

Feeding, growth and nutritional status of restocked salmon parr along the longitudinal gradient of a large European river: the Allier

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Ecology of Freshwater Fish 2009: 18: 282–296. © 2008 John Wiley & Sons A/S

Abstract – The feeding, growth and nutritional status of salmon parr (0+) released at fry stage in different riffles were studied in a large temperate river (Allier, France) throughout the active feeding period. Significant differences were observed along the upstream–downstream gradient. Parr growth performance and energy storage were higher in downstream riffles and low in the most upstream one. These longitudinal growth variations are discussed in the context of diet and food availability differences, habitat variables and intra- and inter-species competition. The most favourable site for optimum growth and nutritional status appeared to be the intermediary riffle located in the grayling zone.

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Key words: feeding and growth; nutritional status; upstream–downstream gradient; large temperate river; *Salmo salar* L.

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Accepted for publication November 8, 2008

Introduction

Atlantic salmon (*Salmo salar* L.) have already disappeared from most of the large European rivers and have been listed as endangered species (Hendry & Cragg-Hine 2003). In France, a wild population seems to subsist in the Loire basin with production areas mostly located in the upper part of its main tributary, the Allier (Thibault 1994). Consequently, serious conservation attempts have been made by French and European programmes on the Loire-Allier axis. Efficient conservation depends on sound understanding of *S. salar*'s life history, including growth, reproduction and mortality.

Salmo salar is an anadromous species which migrates long distances from rivers to the sea (900 km on the Loire-Allier axis). The survival of young salmon after entering the sea depends on local environmental conditions. There is an ecological 'smolt window' during which the probability of

survival is maximal (McCormick et al. 1998; Riley et al. 2002). Consequently, differences in migration onset timing may be crucial for survival (McCormick et al. 1999). The timing of smolt migration to the sea depends on climatic and anthropic conditions (photo-period, temperature, flow, dams) but is also linked to the smolts' physiological status, which is in turn highly dependent on parr-stage growth (Duston & Saunders 1997; McCormick et al. 1998; Riley et al. 2002; Strothotte et al. 2005). Slow parr growth will tend to delay smolting, resulting in a shift in smolt departure time. Parr growth is influenced by habitat characteristics such as flow and temperature (Jensen 2003), density-dependent factors (competition, predation) (Grant & Imre 2005), and food supply availability (Richardson 1993; Erkinaro & Erkinaro 1998). Feeding is therefore of prime importance during juvenile salmon's freshwater residential stage (McCormick et al. 1998; Amundsen et al. 2001). Food and more particularly macroinvertebrate production in

different sections of a river vary according to stream order and river zonation (Vannote et al. 1980). However, it remains unclear how food abundance and quality interact with parr growth along the upstream–downstream gradient of large European rivers. We hypothesised that different rearing conditions within the River Allier could be related to differences in available prey type and density along the upstream–downstream gradient, influencing parr growth.

The objectives of the present study were to investigate the relationship between variability in the growth performance of *S. salar* and the spatial variability of the abundance and composition of invertebrate fauna along an upstream–downstream gradient in the River Allier. As growing salmon parr may allocate energy to lipid deposition (Naesje et al. 2006), we focused on temporal and spatial variations in neutral lipid (NL) contents and on parr condition factors. Detailed analysis of diet, growth and physiological status of age 0+ parr was performed, and results were compared along the upstream–downstream gradient. Finally, the results of this study will help identify the best stocking area in the River Allier.

Study area

The River Allier has its source in the French Massif Central at an altitude of 1,473 m on a flat metamorphic plateau (Fig. 1). This high plateau rapidly gives way to deep granite and basalt gorges only interrupted by a few intra-mountain basins. This area, known as the Upper Allier, was our main study location, and has been historically known as a natural breeding area for Atlantic salmon. It is a fourth to fifth order stream (Strahler 1957) with a watershed of 2,900 km². The

mineral substratum is covered by epilithic biofilm. In spring and summer, stream-submerged macrophytes (*Ranunculus* and *Callitriche*) develop in downstream reaches, but do not induce excessive in-stream cover.

Five sites were chosen according to their upstream–downstream distribution on the salmon breeding linear and natural feeding area of the parr (Fig. 1). This linear covered more than 170 km and included the rhithron and epipotamon zones according to the classification of Illies & Botosaneanu (1963) (see Aarts & Nienhuis 2003 for a description of longitudinal zonation in European rivers). Study sites (see Table 1) were selected (1) to allow sampling in pool-riffle sequences placed along Huet's longitudinal zonation (Huet 1959), (2) as being part of reaches representative of the main river, with or without anthropogenic influence, and (3) because no natural spawning was observed in reaches during autumn 2005 (Bach et al. 2007). Site 1 was situated approximately 32 km from the sources in a granite and gneiss plateau dominated by forest and pasture. The reach was located in the trout zone, free of human disturbance. Site 2 was located in the granite and basalt gorges, 66 km from the sources (upper grayling zone); although the catchment area had little human land use, the reach was under the influence of the Naussac regulatory dam. Site 3 was situated at the end of the gorges (106 km from the sources) and belonged to the lower grayling zone; the catchment area exhibited the same characteristics as Site 2, and the hydroelectric dam of Poutes-Monistrol (20 km upstream) could also affect the natural flow regime. Site 4 was located in a small agricultural basin, 123 km from the sources; the reach was located in the upper barbel zone, and water quality suffered from discharge from the wastewater

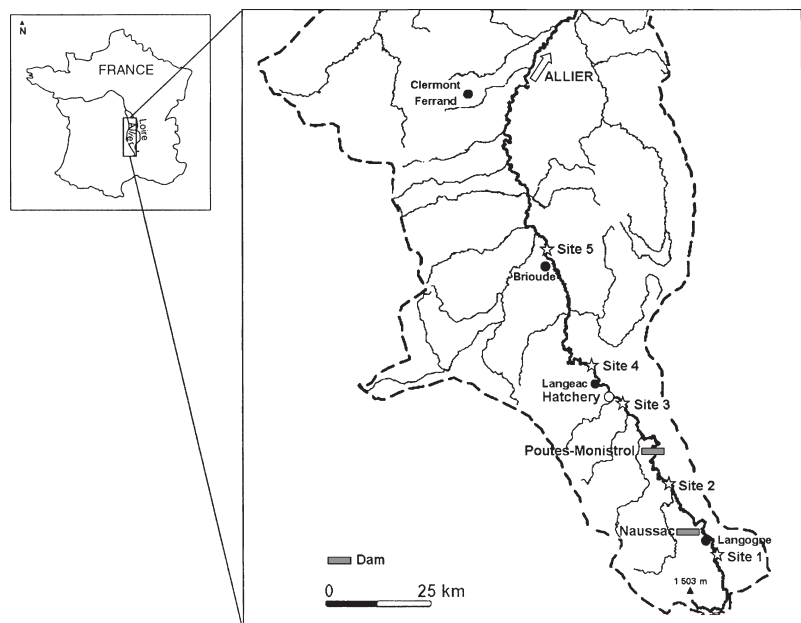


Fig. 1. Situation of the study area in France and location of the restocking riffles (white stars) and Chanteuges salmon hatchery (white circle) on the River Allier.

Table 1. Physical and biological characteristics of the five restocking riffles along the upstream-downstream gradient (mean values \pm SE).

