

INVERTEBRATE ACCESSIBILITY AND VULNERABILITY IN THE ANALYSIS OF BROWN TROUT (*SALMO TRUTTA* L.) SUMMER HABITAT SUITABILITY

V. DE CRESPIN DE BILLY,^{a,b*} B. DUMONT,^a T. LAGARRIGUE,^c P. BARAN,^c and B. STATZNER^b

^a Cemagref, Unité de recherche "Hydrobiologie", BP 31 le Tholonet, 13612 Aix-en-Provence cedex 1, France

^b CNRS, Ecologie des Hydrosystèmes Fluviaux, Université Lyon 1, 69622 Villeurbanne cedex, France

^c ENSAT, Laboratoire Environnement Aquatique, BP 107 Auzeville, 31326 Castanet Tolosan, France

ABSTRACT

Water discharge regulation can affect food availability, accessibility and vulnerability and thus, the trophic habitat suitability for lotic salmonids. To analyse brown trout habitat suitability, we therefore combined the relative importance of the food availability (overall abundance of benthic and drifting invertebrates), with the potential food vulnerability (accessibility, conspicuousness and ease of handling), the latter depending on both physical habitat characteristics (flow patterns and structural complexity of habitat) and invertebrate traits (size and other biological traits). We considered the trophic patterns of trout at two spatial scales: the reach scale (unregulated reach versus regulated reach) and the macrohabitat scale (e.g. riffles and pools).

Discharge regulation reduced trout abundance, biomass, and temperature-independent growth rates. In the regulated reach, trout had a lower total prey consumption, a higher consumption of terrestrial invertebrates and a higher diet diversity than in the unregulated reach, indicating that trout were food-limited. However, the potential availability of food supplies per individual trout was similar for the two reaches. Thus, trout prey consumption in the regulated reach should have been predominantly affected by the decrease in both the availability of large invertebrates in the drift and their vulnerability in the total food supplies.

There were no macrohabitat-specific differences in the total prey consumption and in the potential food availability within each reach. However, brown trout diets differed between the macrohabitats of each reach, in relation to differences in potential invertebrate vulnerability.

Therefore, the potential vulnerability of invertebrates to predation was more relevant in the ecological evaluation of salmonid habitat suitability than the total food availability. The analysis at the macrohabitat scale provided a better understanding of the switches in brown trout diet and enabled a finer and more realistic analysis of trout feeding patterns. Copyright © 2002 John Wiley & Sons, Ltd.

KEY WORDS: benthos; drift; brown trout; growth; food availability; two-scale approach

INTRODUCTION

Water discharge regulation in streams strongly modifies the structural complexity and diversity of the physical habitat which in turn affects biological patterns of freshwater organisms. To restore streams and to maintain fish populations (usually salmonids), stream managers are mainly concerned with predicting fish abundance and the assessment of the minimum flows required. Many tools have been developed for the habitat management of organisms living in regulated streams (see Jowett, 1992). For instance, models based on the assessment of microhabitat preferences of salmonids (water depth, velocity, substrate and cover) have been used to measure microhabitat suitability (Instream Flow Incremental Methodology; Bovee, 1982; Nestler *et al.*, 1989). However, microhabitat preferences and use also vary according to biotic factors such as the diel activity of salmonids (Roussel and Bardonnnet, 1997; Heggenes *et al.*, 1999), inter- and intra-specific interactions (Nielsen, 1992; Greenberg *et al.*, 1997; Vehanen *et al.*, 1999) and food availability (Grant and Noakes, 1987).

* Correspondence to: V. de Crespin de Billy, Equipe de Démoécologie, UPRES EBSE, Université de Metz, Avenue du général Delestraint, 57070 Metz, France. E-mail: debilly@sciences.univ_metz.fr

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There is currently a need to identify the relevance of biotic factors for estimating habitat suitability of salmonids. Many authors have pointed out the importance of food availability as a limiting factor for salmonids, despite their opportunistic feeding behaviour (see Poff and Huryn, 1998). Food availability is often defined as the overall abundance or biomass of benthic invertebrates (Jowett, 1995). However, salmonids are visual and size-selective feeders that mainly use drifting invertebrates (Bannon and Ringler, 1986). Thus, changes in prey vulnerability, i.e. in accessibility, conspicuousness and ease of handling, can also modify fish foraging behaviour (Grant and Noakes, 1987) and affect their production (Smith, 1961). Hence, Poff and Huryn (1998) stated that 'invertebrate production' is not necessarily equivalent to 'prey production'.

