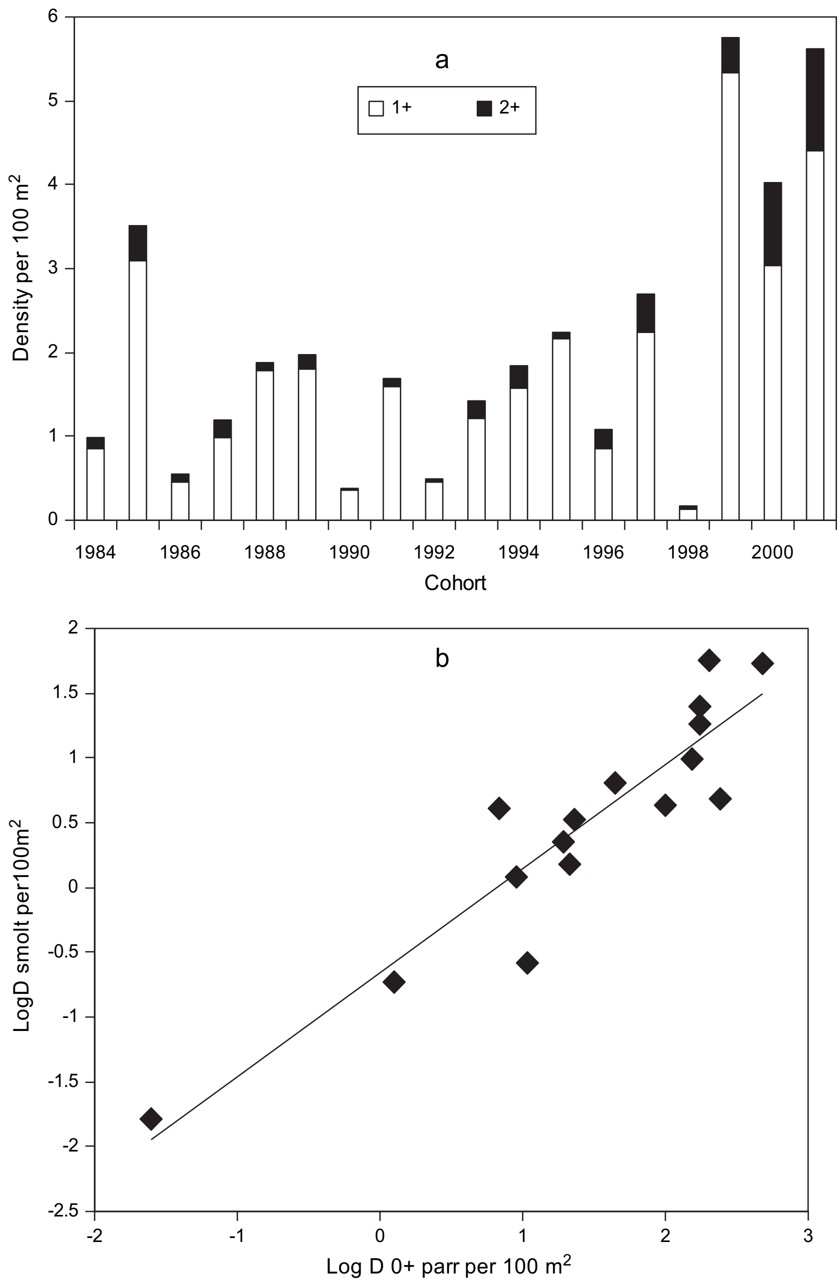

Figure 6. (a) Number of salmon smolts by cohort and age class, and (b) the relationship between smolt and 0+ parr density (the line is the linear regression) in the River Oir, 1984–2001.