	Site 1	Site 2	Site 3	Site 4	Site 5
Physical characteristics					
Catchment area (km ²)	48.8	514	1351	1781	2269
Altitude (m)	1000	740	540	495	434
Riffle slope (%)†	0.90	1.70	1.40	0.80	0.20
Riffle length (m)†	42	59	52	36	124
Riffle width (m)†	5.50	25	19	22	26
Water velocity (cm·s ⁻¹)†	26.8 (\pm 4.4)	47.4 (\pm 3.8)	87.1 (\pm 6.5)	68.8 (\pm 4.5)	77.7 (\pm 4.9)
Water depth (cm)†	16.7 (\pm 1.2)	44.0 (\pm 2.9)	34.1 (\pm 2.4)	43.0 (\pm 4.1)	47.9 (\pm 2.5)
Water temperature (°C)	14.0 (\pm 3. 8)	14.3 (\pm 4.2)	16.2(\pm 3.0)	18.1 (\pm 3.6)	17.9 (\pm 3.8)
Substrate types (%)‡					
Boulder		4	1		
Cobble	30	48	40	52	32
Pebble	52	34	43	35	65
Gravel		1			2
Biological characteristics					
Fish zonations§	Trout zone	Grayling zone	Grayling zone	Barbel zone	Barbel zone
Density of <i>S. salar</i> (fish. 100 m ⁻²)¶	30.14 (\pm 9.11)	28.37 (\pm 9.12)	25.53 (\pm 3.07)	9.22 (\pm 0.39)	7.45 (\pm 2.54)
Density (fish. 100 m ⁻²)					
Barbel (<i>Barbus barbus</i> ; 0+)			7.5 (\pm 2.0)	17.0 (\pm 8.1)	13.3 (\pm 3.6)
Bullhead (<i>Cottus gobio</i>)	130.8 (\pm 11.7)				
Grayling (<i>Thymallus thymallus</i> ; 0+)		2 (\pm 0.4)			
Gudgeon (<i>Gobio gobio</i>)	12.2 (\pm 5.9)	4.5 (\pm 1.7)	8.2 (\pm 2.4)	8.1 (\pm 1.1)	18.3 (\pm 12.8)
Minnow (<i>Phoxinus phoxinus</i>)	33.3 (\pm 12.6)	8.0 (\pm 2.7)	5.7 (\pm 3.0)	19.1 (\pm 8.4)	12.2 (\pm 2.0)
Spirilin (<i>Alburnoides bipunctatus</i>)		5.0 (\pm 1.1)	8.6 (\pm 2.7)	16.5 (\pm 6.4)	7.5 (\pm 1.8)
Stone loach (<i>Barbatula barbatula</i>)	43.3 (\pm 7.1)	26.0 (\pm 6.8)	57.1 (\pm 13.7)	21.9(\pm 4.1)	40.6 (\pm 9.1)
Trout (<i>Salmo trutta</i> ; Adults)	17.5 (\pm 9.9)	5.5 (\pm 1.3)			

†Determined in September 2006 during the low water period.

‡Wentworth (1922) classification.

§Huet's European river zonation scheme (1959).

¶Mean values obtained from annual electrofishing surveys monitored by ONEMA and Chanteuges hatchery in late October 2006 (Bach et al. 2007).

treatment plant of the town of Langeac (pop. 4,100). The last study reach (Site 5, barbel zone) lay 162 km from the sources, at the beginning of the southern Limagne graben, a major intensive agricultural plain; here, the river starts to meander and its water quality was only Grade B according to the national river water quality indicator, owing to ambient nutrient (N-NO₃⁻ and P-PO₄³⁻) concentrations (Anonyme 2003). The physical parameters of each riffle are described in more detail in Table 1.

Materials and methods

Sampling

Atlantic salmon parr

The fish used in the study originated from wild spawning *S. salar* caught each autumn in the river. Juveniles were reared from the egg stage in the Chanteuges salmon hatchery (see Fig. 1) and fed with commercial pellets for 6 weeks. In late May 2006, juveniles (0+ parr, total length ranging from 3 to 4 cm) were released in the selected Upper Allier riffles. The number of released fry could not be chosen, because the restocking procedure was supervised and executed only by the regional agency of the French ONEMA (National Office of Water and Aquatic

Environments). Nevertheless, we made sure that restocked salmon densities were approximately adapted to riffle area, ranging between 10 and 15 fry·m⁻². After 3 weeks of acclimatisation, sampling started and was conducted monthly during the period of maximal growth (June–October) and hence of high food demand. Sampling was performed in the riffles of Sites 1–5. To capture salmon juvenile, a Dream Electronic® portable electrofishing unit with an anode of 25 cm diameter was activated at points randomly selected in area with water depth <50 cm. All fish immobilised by the electric field were collected immediately with a separate dip net. Fish were caught at 5–15 points within the riffle and the distance between points was at least 2 m. Because our sampling locations were situated in restricted Atlantic salmon fishing areas, we were not allowed to capture more than twenty 0+ parr per site and date.

Six to nineteen 0+ parr were collected at each site and date. Total lengths and wet weights were immediately recorded in the field. Stomach contents were extracted by pulsed gastric lavage (Kamler & Pope 2001) and diet materials were preserved in 4% formaldehyde. Two subsamples of 3–7 fish were immediately frozen in liquid nitrogen prior to otolith growth determination and lipid analysis. A total of 225 parr were thus collected during this study.

In the Chanteuges salmon hatchery, a stock of unreleased juveniles was reared in triplicate circular fibreglass tanks (1,000 L), containing 1,250 fish each. Constant water flow (pumped from the River Allier) and a current speed of 8–10 cm·s⁻¹ were maintained in all tanks under natural photoperiod. All parr were fed with Nutra HP[®] commercial diet (Skretting, France) throughout the study. Sampling was carried out on the same dates as electrofishing. A mean 12 fish were anaesthetised, weighed, measured and immediately frozen in liquid nitrogen prior to lipid analysis.

Additional data on riffle fish communities (see Table 1) were obtained from the annual electrofishing surveys monitored by ONEMA and the Chanteuges salmon hatchery (Bach et al. 2007). Abundance of salmon parr was estimated in October 2006 using the standardised protocol of Prevost & Nihouarn (1999). Densities (fish·100 m⁻²) were calculated from equations of direct proportionality between CPUE-type (number of individuals caught for one standard unit of effort of five minutes) abundance indices and removal density estimates. For other species inhabiting the riffles, several points were fished and the relative densities were related to the surface area sampled (Garner 1997; Bischoff & Freyhof 1999). All fish were captured with a Dream Electronic[®] portable electrofishing unit.

Macroinvertebrate fauna

To assess the abundance of potential macroinvertebrate prey in the environment, benthic fauna were collected at the same time periods as the parr were sampled. For schedule reasons, this could not be done in July and September. On each site, four samples were collected from randomly selected locations to give a good representation of habitats found in riffles. Sampling used a Surber benthic sampler (area, 0.1 m²; mesh size, 250- μ m) and samples were stored in an ice tank until taken to the laboratory. There, specimens were preserved in 70% ethanol in plastic bottles. The composition and relative abundance of the macroinvertebrate drift was not examined, assuming that long pools, characteristic of the River Allier, would act as barriers to stream drift (Martin & Knight 1989), so that invertebrates drifting in the riffle would mainly be species originating from the activity of benthic riffle fauna. This assumption was reinforced by the lack of any flood event during the survey, and the stable flow regime conditions.

Laboratory analysis

Growth and nutritional condition of Atlantic salmon parr

To estimate the growth trajectories of the fish in the various riffles, body size (total length and wet weight)

was assessed by otolith growth and evaluation of individual NL contents.

Sagittal otoliths were extracted from 3 to 7 randomly chosen fish per month and per site. Each otolith was prepared according to an adapted method described by Rakocinski et al. (2006). They were glued (Crystalbond 509, AREMCO) on a glass slide and polished in the sagittal plane. Preparations were viewed by an image analysis system using an Olympus BH-2 MTV-3 microscope coupled to a high-resolution video camera (Sis ALTRA 20) and a computer equipped with AnalySiSgetIT software. Length and width, core size and distance to each daily increment were measured along the longitudinal axis of sectioned otoliths by ImageJ software.

To determine NL content, 3–7 frozen fish were freeze-dried and weighed (Mettler AE163 electrobalance) to determine dry mass. Total lipids were then extracted from each salmon carcass (including intestine and empty stomach) following a modified version of Folch et al.'s procedure (Folch et al. 1957). Lipid classes were separated and NL quantified using the Iatroscan Th10 mark IV analyser, which combines TLC and flame ionisation detection, following the method described elsewhere (Desvillettes et al. 1997).