According to several authors, invertebrate vulnerability depends on physical habitat characteristics: (i) high structural complexity of habitat alters the visual field and foraging efficiency of fish (Wilzbach *et al.*, 1986); (ii) low water depth affects the accessibility of suitable feeding habitat (Braaten *et al.*, 1997); and (iii) a decrease in current velocity may reduce the encounter rate of salmonids with drifting prey (Nislow *et al.*, 1999). However, the invertebrate vulnerability can also be affected by their own traits (e.g. size, mobility, drift behaviour; Ware, 1973; Rader, 1997). So, to understand the limits on salmonid production, Poff and Huryn (1998) suggested that both the availability and potential vulnerability of food supply should be considered (i.e. prey abundance and traits, respectively).

The taxonomic composition, density and drift rate of benthic invertebrates depend on habitat characteristics (Statzner and Borchard, 1994). Thus, discharge regulation should modify both the availability and vulnerability of food supply for salmonids. These features could therefore constitute relevant ecological descriptors of salmonid habitat suitability. Fish growth, an integrative expression of the well-being of fish in streams in general and of food availability in particular (Cada *et al.*, 1987), can also be used as a descriptor of the habitat suitability.

Growth and trophic patterns of fish have to be studied at an appropriate spatial scale, as there is a scale-dependence in patterns and processes (Cooper *et al.*, 1998). In principle, salmonid growth should be analysed on a large scale (e.g. the catchment), as it depends on conditions experienced by the fish over a lifetime and may not reflect the site conditions where the fish is captured. However, in regulated rivers, fish cannot circulate freely among reaches, and growth patterns should therefore be compared on the reach scale. Concerning trophic patterns of lotic salmonids, Armstrong *et al.* (1998) noted that 'food may be limiting due to the eutrophic state of the catchment', so trophic patterns should also be analysed on a large scale. However, the structural complexity of habitats and the associated composition of invertebrate communities depends on the local habitat pattern (e.g. Lancaster and Mole, 1999), and many authors have reported macrohabitat-specific differences in brown trout diets (i.e. between pools and riffles *sensu* Frissel *et al.*, 1986).

Therefore, we chose an unregulated and a regulated reach of a small Pyrenean mountain river and a two-scale approach (reach and macrohabitat scale) to analyse (i) the effects of habitat characteristics on the availability and potential vulnerability of food supply, as well as on brown trout (*Salmo trutta* L.) diets; (ii) the relevance of food characteristics for measuring the habitat suitability of brown trout; and (iii) the suitability of the spatial scales that were studied for detecting potential food availability and vulnerability. Baran *et al.* (1995) previously observed that discharge regulation reduced the weighted usable area (WUA) and cover for brown trout in this Pyrenean stream, as well as trout density and biomass. We completed this previous study by comparing growth patterns of brown trout between the unregulated and the regulated reach. However, our focus was the concurrent analysis of feeding habits of medium to large sized brown trout and their potential prey.

MATERIAL AND METHODS

Study area

The Neste d'Aure is a small French Pyrenean mountain river (Figure 1a). Its origin is at 1100 m, at the confluence of the Neste de Couplan and the Neste d'Aragnouet, and it flows into the Garonne River. We studied two sites on the Neste d'Aure (Figure 1b): (i) a reference site which is a semi-natural reach as it has an unregulated discharge; and (ii) a site in the regulated reach, 3.5 km downstream from the Arreau