confirmed by *in situ* experiments on under-gravel survival (Claude, 1996). Artificial spawning redds (small cylindrical cages filled with gravel of suitable size and eggs taken from wild spawners) were buried at several points in the bed of the Oir and La Roche Brook. Survival from eyed egg to hatching ranged from 22.3% to 35.3%, and from 8.1% to 11% until emergence (Claude, 1996). Other experiments using the same method have been carried out with brown trout green eggs in two tributaries of the River Oir having different geological substrata (granite mixed with hornfels schist in La Roche Brook, and sedimentary schist in the Moulinet Brook). Results (Table 2) showed that:

(i) Average survival until emergence (0.81–10.6%;) was low compared with results obtained by the same method on the Catamaran Brook (40–62%;

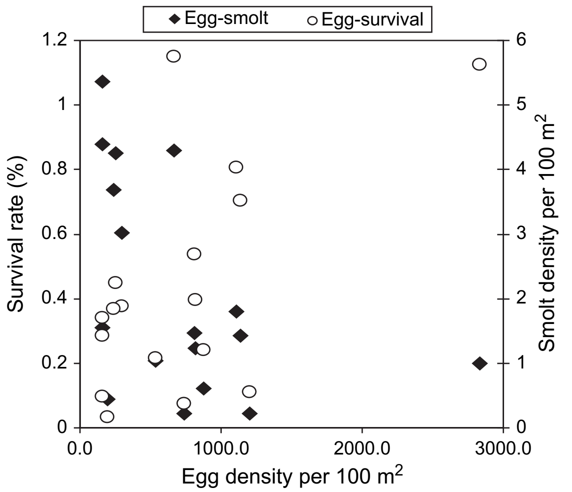

Figure 7. Relationship between the initial stock size (egg density), smolt density, and the egg-to-smolt survival rate in the River Oir, 1985–2001.

R. Cunjak, pers. comm., in Bardonnet and Baglinière, 2000). However, the values obtained for the Oir were probably underestimated for salmon because of the small size of gravel used. Indeed, similar experiments on brown trout eggs showed a better survival when the gravel size was increased (Table 3), in accord with the findings of Witzel and MacCrimmon (1983).

(ii) Survival rates were much lower in the brook with a sedimentary schist substratum (Moulinet), which is finer and more easily choked than the prevailing substratum in the Oir drainage system. In La Roche Brook, annual turbidity values were twofold lower (6.7–10.6 nephelometric turbidity units) than in the Moulinet Brook (12.3–18.3 nephelometric turbidity units; unpublished data from Ecology and Ecotoxicology Experimental Unit, INRA Rennes). In this tributary, moreover, concentrations of suspended matter measured during water floods in winter were very high ($96\ mg\ l^{-1}$) and close to the class 4 threshold limit ($100\ mg\ l^{-1}$: bad water quality) in the quality grid of the Water Authorities and Ecology Ministry (Anon., 2003). Silt deposition leads to low dissolved oxygen in the gravel, as well as denitrification that causes the formation of nitrites that would induce increased mortality (Magee *et al.*, 1996; Massa *et al.*, 2000a).

(iii) Survival rates depend on the water discharge during incubation. The mortality between fertilization and hatching was high (up to >55%) when discharge was low (increasing silt deposition), but decreased during

Table 1. Smolt age and production, egg-to-0+ parr and egg-to-smolt survival rates in some northern American and European Atlantic salmon populations.