Stomach contents and benthic sample analysis

Per site and date, 6–19 preserved stomach contents were analysed under a binocular loop. Food items were identified and enumerated. Macroinvertebrates were identified to genus level for Diptera, Ephemeroptera and Trichoptera and to family level for other taxa. When insect prey was damaged, only cephalic capsules were counted. Prey items were measured in a minimum of three alimentary tract contents per site and month. The total body length of each individual prey was determined with an image analysis system (LEICA Qwin) to the nearest 0.01 mm from the anterior head to the end of the last abdominal segment, excluding cerci and other appendages (Towers et al. 1994).

Preserved benthic macroinvertebrates were sorted out, counted and identified as described above. The dry mass (60 °C for >48 h) of each sample was determined using a Mettler AE163 electrobalance.

Data analysis

Growth parameters

The effects of site and date on parr growth were determined by examining total length and wet weight evolution and daily growth rate calculated from otolith analysis. The length–weight relationship for fish in the various riffles and in the hatchery were established using the common formula (Ricker 1975):

$$W = a \cdot TL^b$$

where W is body weight of fish in g, TL body length of fish in cm, and a and b are constants. Total length and weight were \log_{10} -transformed and least square regressions ($\log_{10} W \times \log_{10} TL$) were performed to determine the length-weight relationship ($\log_{10} W = \log_{10} a + b \cdot \log_{10} TL$) for all sampled salmon parr by site. The exponential form of the slope (b -value) and intercept (a -value) thus obtained were used to calculate the relative condition factor (K_n -factor) for each fish according to the following equation (Le Cren 1951):

$$K_n = W/a \cdot TL^b$$

where W is body weight in g, TL is body length in cm, and a and b are the exponential forms of the intercept and slope, respectively. To identify significant effects of site, hatchery and date, a two-way analysis of variance (ANOVA) was performed on each dependent variable followed by a *post hoc* pair-wise comparison Tukey test on fish size and weight, daily growth rate, condition factor and total lipid concentration. All data were checked for normality and variance homogeneity before analysis, and log-transformed when necessary.

Prey availability and diet analysis

To facilitate analysis, the various invertebrate items found in the stomachs and benthic samples were categorised as Coleoptera larvae and adults, Diptera larvae and pupae, Ephemeroptera nymphs, Plecoptera nymphs, Trichoptera larvae, and other prey (for items <5% abundance). The density, biomass and relative composition of benthic invertebrates were determined in order to study variations in prey availability during the survey in each restocking riffle. After \log_{10} -transformation, invertebrate density and biomass were analysed by two-way ANOVA followed by a *post hoc* pair-wise comparison Tukey test to test for site and date effects.

Salmon parr diet was defined by the common numerical method. Percentage abundance ($\%A_i$) and frequency of occurrence (F_i) were calculated for each prey category using the following formula (Amundsen et al. 1996):

$$\%A_i = (\Sigma S_i / \Sigma S_t) \times 100 \text{ and } F_i = (N_i / N) \times 100$$

where S_i is the stomach content (in this case, number) comprised of prey i , S_t is the total stomach content for all prey categories in t fish, N_i is the number of fish with prey i in their stomach, and N the total number of fish with stomach contents.

The graphical analysis proposed by Amundsen et al. (1996) was used to interpret the whole dataset

of prey categories identified in stomach contents. This is a modification of Costello's method (Costello 1990) which allows foraging behaviour and prey importance to be analysed by a two-dimensional representation of frequency of occurrence (F_i) and prey-specific abundance. The prey-specific abundance ($\%P_i$) takes into account only those predators in which the actual prey occurs (Amundsen et al. 1996):

$$\%P_i = (\Sigma S_i / \Sigma S_{ti}) \times 100$$

where S_i is the stomach content (in this case, number) comprised of prey i , and S_{ti} the total stomach content in only those fish that consumed prey i . According to Amundsen et al. (1996), the interpretation of the diagram (prey importance, feeding strategy and inter- and intra-individual components of the niche width) can be obtained by examining the distribution of prey categories (points) along the diagonal and axes of the graphic (see Fig. 2).

In addition, possible size selectivity was assessed by examining prey size evolution throughout the survey in each restocking riffle. Effects of date and site on prey size were assessed by two-way analysis of

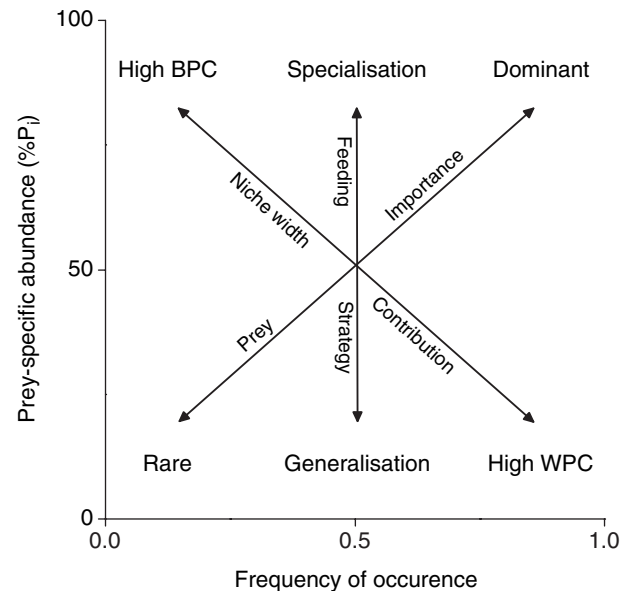


Fig. 2. Modified Costello graph showing explanatory axes (adapted from Amundsen et al. 1996). (1) Prey prevalence is represented in the diagonal from lower left (rare prey) to upper right (dominant prey); (2) feeding strategy is represented in the vertical axis from bottom (generalisation) to top (specialisation): specialisation by individual predators (upper left of the diagram) and specialisation of the predator population (upper right); and (3) The contribution of between- and within-phenotype (or individual) components to niche width is represented in the diagonal from lower right (most of the individuals utilize many resource types simultaneously: high within-phenotype component (WPC) to upper left [different individuals specialize in different resource types: high between-phenotype component (BPC)]).

variance (ANOVA). When significant differences were found, they were located by *post-hoc* Tukey test. All statistical analyses were performed using SYSTAT 12 software and were considered significant at $P < 0.05$.

Results

Fish samples

Growth parameters

Significant variation in growth performances of *S. salar* parr was observed between restocking riffles and hatchery (ANOVAS and *post-hoc* Tukey tests: TL: $F_{5, 255} = 13.70$, $P < 0.01$, W: $F_{5, 255} = 17.18$, $P < 0.01$; Fig. 3a,b). The maximum length and weight were reached in Site 3 (TL = 9.78 ± 0.35 cm, $W = 9.08 \pm 1.31$ g) and Site 5 (TL = 9.38 ± 0.50 cm, $W = 8.41 \pm 1.45$ g) while lower growth performances were observed in Sites 4 and 2 (Site 4: TL = 8.09 ± 0.45 cm, $W = 5.29 \pm 0.97$ g; Site 2: TL = 8.06 ± 0.45 cm, $W = 5.49 \pm 0.99$ g), and especially in Site 1 (TL = 6.98 ± 0.19 cm, $W = 2.95 \pm 0.27$ g). Thus, it appeared that the total length and wet weight of parr varied according to the upstream–downstream gradient, with better growth in fish from downstream (Sites 3, 4 and 5) than upstream riffles (Sites 1 and 2). In the hatchery, the maximum length and weight of reared fish was greater than that of the restocked fish, reaching a maximum of 11.00 ± 0.98 cm and 19.82 ± 5.04 g respectively. Furthermore, it is of interest to note that salmon growth recorded in the intermediary riffle (Site 3) was closest to that observed in the hatchery, although growth increased more regularly in the latter (Fig. 3a,b). In downstream sites, a greatest length and weight increase was observed between July and August, especially in Site 3.