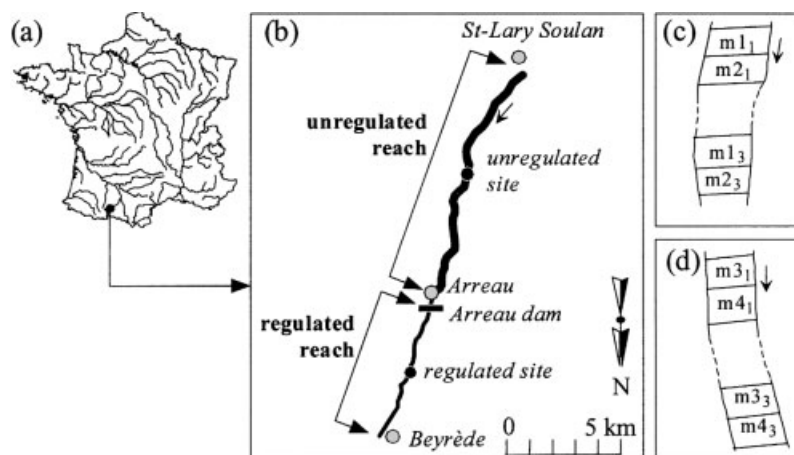


Figure 1. Geographic location of the catchment of the Neste d'Aure within France (a), and the studied spatial scales with (b) the reach scale and (c, d) the macrohabitat scale. m1, m2, m3 and m4 correspond to the four macrohabitat types studied. Subscript numbers (e.g. m1₁) indicate one of the three replicates sampled for each macrohabitat type. (c) and (d) are not to scale

Dam. The regulated reach is in a straight channel section in a confined valley where human interventions on the morphology are limited, while the semi-natural reach is situated in a glacial valley characterized by a wide alluvial plain where human interventions like channelization have increased the channel slope. Human activities have therefore potentially decreased habitat diversity in the plain of the unregulated reach (Gordon *et al.*, 1992). Because the reference site is not completely natural, the comparisons between the two reaches were less suitable for measuring the impact of constantly reduced discharge on invertebrate communities. However, the study sites were suitable for analysing the availability and potential vulnerability of the food supply and brown trout feeding habits in different habitat types.

In the regulated reach, the fish assemblage consisted exclusively of brown trout, while in the unregulated reach, 4.7% of the fish were sculpin (*Cottus gobio*, L.). Major interactions between these two species are possible, including predation on each other's eggs and larvae and competition for food resources or habitat (Foote and Brown, 1998). However, in the study reach, the low abundance of sculpin did not affect trout abundance (Baran, 1995) and could not have modified their feeding habits (see Hudson *et al.*, 1995).

General sampling design

In 1995, we analysed the structure and the growth of brown trout populations in the two reaches. In 1998, we analysed the structure of brown trout populations, as well as habitat characteristics, trout feeding habits and invertebrate traits. In the unregulated reach, we could only sample one side of the river because the current velocity was too high on the other side. However, the latter was unsuitable habitat for brown trout (Baran, unpublished data).

Chemical and physical habitat characteristics

In 1995, we measured conductivity, pH and dissolved oxygen with a 30 SCT YSI Conductivity Bridge, a pH 320 SET Microprocessor pH-Meter (WTW) and a 57 YSI dissolved oxygen meter, respectively. At the same time, we collected two water samples per reach, and analysed concentrations of calcium (Ca²⁺), ammonium (NH₄-N), nitrate (NO₃-N), phosphate (PO₄-P) and magnesium (Mg²⁺) using standard AFNOR methods (Rodier, 1984). We measured stream temperature every 40 minutes from September 1994 to January 1996 in the two reaches using Pekly Indic 8000 thermometers.

In July 1998, we identified representative macrohabitats in each reach in terms of their velocity and turbulence. We found two different macrohabitats in the unregulated reach (referred to as m1 and m2) and in the regulated reach (m3 and m4). Usual macrohabitat classifications did not accurately discriminate these

macrohabitats. According to the classification of Jowett (1993), m1 was a riffle, m2 and m3 were runs, and m4 was a pool. So, we ranked the macrohabitat types from 1 to 4 according to their Froude number (e.g. m1: flow most torrential; m4: flow least torrential; see Data analysis section and Table VI for macrohabitat description).