River	Egg-to-0+ parr survival (%)		Egg-to-smolt survival (%)		Smolt age (year)	Smolt production per 100 m^2	Reference
	Mean	CV	Mean	CV			
Polett	3.89	63.7	1.98	69.7	2.1	2.6	Elson (1975)
Big salmon			0.17		2.6	2.2–5.8	Jessop (1975, 1986)
Western Arm Brook			1.74	47.7	3.9	9.66	Chadwick (1981), Chaput *et al.* (1992)
Trinité			3.24	38.9	2.95	5.8	Caron (1992)
Bec-Scie			1.56		2.96	3.4	Caron (1992)
Conne			0.54	17.9	3.3	5.2	Dempson *et al.* (1995), Dempson and Furey (1997)
Northeast Brook			0.44	14.5	4		O'Connell *et al.* (1992)
Freshwater Brook			52	51.5	3		O'Connell *et al.* (1992)
Southwest Miramichi	26	65.3	0.36	48	3.2		Cunjak and Therrien (1998)
Northwest Miramichi			0.7	46.5			Chaput *et al.* (1998)
Fender Burn	12.92	12.2			2.4	4.2	Egglishaw and Shackley (1980)
Shelligan Burn	16.45	71.7					Gardiner and Shackley (1991)
Bran							Mills (1964)
Girnock Burn			0.87	52	2.8	7.3	Buck and Hay (1984), Hay (1991)
Wye					2	4.3	Gee *et al.* (1978)
Exe					2	6.9	Nott (1970)
Bush			1.19	48.7	1.8	6	Kennedy and Crozier (1993), Crozier and Kennedy (1995b)
Burrishoole			0.59	24.3	2	5.3	Anon. (1970–1994)
Nivelle	0.97	78.2			1.09		Dumas and Prouzet (2003)
Oir	1.08	72.5	0.42	79.2	1.1	2.1	This paper

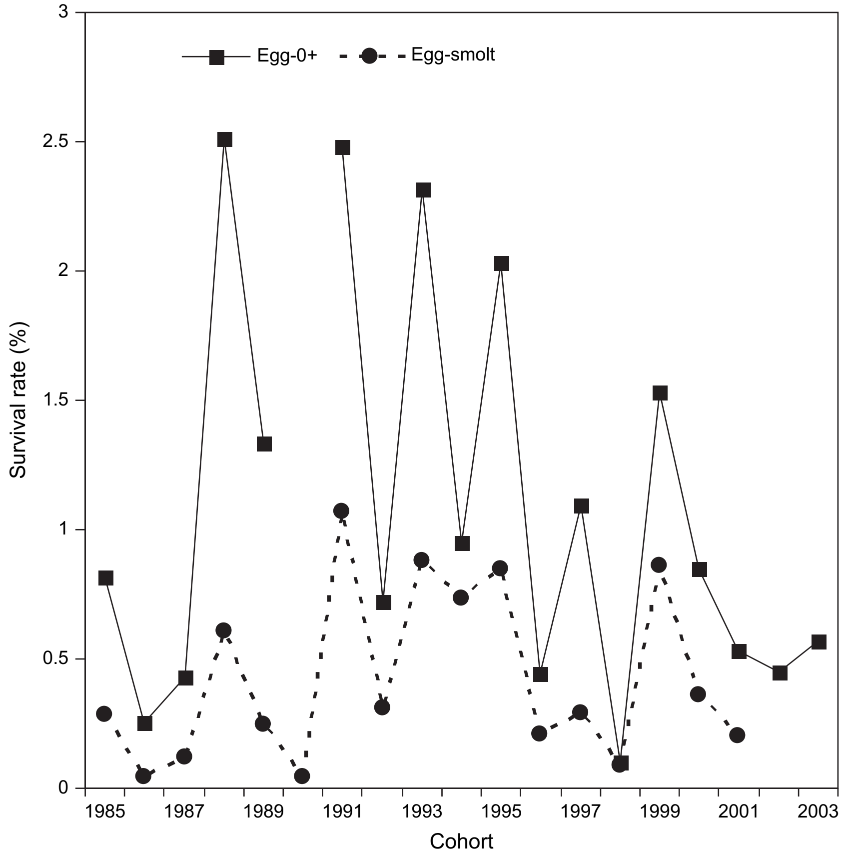

Figure 8. Survival rate (%) from egg-to-0+ parr and -to-smolt by cohort in the River Oir, 1985–2003 (no data for egg-to-0+ parr in 1990).

successive periods of high discharge (washing of spawning beds by removing suspended matter; Massa *et al.*, 2000b).

These observations and experiments underscore the importance of the quality of the spawning substratum in supporting good salmon production, particularly in the La Roche Brook.