These significant differences in parr growth patterns along the upstream–downstream gradient were confirmed by otolith analysis ($F_{4, 67} = 8.26$, $P < 0.01$; Fig. 4). Tukey's *post-hoc* test indicated that parr otolith daily growth did not differ between the first and second sites (around $2.27 \pm 0.05 \mu\text{m}\cdot\text{day}^{-1}$). These upstream riffles were separated from the three others (Sites 3, 4 and 5), where mean daily otolith growth was significantly higher, ranging from 2.63 ± 0.15 to $3.13 \pm 0.22 \mu\text{m}\cdot\text{day}^{-1}$ (Fig. 4).

Condition factors

Parr condition factors varied significantly with restocking riffle and hatchery tank (ANOVAS and *post-hoc* Tukey tests: $F_{5, 255} = 11.41$, $P < 0.01$; Fig. 3c). They also showed monthly variations in each site and in the hatchery, with the exception of Site 5 ($F_{3, 26} = 0.69$, $P = 0.57$). At the beginning of the survey, the relative condition factors appeared higher for hatchery-reared

parr ($K_n = 1.03 \pm 0.05$) and restocked parr from Site 3 ($K_n = 0.82 \pm 0.04$) and Site 4 ($K_n = 0.96 \pm 0.03$) than in upstream sites (Site 1: $K_n = 0.49 \pm 0.03$; Site 2: $K_n = 0.46 \pm 0.09$). Values reached at the end of the study (October) showed no significant differences between sampling zones ($F_{4, 40} = 0.49$, $P = 0.75$), while the condition factor was highest for hatchery parr ($K_n = 1.07 \pm 0.08$; Fig. 3c).

Lipid deposition

Neutral lipid contents evolution varied significantly with site and hatchery (ANOVAS and *post-hoc* Tukey tests: $F_{5, 90} = 4.37$, $P < 0.01$) (Fig. 3d). NL deposition was significantly higher in fish growing in Sites 2, 3, 4 and 5, while the amounts deposited in fish from Site 1 were the lowest observed. Moreover, NL storage was higher in hatchery-reared parr than in any riffle restocked fish. Monthly variations were also observed in each restocking riffle ($F_{4, 90} = 15.61$, $P < 0.01$), except in Sites 1 and 5. The NL concentration per fish increased markedly from July to August in Site 4, and from July to September in Sites 2, 3 and 5. In October, a tendency towards a decrease was then observed in parr from those riffles, but was not statistically significant (Fig. 3d).

Available food resources

The total density of all benthic macroinvertebrates significantly differed with riffle and month (ANOVAS and *post-hoc* Tukey tests: riffles, $F_{4, 53} = 2.92$, $P = 0.03$; months, $F_{2, 53} = 3.38$, $P = 0.04$), but their interaction was not significant ($F_{8, 53} = 1.92$, $P = 0.09$; Fig. 5a). Significant differences in macroinvertebrate biomass were observed only between sites ($F_{4, 53} = 5.06$, $P = 0.01$), and not months ($F_{2, 53} = 0.08$, $P = 0.92$; Fig. 5b). Site 2, with mineral microhabitats (no submerged macrophytes), exhibited the lowest recorded macroinvertebrate density and biomass, with minimum values found in October in this riffle ($3\ 657.47 \pm 741.73 \text{ ind}\cdot\text{m}^{-2}$, $0.57 \pm 0.13 \text{ g}\cdot\text{m}^{-2}$, respectively). On the other hand, the highest values ($36\ 737.30 \pm 18\ 880.28 \text{ ind}\cdot\text{m}^{-2}$, $4.07 \pm 1.06 \text{ g}\cdot\text{m}^{-2}$, respectively) were observed, in August, in Site 4, which presented microhabitats of aquatic vegetation (hydrophytes). Within a given riffle, no significant differences in density and biomass were observed from June to October, and this was true for all riffles (Fig. 5a,b), although densities showed a slight tendency to be greater in August, except in the last downstream riffle (Site 5, see Fig. 5a).

A total of 67 different invertebrate taxa were recorded in the benthic samples, with a majority of insect larvae and pupae (mean = 94%). The incidence and relative composition of these taxonomic groups differed slightly along the upstream–downstream

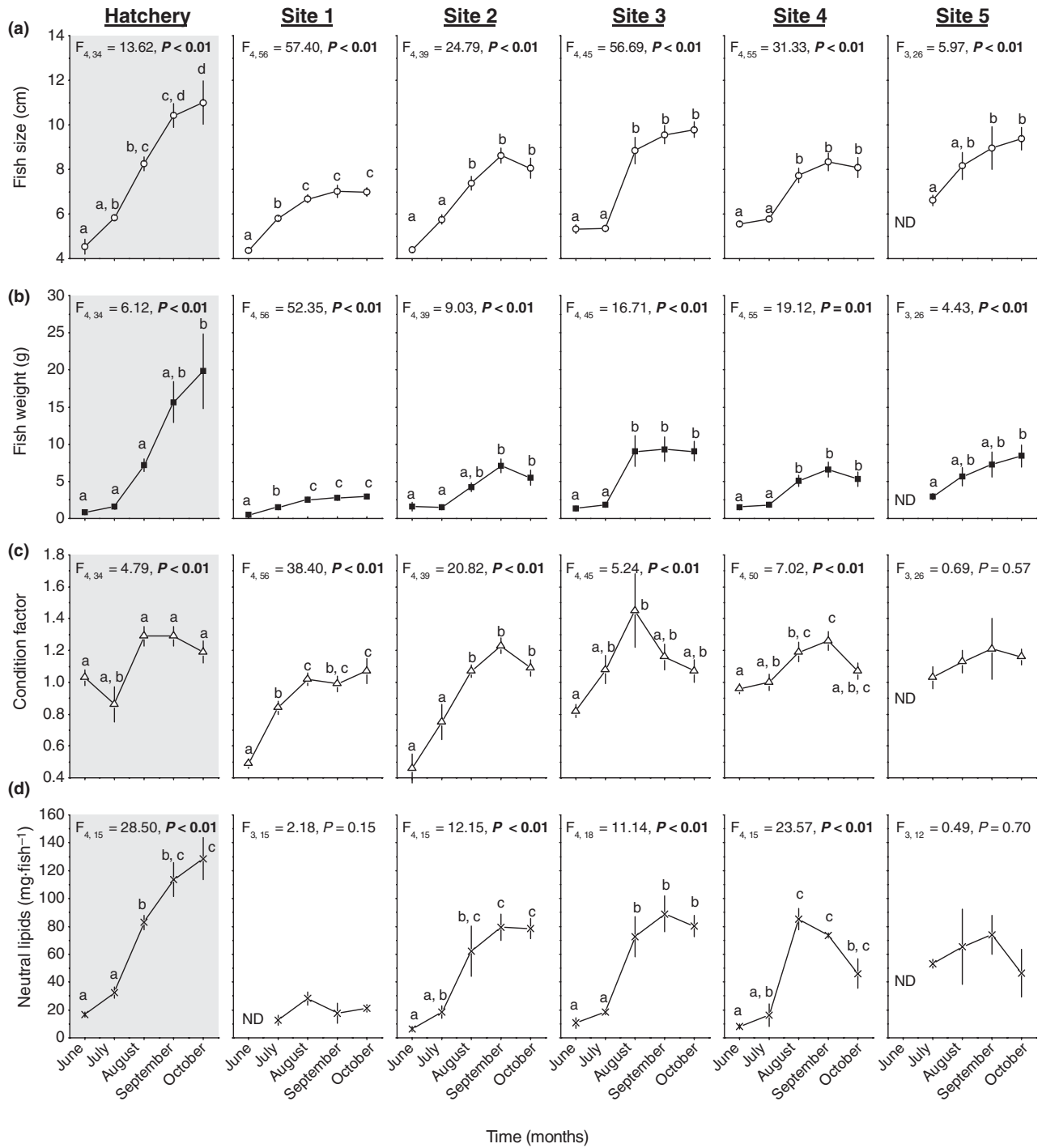


Fig. 3. Temporal/seasonal changes (June to October) in total length (mean, cm; a), wet weight (mean, g; b), condition factor (mean; c) and neutral lipid contents (mean, mg·fish⁻¹; d) of reared parr in the hatchery (in grey) and parr sampled in the five restocking sites. *F* and *P*-values are the result of two-way ANOVAs. Different letters indicate significant differences (ND = No data).

gradient (Fig. 5c). Diptera larvae dominated the benthic fauna of the Upper Allier: Chironomid larvae were most abundant in upstream (Sites 1 and 2) and Simuliid larvae in downstream riffles (Sites 3–5). Caddisfly larvae were the second most frequent invertebrate groups found in all sampled riffles. The

third most abundant group was mayfly nymphs, with only one dominant family (Baetidae). Ephemeroptera nymphs were present in each riffle throughout the sampling period (Fig. 5c).