Three replicates per pair of macrohabitats were randomly chosen along each reach (Figure 1c and d). The surface area of the macrohabitats was quite similar within each reach (60% of m1 and 40% of m2 in the unregulated reach; 48% of m3 and 52% of m4 in the regulated reach). In the unregulated reach, the two replicates (m2₁ and m2₂) were separated by an island. We measured wetted widths and lengths as well as depth with a metre stick, velocity (at 0.2, 0.4 and 0.8 × depth) with an electromagnetic current meter (Flo-Mate, 2000 portable flow meter) and substrate characteristics by recording the largest size (maximum diameter) and height (level above the stream bed) of randomly selected particles. The grain size investigation included measurements of the largest size of four additional particles nearest to the location of each of about 30 randomly selected particles. Depth and velocity were recorded independently from particle size at about 30 locations regularly spaced across five transects per replicate.

Structure and growth of brown trout populations

In 1995 and 1998, we sampled fish at low flow (September) by electrofishing and using a removal method (i.e. two removals per reach and per sampling year; see De Lury, 1951). We measured total fish length (to the nearest millimetre) and weight (to the nearest gram) and in 1995, removed scales above the lateral line and behind the dorsal fin.

Potential food and trout diet

In July 1998, we collected the benthic fauna with a Surber sampler (mesh size = 250 µm, area sampled = 0.1 m²). Three samples were randomly taken from each macrohabitat replicate (i.e. nine samples per macrohabitat type and 18 per reach). We sampled drift and trout gut contents the day after collecting the benthos to avoid the effect that benthos sampling would have on the evaluation of drift and trout diet. We used both water column and surface drift nets (mesh size = 250 µm, length = 2 m), which had a rectangular opening (0.10 × 0.25 m and 0.15 × 0.25 m for water column and surface drift nets, respectively). Surface drift nets were submerged 5 to 10 cm into the water to sample only surface invertebrates, and water column drift nets were set at the average current velocity (60% of the depth). We used two column and surface drift nets in each macrohabitat (i.e. four samples were taken per macrohabitat type and eight per reach), upstream from the electrofishing area to avoid disturbance of the drift sampling.

One hour before dawn, we opened the drift nets from the bank to prevent invertebrates being dislodged. Water velocity was measured the day before and at the end of each sampling period in the opening of each net to determine the volume of water filtered over the time the drift nets were opened (generally 4–4:30h). Three hours after dawn, we collected trout for diet analysis by electrofishing each replicate of the macrohabitats (i.e. three samples were taken per macrohabitat type and six per reach). The fish were immediately anaesthetized using Tricaine Methanesulfonate (MS-222), and then weighed and measured. We collected the gut contents of fish by stomach flushing, a non-destructive method (Meehan and Miller, 1978). Because one purpose of the study was to analyse the effects of habitat characteristics on trout feeding habits, we analysed the gut contents of trout longer than 110 mm that occurred in each of the macrohabitat types. We preserved all invertebrate samples in formaldehyde (4%).

In the laboratory, we identified invertebrates to the lowest possible taxonomic level. We counted both aquatic and terrestrial items in benthos and drift samples, i.e. all invertebrates that could constitute a potential prey for trout. Terrestrial taxa occurring in the benthos were individuals which may have lain on the bottom substrate. Development stages of a taxon such as larva, pupa and pre-adult were considered as different taxa. Terrestrial invertebrates and aerial stages of amphibiotic insects were included in the terrestrial item category. We measured invertebrate length from the most anterior point of the head to the tip of the abdomen and grouped them by 1 mm size classes. We also estimated the wet-weight of gut contents to the nearest 0.1 mg with a microprecision balance (Mettler AE260 Delta Range).