Conclusion

Analysis of a 20-year data set on biological and ecological data series related to the salmon population of the River Oir, combined with recent research on stock-recruitment relationships and population dynamics, leads to a conclusion that the salmon population there is characterized by strong interannual variability resulting from two synergetic factors. The first is the high variability in spawning, mainly the result of a fluctuation in the abundance of spawners and the relative decrease in numbers of MSW in the 1990s. This decline has been observed in the whole range of the species, and seems to be the consequence of lesser survival in the

Table 2. Survival rate (%) from green egg to hatching or emergence in brown trout in two tributaries of the River Oir (after Massa *et al.*, 1998; Massa, 2000; Ecology and Ecotoxicology Experimental Unit INRA Rennes, unpublished data).

		Survival (%)	
Year	Under-gravel phase	Moulinet	La Roche
1996	Egg to emergence	0	20
1997	Egg to hatching	3.3	7.7
	Egg to emergence	2.8	6.3
1998	Egg to hatching	1.5	4.6
	Egg to emergence	0.76	2.8
1999	Egg to hatching	10	54
	Egg to emergence	0.5	17.8
2000	Egg to emergence	0	2.4
2001	Egg to hatching	3.1	—
	Egg to emergence	—	14.1
Mean	Egg to hatching	4.9	20.8
	Egg to emergence	0.812	10.6

Table 3. Survival rate (%) from green egg to eyed egg in brown trout according to the gravel size suitable for trout or salmon (Ecology and Ecotoxicology Experimental Unit INRA Rennes, unpublished data).

Group	Survival (%)
Control group in hatchery	88.7
Vibert Box "trout model"	46.4−57.3
Vibert Box "salmon model"	71−75.2

North Atlantic, and is a trend that does not appear to be showing any signs of reversal in southern European salmon populations (ICES, 2003). The second and perhaps more important factor is the highly variable smolt productivity of this river system, already documented by Prévost *et al.* (1996), which leads to very poor production in some years. Given the geological (schist) and pedological (thick and silty soils) context of the drainage basin, the egg-to-smolt survival rate may be strongly influenced by the extent of silt deposition on spawning redds. This silt deposition is also responsible for an overall degradation of habitat quality, and is largely attributable to agricultural practices (Armour *et al.*, 1991; Knapp and Matthews, 1996). Indeed, the erosion is increased by cattle grazing and trampling in riparian zones, as well as the corn culture that leaves the soil bare in autumn and winter, resulting in significant silt deposition. In such an anthropogenically impacted river system, the bottleneck in the production of salmon juveniles appears to take place more during the under-gravel phase incubation than during the first months of life of the salmon (spatial competition, predation, density-dependent mortality). The study has also emphasized the importance of in-stream habitat quality, notably on the spawning grounds, and has stressed the advantage of preserving some productive areas, such as La Roche Brook, in order to sustain a sufficient level of salmon production.

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References

Anon. 1970−1994. Annual Report. The Salmon Research Agency of Ireland Incorporated. Reports XV−XXXIX.

Anon. 1997. Seuils de qualité pour les micropolluants organiques et minéraux dans les eaux superficielles. Rapport de synthèse, comité inter-agences. 21 pp.

Anon. 2003. Systèmes d'évaluation de la qualité de l'eau des cours d'eau. Gilles d'évaluation SEQ-Eau (version 2). MEDD et Agences de l'eau. 40 pp.

Armour, C. L., Duff, D. A., and Elmore, W. 1991. The effects of livestock grazing on riparian and stream ecosystems. Fisheries, 16: 7−11.

Baglinière, J. L. 1979. Les principales populations de poissons sur une rivière à salmonidés de Bretagne-sud, le Scorff. Cybium, 7: 53−74.

Baglinière, J. L., and Arribe-Moutounet, D. 1985. Microrépartition des populations de Truite commune (*Salmo trutta* L.), de juvénile de Saumon atlantique (*Salmo salar* L.) et des autres espèces présentes dans la partie haute du Scorff (Bretagne). Hydrobiologia, 120: 229−239.