In all concerned riffles, there were no clear seasonal changes in macroinvertebrate taxonomic assemblage

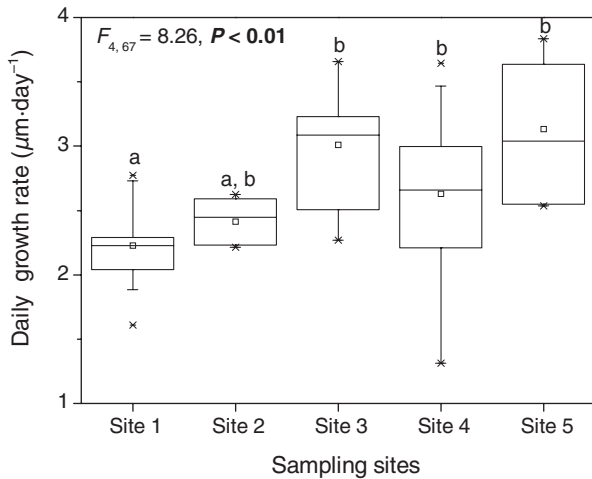


Fig. 4. Mean daily growth rates ($\mu\text{m}\cdot\text{day}^{-1}$) of parr otoliths estimated from analysis undertaken with fish from the five restocking sites (June–October). F and P -values are the result of one-way ANOVA. Different letters indicate significant differences.

for the majority of families encountered. It seemed, however, that the amount of Diptera larvae tended to decrease with time as a consequence of adult emergence. In contrast, the amount of Trichoptera larvae increased from June to October following the development of the young instar cohorts (Fig. 5c).

Feeding of salmon parr

Fish diet

Over the entire survey, a total of 225 stomachs were examined, with only 10% empty stomachs. 21 prey taxa, mostly aquatic insects (mean = 98%), were identified from the full stomachs. In all riffles and over the whole survey, the dominant salmon parr prey were Diptera larvae ($A_i = 64\%$), Ephemeroptera nymphs ($A_i = 27\%$) and Trichoptera larvae ($A_i = 7\%$; Fig. 6a). Other taxa, such as Coleoptera, Gastropoda, Hydracarina, Oligochaeta and Plecoptera, were also consumed, but generally constituted < 1% of the salmon diet and could be regarded as secondary or occasional prey (Fig. 6).

Some gradual dietary changes in the resources used by salmon parr were observed from June to October and differences also occurred between riffles (Fig. 6). Mayfly nymphs (mainly Baetidae) decreased in importance with time in Sites 2 (62 to 9%), 3 (54 to 6%) and 4 (92 to 7%), whereas Diptera larvae increased (Site 2: 30 to 55%; Site 3: 40 to 87%; Site 4: 8 to 86%). More specifically, Chironomid larvae provided major contributions to diet in Sites 2 and 4, while Simuliid larvae were predominant in Site 3. In Site 5, the mayfly Baetid dominated the diet throughout the sampling period, ranging from 40% to 76% of

stomach contents. In the first (upstream) site, Chironomid larvae predominated, constituting from 43% to 83% of the salmon diet. Trichoptera larvae were also eaten by salmon parr but in lower proportions than the main prey taxa (Diptera and Ephemeroptera). These Trichoptera were more abundant in the stomachs of parr sampled in the two upstream riffles (Site 1: $A_i = 8\%$; Site 2: $A_i = 18\%$; Fig. 6).

Generally speaking, diet composition diversified as of August, with a greater contribution of secondary and occasional prey (Fig. 6a). The diversification of invertebrates in the salmon parr diet reflected that found in benthic samples (Fig. 5c). Despite this, 0+ salmon parr collected in the Upper Allier exhibited only slight seasonal variation in diet.

Feeding strategy and prey selection

The modified Costello plot confirmed previous observations made from Fig. 6. Considering the prey importance axis (see Fig. 2), parr diet was mostly based on rare items except for one or two prey categories which tended to be dominant prey (Fig. 7). The dominant preys appeared to vary from riffle to riffle. Indeed, Chironomid larvae were more prominent in the stomachs of parr from Sites 1 ($F_i > 0.80$, $\%P_i > 40\%$) and 2 ($F_i > 0.60$, $\%P_i > 40\%$), Simuliid larvae in Site 3 ($F_i > 0.50$, $\%P_i > 30\%$), and Baetid nymphs in Sites 4 ($F_i > 0.80$, $\%P_i > 30\%$) and 5 ($F_i > 0.80$, $\%P_i > 30\%$; Fig. 7). In the first three riffles, the most common prey found in stomach contents appeared to be that most available in the benthic fauna (see Fig. 5c). In the other sites, results were not so clear. Baetid nymphs were consumed heavily in Sites 4 and 5 but were not frequent in the environment (Fig. 5c and 7).

To assess possible prey size selectivity, the mean size evolution of prey was observed throughout the studied period in each restocking riffle (Fig. 8). A significant increase in prey size with time was observed in each riffle (ANOVA and *post-hoc* Tukey test: Sites, $F_{4, 2152} = 21.01$, $P < 0.01$; Dates, $F_{4, 2152} = 55.99$, $P < 0.01$), except in the last site, where no difference in prey size between months was recorded ($F_{3, 131} = 2.30$, $P = 0.08$). Thus, size of invertebrate prey increased with fish size in all sites whereas prey type stayed the same.

Discussion

The growth of restocked salmon parr in the River Allier varied along an upstream–downstream gradient. The highest growth performances were observed for parr from downstream riffles (Sites 3, 4 and 5), with optimal values recorded in the intermediary riffle (Site 3), whereas the lowest were found in the upstream riffle (Site 1). The same pattern was observed for NL