Data analysis

We calculated total trout biomass (kg ha^{-1}) and density (number of individuals (ind ha^{-1})) per reach using the method of Seber and Le Cren (1967). We determined length–age relationships from scale readings (Francis, 1990). Growth curves were fitted using the Von Bertalanffy (1960) growth function. We calculated the ecological growth coefficient (*EGC*) that introduces a correction factor to the growth rate and allows comparisons among reaches having different temperature regimes (Preall and Ringler, 1989). This coefficient computes the ratio of the observed individual growth rate ($G\%_{obs}$) to the predicted maximum growth rate ($G\%_{max}$), as:

$$EGC = [G\%_{obs}/G\%_{max}] \times 100$$

with $G\%_{obs}$ and $G\%_{max}$ in percentage increase in wet body weight per day. $G\%_{max}$ was estimated using the growth model of Elliott *et al.* (1995), with monthly mean water temperatures (data from September 1994 to September 1995). The *EGC* of individuals allowed us to calculate the mean *EGC* of age classes.

We determined the food availability using the invertebrate density in the benthos (invertebrate abundance/surface sampled: ind m^{-2}) and in the drift (invertebrate abundance/volume of water filtered: ind m^{-3}). We then calculated the food availability per individual trout, by weighting the benthic and drifting invertebrate density by the trout density (invertebrate m^{-2} /trout m^{-2} and invertebrate m^{-3} /trout m^{-3}).

We analysed the potential vulnerability of food supply by the use of both habitat and invertebrate characteristics. First, we deduced the potential accessibility and conspicuousness of invertebrates on the bottom substrates and in the drift from the analysis of the structural complexity and flow characteristic of habitats. We combined the bottom substrate (see Wilzbach *et al.*, 1986) and water depth (see Braaten *et al.*, 1997) using the relative roughness, R_{rel} (Gordon *et al.*, 1992):

$$R_{rel} = k/D$$

where k is particle height (cm), and D is water depth (cm). We computed the mean water velocity and dimensionless hydraulic characteristics such as the Froude (F_r) and Reynolds (R_e) numbers:

$$F_r = V/\sqrt{gD}$$

$$R_e = VD/\nu$$

where V is mean water column velocity (cm s^{-1}) = $0.25(V_{0.2} + V_{0.8} + 2V_{0.4})$; g is gravity (cm s^{-2}), and ν is kinematic viscosity computed for 13 °C.

Second, to analyse the potential food accessibility in the full drift, we computed the invertebrate drift flow in the water column and at the surface (invertebrate abundance/(area of water column going through the drift net opening \times time sampled): $\text{ind m}^{-2}\text{s}^{-1}$). Third, several traits of invertebrates, such as their size, mobility, drift behaviour and morphological defences may affect trout foraging behaviour (Ware, 1973; Bannon and Ringler, 1986; Feldman and Savitz, 1999). Therefore, to estimate the potential vulnerability of food supply, we used two complementary approaches: (i) invertebrate length (directly measured on individuals); and (ii) Rader's (1997) model. The latter ranks amphibiotic invertebrates according to their likelihood of entering the drift and importance as a food resource for salmonids. In this model, the potential invertebrate vulnerability is based on their (i) tendency to drift intentionally; (ii) likelihood of being accidentally dislodged by the current described in terms of habitat use, flow exposure, mobility, body shape (the drag index which also included body width and height); (iii) drift distance; (iv) adult drift; (v) benthic exposure; and (vi) potential body size (so that our size measurements of invertebrates were not redundant with this potential size measure); and (vii) abundance. Scores of potential invertebrate vulnerability varied from low (*Bivalvia*: 2.0) to high (*Baetis*: 93.0) potential vulnerability.

We analysed trout prey consumption using the capture index (CI = abundance of prey items consumed/weight of the fish: ind g^{-1}) and the fullness index (FI = weight of fresh gut content/weight

of the fish: mg g^{-1}). The use of prey data divided by the fish weight gave an analysis that was unbiased by weight differences in the fish populations (Lauters *et al.*, 1996).

We analysed the characteristics of food supplies and trout diet using the taxonomic diversity (Simpson index S):

$$S = 1 - \sum_{j=1}^p p_{j/i}^2$$

(where i and j are the samples and the taxa respectively), the relative taxa abundance (abundance of invertebrate i / abundance of all invertebrates in the sample) and the percentage prey occurrence in trout gut contents (number of fish specimens containing the invertebrate i / total number of fish specimens).