Baglinière, J. L., and Champigneulle, A. 1982. Densité de populations de truite commune (*Salmo trutta* L.) et de juvéniles de saumon atlantique (*Salmo salar* L.) sur le cours principal du Scorff (Bretagne): preferendums physiques et variations annuelles (1976−1980). Acta Oecologica Oecologia 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 River Scorff, Brittany. Journal of Fish Biology, 29: 467−482.

Baglinière, J. L., Denais, L., Rivot, E., Porcher, J. P., Prévost, E., Marchand, F., and Vauclin, V. 2004. Length and age structure modifications of the Atlantic salmon (*Salmo salar*) populations of Brittany and Lower Normandy from 1972 to 2002. Technical report, INRA-CSP. 24 pp.

Baglinière, J-L., Maisse, G., and Nihouarn, A. 1993. Comparison of two methods of estimating Atlantic salmon (*Salmo salar*) wild smolt production. *In* Production of Juvenile Atlantic Salmon, *Salmo salar*, in Natural Waters, pp. 189−201. Ed. by R. J. Gibson, and R. E. Cutting. Canadian Special Publications of Fisheries and Aquatic Sciences, 118.

Baglinière, J. L., Maisse, G., Nihouarn, A., Porcher, J. P., and Le Gloannec, P. M. 1988. Comparaison de deux méthodes d'estimation de la production naturelle de smolts de saumon atlantique (*Salmo salar* L.). Bulletin Français de la Pêche et de la Pisciculture, 308: 24−34.

Baglinière, J. L., Marchand, F., Nihouarn, A., and Delanoë, R. 2002. Caractéristiques biologiques, niveau d'abundance et fonctionnement de la population de juvéniles de saumon (*Salmo salar*) du bassin de l'Oir (Manche, Basse-Normandie) de 1996 à 2001. Rapport UMR INRA-Agrocampus ENSA, Ecobiologie et Qualité de Hydrosystèmes Continentaux, Rennes. 15 pp.

Baglinière, J. L., Ombredane, D., and Marchand, F. 2000. Critères morphologiques pour l'identification des deux formes (rivière et mer) de truite (*Salmo trutta*) présentes sur un même bassin. Bulletin Français de la Pêche et de la Pisciculture, 357−360: 375−383.

Bardonnet, A., and Baglinière, J-L. 2000. Freshwater habitat of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences, 57: 497−508.

Buck, R. J. G., and Hay, D. W. 1984. The relation between stock size and progeny of Atlantic salmon (*Salmo salar*) in a Scottish stream. Journal of Fish Biology, 23: 1−11.

Caron, F. 1992. Relation entre le nombre d'œufs déposés et la production de saumoneaux dans les rivières de la Trinité et de Bec-Scie. CAFSAC Research Document, 92/125. 23 pp.

Chadwick, E. M. P. 1981. Biological characteristics of Atlantic salmon in Western Arm Brook, Newfoundland. Canadian Technical Report of Fisheries and Aquatic Sciences, 1024. 45 pp.

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.

Chaput, G., Mullins, C. C., and Chadwick, E. M. P. 1992. Stock-recruitment relationship for Atlantic salmon from Western Arm Brook, Newfoundland. CAFSAC Research Document, 92/123. 13 pp.

Claude, A. 1996. Deux éléments de recrutement chez le salmon atlantique (*Salmo salar* L.) dans le Massif Armoricain: quantification des surfaces d'habitat favorable aux juvéniles et estimation de la survie au stade embryo-larvaire sur le Scorff (Morbihan) et l'Oir, affluent de la Sélune (Manche). Certificat d'Etudes Supérieure Agronomique, Option Halieutique, Ecole Nationale Supérieure Agronomique de Rennes. 44 pp.