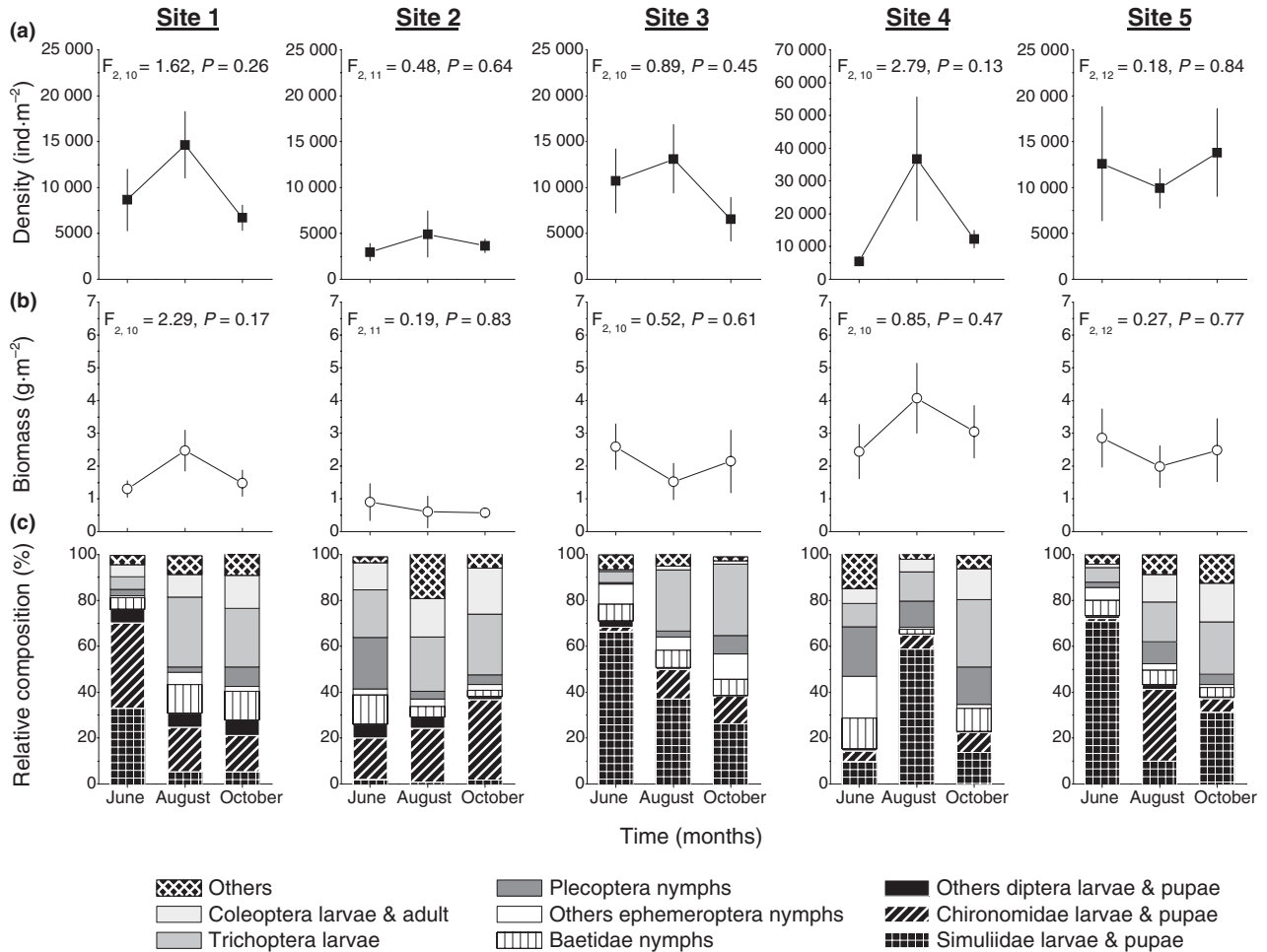


Fig. 5. Seasonal changes in density (mean, ind.m⁻²; a), biomass (mean, g.m⁻²; b) and taxonomic composition (%; c) of macroinvertebrates collected in the five riffles. *F* and *P*-values are the result of two-way ANOVAS.

composition and condition factors, with the lowest values recorded in the first site. The physiological status of restocked parr increased throughout the study period without reaching that of hatchery parr. However, a discrepancy in monthly evolution between lipid storage and condition factor was observed in the first riffle. These findings support the contention that the condition factor may be a relatively poor indicator of the energy status of both Atlantic salmon and of several other fish species (Simpson et al. 1992; Saliu et al. 2007), although it has often been assumed to indicate the lipid content/energy reserve of fish (Herbinger & Friars 1991; Johansen & Jobling 1998). The observed differences between hatchery parr and parr from upstream and downstream locations suggest sufficiently variable rearing conditions within the River Allier to influence growth and energy storage. It was hypothesised that this could be related to differences in available prey type and density along the upstream–downstream gradient, as well as differential expenditure between riffles (Shackley et al. 1994; Dempson et al. 2004).

Macroinvertebrate quantities in the bottom fauna tended to be highest in downstream sites, although the observed differences were not statistically significant owing to the wide standard errors. These variations, linked to the benthic fauna sampling design, were the direct result of microhabitat diversity in downstream riffles from Sites 3 to 5. In those riffles, contrary to what was observed upstream, the microhabitats of aquatic vegetation (hydrophytes) contained the richest fauna in terms of density. In contrast, mineral microhabitats were poorer in fauna. These findings agreed with previous studies undertaken in large temperate rivers, such as the Upper Rhone (Cogerino et al. 1995) or River Sieg, a Rhine tributary (Bischoff & Freyhof 1999). Macroinvertebrate assemblages in our studied riffles were greater than or equal to the relative total density of macroinvertebrate assemblages described from the Allier river basin (Nelva et al. 1979; Beauger et al. 2006). The lower densities and biomass recorded in Site 2 resulted from a specificity of this reach, which has torrential flow (see Table 1) and shows only mineral microhabitats, making densities closer to those

Feeding, growth and nutritional status of parr in French river

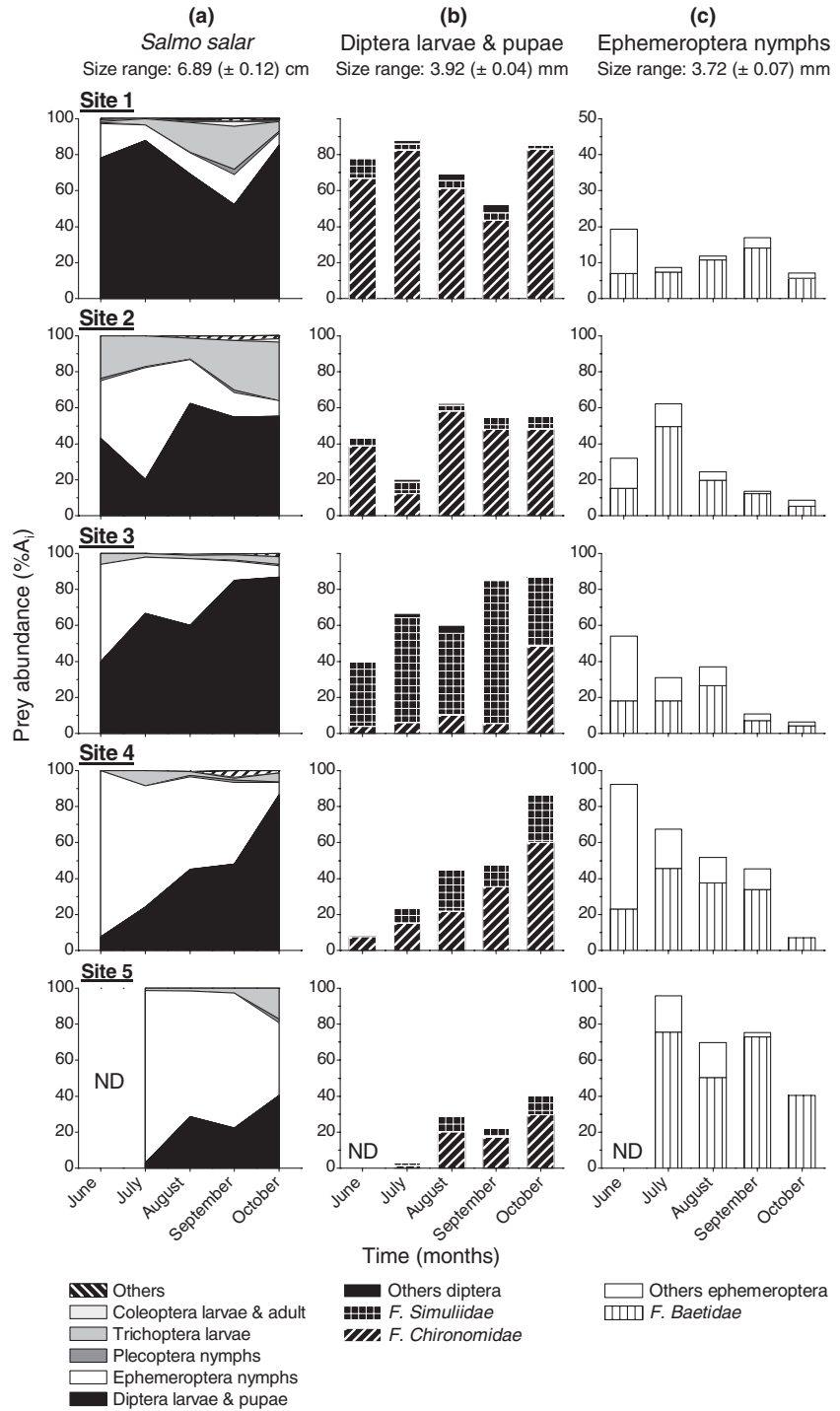


Fig. 6. Prey abundance in the stomach samples (a) and family composition of Diptera larvae and pupae (b) and Ephemeroptera nymphs (c) in the diet of *Salmo salar* parr in the five restocking riffles from June to October (ND = No data).

reported for mountain streams (Lagarrigue et al. 2001).