We deduced brown trout foraging behaviour by calculating the prey-selection index (V) as described by Pearre (1982):

$$V = (a_d b_e - a_e b_d) / \sqrt{a \times b \times d \times e}$$

where a_d and a_e are the numbers of a given prey taxon in the diet and the environment respectively, b_d and b_e are the numbers of all other prey taxa in the diet and the environment, and $a = a_d + a_e$, $b = b_d + b_e$, $d = a_d + b_d$, $e = a_e + b_e$. V can range from -1 to $+1$, representing complete avoidance or inaccessibility and preference, respectively, while 0 indicates random feeding. We considered that prey items were preferred, randomly selected or avoided, when indices indicated the same trend in the three potential food supplies (benthos, water column and surface drift). The statistical significance of V was determined using χ^2 tables after calculating NV^2 (for one degree of freedom), where $N = a_d + a_e + b_d + b_e$. Only the most abundant invertebrate taxa (representing more than 5% of the total abundance in either benthos, column drift, surface drift or gut contents) were included in this analysis.

To determine differences in average invertebrate size, the large number of invertebrates measured allowed use of a paired t -test. To compare habitat characteristics, abundance, biomass and growth patterns of brown trout, invertebrate density, drift flow and trout prey consumption between the two reaches, we used one-way analysis of variance by ranks (Wilcoxon two-sample test) because of the smaller sample size. We compared habitat characteristics and benthic invertebrate density between each pair of macrohabitats using the same non-parametric test. To limit the overall experimental error rate, we tested each comparison using the Bonferroni correction. As these comparisons were not independent, we had to treat the probability tests (P) with caution.

RESULTS

Analyses on the reach scale

Chemical and physical habitat characteristics. The chemical characteristics of the water were similar for the two reaches (Table I). Mean annual and summer temperature were higher in the regulated than in the unregulated reach (Table II). The latter had a lower structural habitat complexity than the former (higher depth and lower relative roughness). However, the unregulated reach was faster flowing and had higher torrential characteristics.

Structure and growth of brown trout populations. In 1995 trout collections yielded 3912 ind ha^{-1} and 217 kg ha^{-1} in the unregulated reach, and 1768 ind ha^{-1} and 68 kg ha^{-1} in the regulated reach; and in 1998 yields were 1397 ind ha^{-1} and 77 kg ha^{-1} in the unregulated reach, and 454 ind ha^{-1} and 30 kg ha^{-1} in the regulated reach.

Trout growth in 1995 showed an excellent fit (unregulated: $r^2 = 0.995$; regulated: $r^2 = 0.993$) to the Von Bertalanffy growth function (Figure 2). Trout older than one year grew faster in the unregulated reach; their lengths by age were lower in the regulated reach (Wilcoxon, $P < 0.05$). The *EGC* decreased with increase in

Table I. Main characteristics and water chemistry of the reaches at the study sites (see Figure 1)

	Unregulated reach	Regulated reach
Altitude (m)	760	660
Slope (%)	1.05	1.10
Mean natural annual discharge in 1995 (m^3s^{-1})	14.0	20.0
Discharge in September 1995 (m^3s^{-1}) ^a	6.0	0.9
Discharge in July 1998 (m^3s^{-1}) ^b	9.2	1.2
pH	7.8	7.7
Conductivity ($\mu\text{S cm}^{-1}$)	124	120
Dissolved oxygen O_2 (mg l^{-1})	10.6	10.5
Calcium Ca^{++} (mg l^{-1})	22.8	24.2
Ammonium $\text{NH}_4\text{-N}$ (mg l^{-1})	<0.1	<0.1
Nitrate $\text{NO}_3\text{-N}$ (mg l^{-1})	1.4	1.2
Phosphate $\text{PO}_4\text{-P}$ (mg l^{-1})	<0.05	<0.05
Magnesium Mg^{++} (mg l^{-1})	0.95	1

^a Study of structure and growth of brown trout.

^b Study of structure of physical habitat and trophic relationships of brown trout.