Crozier, W. W., and Kennedy, G. J. A. 1995a. Application of fry (0+) abundance index, based on semi-quantitative electrofishing, to predict Atlantic salmon smolt runs in the River Bush, Northern Ireland. Journal of Fish Biology, 47: 107–114.

Crozier, W. W., and Kennedy, G. J. A. 1995b. The relationship between a summer fry (0+) abundance index, derived from semi-quantitative electrofishing, and egg deposition of Atlantic salmon, in the River Bush, Northern Ireland. Journal of Fish Biology, 47: 1055–1062.

Cunjak, R. A., and Therrien, J. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. Fisheries Management and Ecology, 5: 209–224.

Dempson, J. B., and Furey, G. 1997. Stock status of Atlantic salmon from Conne river, SFA 11, Newfoundland, 1996. CAFSAC Research Document, 97/34. 44 pp.

Dempson, J. B., Reddin, D. G., Furey, G., and Pennell, C. 1995. Evaluation of Atlantic salmon stock status: Conne river, SFA 11, Newfoundland, 1994. CAFSAC Research Document, 95/77. 44 pp.

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

Egglishaw, H. J., and Shackley, P. 1980. Survival and growth of salmon, *Salmo salar*, planted in a Scottish stream. Journal of Fish Biology, 16: 565–584.

Elson, P. F. 1975. Atlantic salmon rivers, smolt production and optimal spawning: an overview of natural production. Special Publications Series of the International Atlantic Salmon Foundation, 6: 96–119.

Fontenelle, G., Douaire, G., Baglinière, J. L., Prouzet, P., and Harache, Y. 1980. Atlantic salmon (*Salmo salar* L. 1766) in Brittany and Lower Normandy: preliminary observations on the general characteristics of adults. Fisheries Management, 11: 49–60.

Gardiner, R., and Shackley, P. 1991. Stock and recruitment and inversely density-dependent growth of salmon, *Salmo salar*, in a Scottish stream. Journal of Fish Biology, 38: 691–696.

Gee, A. S., Milner, N. J., and Hemsworth, R. J. 1978. The effect of density on mortality in juvenile Atlantic salmon (*Salmo salar*). Journal of Animal Ecology, 47: 495–505.

Haury, J., Baglinière, J. L., Cassou, A. I., and Maisse, G. 1995. Analysis of spatial and temporal organisation in a salmonid brook in relation to physical factors and macrophytic vegetation. Hydrobiologia, 300/301: 269–277.

Hay, D. W. 1991. Stock and recruitment relationships. Lessons from the Girnock Project. Atlantic Salmon Trust, Royal Irish Academy Workshop, Dublin. 3 pp.

Heggenes, J., Baglinière, J. L., and Cunjak, R. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in heterogeneous streams. Ecology of Freshwater Fish, 8: 1–21.

Hutchings, J. A., and Jones, M. E. B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences, 55: 22–47.

ICES. 2001. Report of the Working Group on the Atlantic Salmon. ICES Document, CM2001/ACFM: 15. 199 pp.

ICES. 2003. Report of the Working Group on the Atlantic Salmon. ICES Document, CM2001/ACFM: 19. 297 pp.

Jessop, B. M. 1975. Investigations of the salmon (*Salmo salar*) smolt migration of the Big salmon river, New Brunswick, 1966–72. Technical Report Series, No.) MAR/T-75-L. 87 pp.

Jessop, B. M. 1986. Atlantic salmon (*Salmo salar*) of the Big salmon river, New Brunswick, 1966–72. Canadian Technical Report of Fisheries and Aquatic Sciences, 1415. 42 pp.

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 Publications of Fisheries and Aquatic Sciences, 118.

Knapp, A., and Matthews, R. 1996. Livestock grazing, golden trout, and streams in the Golden Trout Wilderness, California: impacts and management implications. North American Journal of Fisheries Management, 16: 805–820.

Magee, J. P., McMahon, T. E., and Thurow, R. F. 1996. Spatial variation in spawning habitat of cutthroat trout in a sediment-rich stream basin. North American Journal of Fisheries Management, 125: 768–779.