In this context of normal prey abundance, 0+ parr can be considered as generalist feeders in the River Allier, with a relatively broad niche width composed of several rare preys caught occasionally. On the other hand, three predominant prey families were observed in the stomach contents: Baetid nymphs, Chironomid

and Simuliid larvae. These types of prey constitute a large part of the salmon parr diet in different temperate and sub-arctic streams (Maitland 1965; Thonney & Gibson 1989; Keeley & Grant 1997). However, this preference varied in the Allier riffles along the upstream–downstream linear: Chironomid larvae were the predominant prey in upstream riffles (Sites 1 and 2), Simuliid larvae in the intermediary riffle (Site 3),

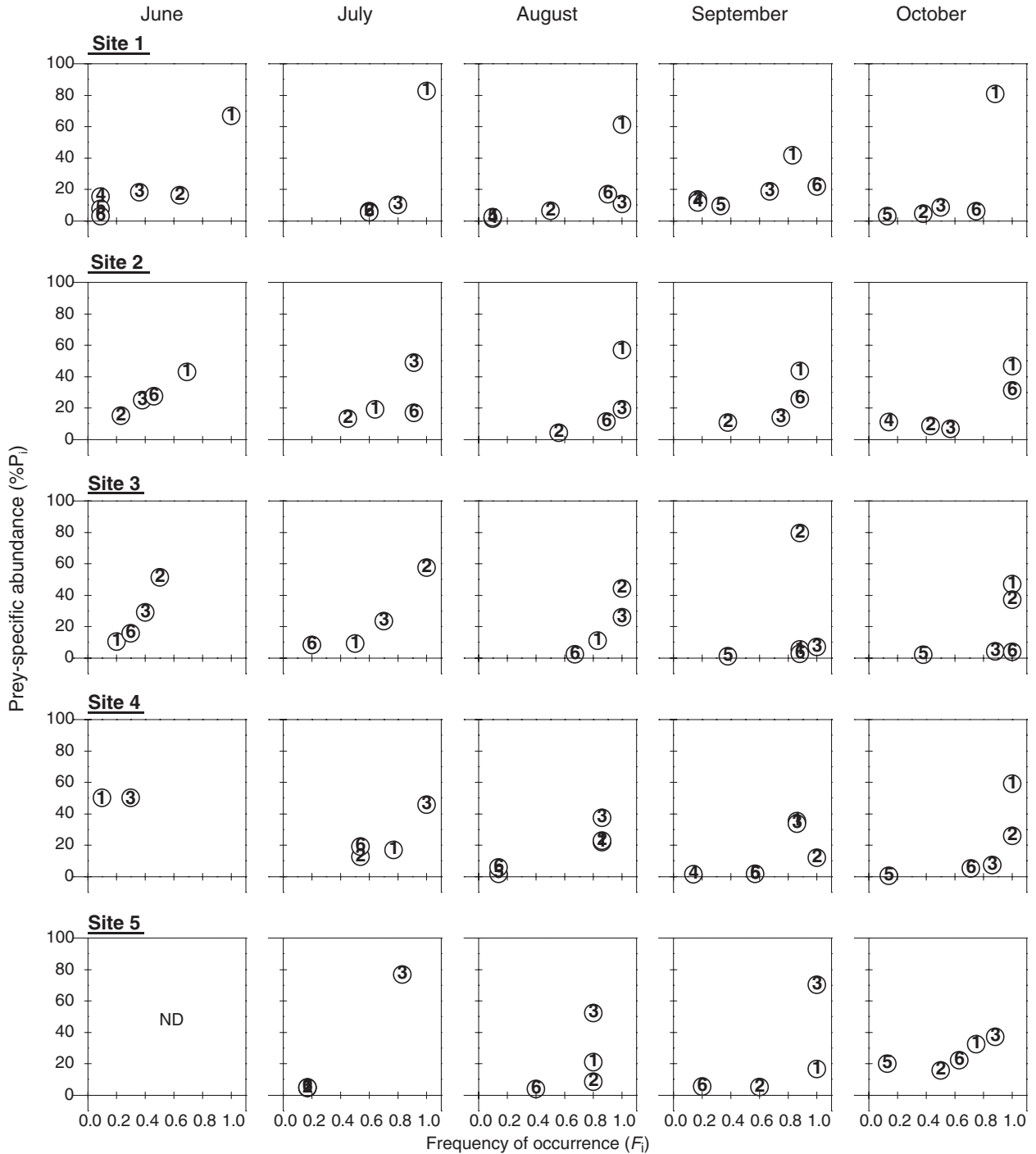


Fig. 7. Feeding strategy diagram in the five restocking riffles according to the Costello method. Prey-specific abundance ($\%P_i$) plotted against frequency of occurrence (F_i) of food items in the diet of *Salmo salar* parr from the River Allier (ND = No data). Food items: 1. F. Chironomidae, 2. F. Simuliidae, 3. F. Baetidae, 4. Coleoptera, 5. Plecoptera, 6. Trichoptera.

and Baetid nymphs in downstream riffles (Sites 4 and 5). In the three upstream sites, 0+ parr fed more intensively on Chironomid and Simuliid larvae because these prey types were locally abundant. This similarity between environment components and salmon diet was already observed in other studies of

stream-dwelling salmonids in North American rivers (Forrester et al. 1994; Keeley & Grant 1997). In addition to their abundance, the life mode of these preys may also explain this preference. They are mostly associated with the bottom and are therefore easy to capture because of their low mobility (Vignes

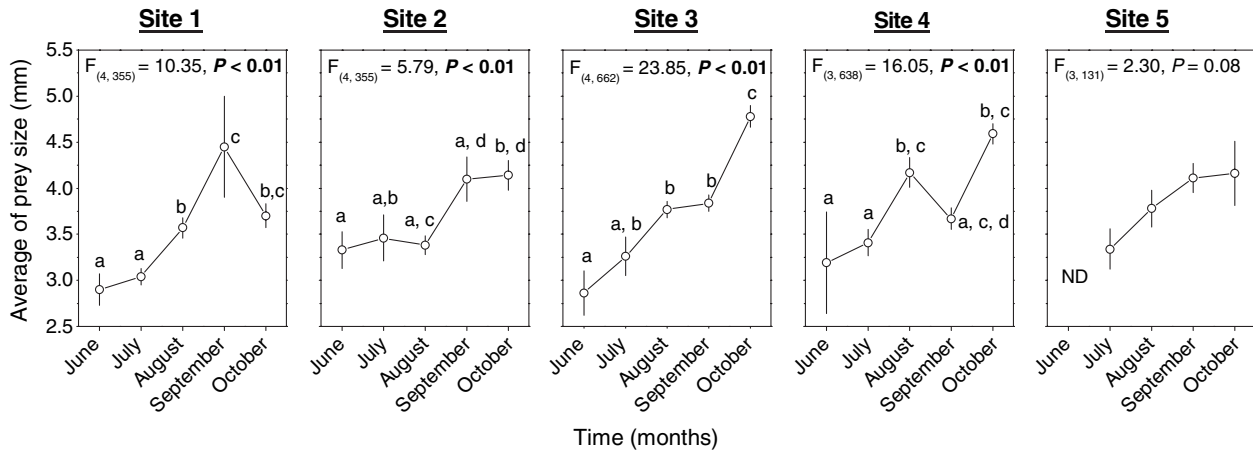


Fig. 8. Mean total length (mm) of *Salmo salar* preys and results of two-way ANOVAs. Different letters indicate significant differences between months in each site (ND = No data).