Massa, F., 2000. Sédiments, physico-chimie du compartiment interstitiel et développement embryo-larvaire de la truite commune (*Salmo trutta*): Etude en milieu naturel anthropisé et en conditions contrôlées. Thèse Doctorate, Université de Paris, VI. 179 pp.

Massa, F., Baglinière, J. L., Prunet, P., and Grimaldi, C. 2000a. Survie embryo-larvaire de la truite (*Salmo trutta*) et conditions chimiques dans la frayère. Cybium, 24(Suppl.): 129–140.

Massa, F., Grimaldi, C., and Baglinière, J. L. 2000b. Conditions hydrologiques et développement embryo-larvaire de la truite commune (*Salmo trutta*): recherche d'un stage critique. *In* Water in the Celtic World: Managing Resources for the 21st Century, pp. 261–267. BHS Occasional Paper, 11.

Massa, F., Grimaldi, C., Baglinière, J. L., and Prunet, P. 1998. Evolution de caractéristiques physico-chimiques des deux zones de frayères à sédimentation contrastée et premiers résultats de survie embryo-larvaire de truite commune. Bulletin Français de la Pêche et de la Pisciculture, 350/351: 359–376.

Mills, D. H. 1964. The ecology of young stages of Atlantic salmon in the River Bran, Ross-shire. Freshwater Salmon Fisheries Research, 32. 58 pp.

Nott, F. J. 1970. River Exe fisheries survey. Devon Authority. 7 pp.

O'Connell, M. F., Dempson, J. B., and Gibson, R. J. 1992. Atlantic salmon (*Salmo salar* L.) egg-to-smolt survival in Newfoundland rivers. CAFSAC Research Document, 92/122. 8 pp.

Porcher, J. P. 1999. Le saumon atlantique en France en 1998. Captures par les pêcheurs amateurs et professionnels en eau douce. Eléments de connaissance et de gestion de stocks. Rapport CSP, DR Bretagne – Basse-Normandie. 47 pp.

Prévost, E., Baglinière, J. L., Nihouarn, A., and Maisse, G. 1996. Premiers éléments d'une relation stock-recrutement chez le salmon atlantique (*Salmo salar*). Cybium, 20(Suppl.): 7–26.

Prévost, E., Chaput, G., and Chadwick, E. M. 2001. Transport of stock-recruitment reference points for Atlantic salmon. *In* Stock, Recruitment and Reference Points. Assessment and Management of Atlantic Salmon, pp. 93–135. Ed. by E. Prévost, and G. Chaput . INRA-Fisheries and Oceans Canada.

Prévost, E., and Porcher, J. P. 1996. Méthodologie d'élaboration de Totaux Autorisés de Captures (TAC) pour le salmon atlantique (*Salmo salar* L.). Evaluation et gestion de poissons migrateurs. GRISAM document scientifique, 1. 18 pp.

Rivot, E. 2003. Investigations bayesiennes de la dynamique de populations de Salmon atlantique (*Salmo salar*). Thèse, Ecole

Nationale Supérieure Agronomique, spécialité halieutique, Rennes. 226 pp.
Rivot, E., Prévost, E., and Parent, E. 2001. How robust are Bayesian posterior inferences based on a Ricker model with regards to measurement errors and prior assumptions about parameters. Canadian Journal of Fisheries and Aquatic Sciences, 69: 1768–1784.
Rivot, E., Prévost, E., Parent, E., and Baglinière, J. L. 2004. A Bayesian state-space modelling framework for fitting a salmon stage-structured population dynamic model to multiple time series of field data. Ecological Modelling, 179: 463–485.
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. J. 1979. Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity. Journal of the Fisheries Research Board of Canada, 36: 132–140.
Witzel, L. D., and MacCrimmon, H. R. 1983. Embryo survival and alevin emergence of brook char, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, relative to redd gravel composition. Canadian Journal of Zoology, 61: 1783–1792.