1998; Amundsen et al. 2001). This would imply that benthic feeding could prevail in these upstream riffles, which has also been demonstrated in other studies of juvenile salmon (Sosiak et al. 1979; Keeley & Grant 1995; Gabler et al. 2001). In downstream riffles (Sites 4 and 5), Simuliid larvae dominated the benthic fauna, whereas Baetid nymphs were preferentially chosen by parr. This poor association between diet and available bottom prey observed in these sites may reflect more substantial drift feeding. Baetidae species are frequently regarded as intentional drifters, particularly when subject to Salmonid predation (Forrester 1994; Rader 1997). Consequently, their strong abundance in salmon parr diet can reflect an increasing drift feeding, as shown in some studies conducted in sub-arctic Norwegian rivers (Amundsen et al. 2001; Gabler et al. 2001).

Prey size was also an important factor in prey choice (Wankowski 1979). Many relationships between prey size and Salmonid body size have been established for small fish. They were often linked to morphological constraints, optimal prey size and feeding energetics (Keeley & Grant 1997). In the Upper Allier, mean prey size increased with fish body size but the type of prey preferentially chosen in each riffle stayed the same. No size-dependent diet segregation occurred here, even if variations in the taxonomic composition of diet have been frequently reported elsewhere between small and large parr (Keeley & Grant 1997; Erkinaro & Erkinaro 1998). In general, the favourite preys of 0+ parr are small-sized and apparently found at high densities in the Upper Allier. According to Steingrímsson & Gíslason (2002), a sufficient supply of large prey items or a greater abundance of small prey, such as Diptera larvae, may maintain the growth of salmonids.

Thus, growth performance and lipid storage were considerable in the intermediary and downstream

riffles (Sites 3, 4 and 5) where Simuliid larvae and Baetid nymphs were predominantly consumed by Atlantic salmon. In contrast, lower values were observed in upstream riffles (Sites 1 and 2) where Chironomid larvae were preferentially selected, especially in Site 1. Whether Simuliid larvae and Baetid nymphs have higher nutritional value than Chironomid larvae remains to be determined. According to Bell et al. (1994), the amount of fatty acid supplied by prey, especially polyunsaturated and monounsaturated components, might be a discriminatory factor in prey's nutritional quality for salmon parr. However, it seems that variations in fatty acid composition between aquatic insects such as Chironomid larvae and Ephemeroptera nymphs are slight (Ghioni et al. 1996), and they remain unknown for Simuliid larvae. Experimental studies on feeding parr have shown that diet with similar fatty acid composition did not induce differences in fish body weight gain or in lipid storage (Polvi & Ackman 1992; Rollin et al. 2003). Therefore, it can be suggested that the low growth and lipid storage rates observed in salmon of the first riffle were not solely linked to the quality and abundance of food. Interactions between food abundance, prey assemblages and several habitat variables could better explain the parr growth performance observed along the river linear.

Some studies have shown that water temperature and velocity are able to interact with food availability in determining the growth performance of Atlantic salmon. Jonsson et al. (2001) estimated that the optimum temperature for growth ranged between 16° and 20 °C. In temperate rivers, Beland et al. (2004) showed that parr prefer areas with water depths ranging from approximately 10–60 cm and water velocities between 30 and 92 cm·s⁻¹. All downstream riffles (Sites 3–5) had mean values approximately within these ranges, while upstream riffles (Sites 1 and

2) had lower values (see Table 1). Here again, the Site 1 was the only one to exhibit a mean water temperature and velocity below these ranges. This might partly explain the difference in growth rate encountered between downstream and upstream riffles. On the other hand, Kemp et al. (2006) showed that fish growth and lipid content were better when the energy costs of foraging were low: i.e., at lower velocity. Accordingly, better growth performance would be found in Site 1. However, these findings are only relevant if prey abundance and competition are not the primary limiting factors. It was hypothesised that food limitation was slight, and – without enough knowledge of prey nutrient contents – competition could be considered as a substantial cause of reduced performance in parr from upstream riffles.

According to Imre et al. (2005), the growth of 0+ salmon seemed to start to decrease when salmon densities exceeded 30–40 fish·100 m⁻². There was a density-dependent limiting factor in response to intra-species competition. However, recorded salmon densities were good in the three upstream riffles (Site 1–3) and low in the last downstream riffles (Sites 4 and 5). Thus, no obvious intra-species competition seemed to lead to parr growth reduction in Site 1 (see Table 1). Considering the small size and densities of other fish species in this site (see Table 1), it can therefore be suggested that inter-species competition affects parr growth and nutritional status in the most upstream riffle (Kennedy & Strange 1986; Gabler & Amundsen 1999). Thus, competition for resources, such as habitat and food, could occur in this area. Such inter-species competition was previously reported by Gabler & Amundsen (1999) in the sub-arctic River Reisa. In addition to Cottidae, brown trout, stone loach and minnow are also known to compete with Atlantic salmon (Maitland 1965; Kennedy & Strange 1986). In contrast, the coexistence of some warmer water species, such as barbel and gudgeon, with wild or restocked salmon has been little studied. Barbel feed almost exclusively on benthic Diptera (Bischoff & Freyhof 1999) and gudgeon can reduce the drift of Baetid nymphs (Winkelmann et al. 2007). The question arises as to whether feeding competition occurred between these fish and salmon in our riffles. Given the lack of detailed studies on the actors involved, it may be suggested that the low densities of parr observed in downstream riffles of the barbel zone (Sites 4 and 5) could be the result of such inter-species competition.

In conclusion, our results show that the growth, lipid storage and condition factors of salmon parr varied along a longitudinal gradient in a large temperate river. Indeed, these restocked parr face different biotic and environmental conditions along the upstream-downstream gradient. Not only temperature and food

availability, but also inter-species competition may interact to determine growth. Site 1 can be considered as the extreme upstream limit for 0+ salmon restocking. The low growth and lipid storage recorded in this area during the active feeding period could be a major cause of overwintering mortality of parr facing harsh climatic conditions (Jobling 2001; Dempson et al. 2004). In contrast, while parr growth performances were good in downstream riffles (Sites 4 and 5), the densities usually found were low. Within these reaches of the downstream gradient, competition with other benthivorous species is suspected and will be examined in further research. Finally, the most favourable site for optimum growth and nutritional status was the intermediary riffle (Site 3), with values close to those achieved in hatchery-reared parr. Located in the grayling zone, reaches similar to Site 3 constitute a linear of about 25 km where progressive modifications in environmental parameters and fish species assemblage occur. To enhance salmon stocks in large European rivers, further studies will be necessary to analyse parr development in such specific intermediary areas of the lotic system.

Acknowledgements

We thank the *Conservatoire National du Saumon Sauvage* for their helpful contribution to electrofishing operations and hatchery samples, and D. Gerdeaux (*Station d'Hydrobiologie Lacustre*, Inra, Thonon) for his advice during the otolith study. We are grateful to M. Nicolas for the preparation and reading of the otoliths. We also thank him, B. Misson and J. Sauvanet for their help during the analysis of stomach contents and macroinvertebrate identification. We express our gratitude to L. Jouve and C. Lemarchand for help and support during the study. The English was revised by I. McGill.

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