Table II. Physical characteristics of the reaches

	Unregulated reach		Regulated reach		P
	n	$\bar{x} \pm 1\text{SE}$	n	$\bar{x} \pm 1\text{SE}$	
Mean annual temperature ($^{\circ}\text{C}$) ^a	18 640	8.8 ± 0.0	18 640	9.5 ± 0.0	***
Highest summer temperature ($^{\circ}\text{C}$) ^b	1116	13.3 ± 0.1	1116	15.1 ± 0.0	***
Width (m) ^c	21	18.1 ± 1.2	32	13.4 ± 0.6	***
Depth (cm) ^c	177	56.1 ± 1.3	191	29.0 ± 0.7	***
Grain size (cm) ^c	962	15.3 ± 0.6	1055	18.9 ± 0.8	***
Relative roughness (%)	194	22.6 ± 2.6	211	32.0 ± 2.0	**
Velocity (cm s^{-1}) ^c	177	90.7 ± 2.5	191	31.6 ± 1.5	***
Froude number	177	0.40 ± 0.01	191	0.20 ± 0.01	***
Reynolds number ($\times 10^6$)	177	0.38 ± 0.01	191	0.07 ± 0.00	***

Means ($\bar{x} \pm 1\text{SE}$) were compared using the Wilcoxon two-sample test, with * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. ns, tests not significantly different.

^a Measured from September 1994 to January 1996

^b Measured in August 1995

^c Measured in July 1998

fish age in both reaches, but for each age class older than one year, the *EGC* was higher in the unregulated than in the regulated reach (Table III).

Potential food and trout diet. The mean size of trout captured for diet analysis was higher in the unregulated reach (Table IV).

The total invertebrate density in the benthos and the column drift were higher in the unregulated reach, as well as the total invertebrate drift flow in the water column and at the surface (Table IV). However, the total invertebrate density at the surface, and the invertebrate density per trout individual in each of the potential food supplies, were similar between the two reaches.

The density of terrestrial invertebrates in the benthos was slightly higher in the unregulated reach, while their densities in the water column and the surface drift did not differ between reaches. The densities of terrestrial invertebrates per trout individual were similar for the two reaches in each of the potential food supplies. The drift flow of terrestrial invertebrates was similar at the surface of the two reaches, but was higher in the water column of the unregulated reach.

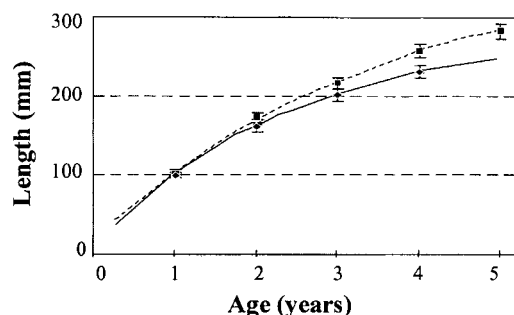


Figure 2. Length–age relationships of brown trout according to the Von Bertalanffy growth function. - - -, unregulated reach; —, regulated reach. Error bars represent ± 1 standard error of the calculated values

Table III. Mean ecological growth coefficient (*EGC*) (according to the model of Preall and Ringler, 1989)

Age (years)	Unregulated reach		Regulated reach		<i>P</i>
	<i>n</i>	$\bar{x} \pm 1SE$	<i>n</i>	$\bar{x} \pm 1SE$	
1	48	93.9 ± 4.3	50	90.1 ± 4.0	<i>ns</i>
2	23	85.8 ± 2.7	30	78.0 ± 2.9	**
3	16	64.3 ± 2.8	13	51.5 ± 2.5	**
4	10	48.4 ± 3.9	8	34.2 ± 3.0	**

Means ($\bar{x} \pm 1SE$) were compared using the Wilcoxon two-sample test. See Table II for further details.

None of the brown trout individuals had empty stomachs. The capture and fullness indices for total invertebrates were higher in the unregulated reach (Table IV). The capture index of terrestrial invertebrates was higher in the regulated reach, but the fullness indices were similar for the two reaches. The mean taxonomic diversity of the potential food supplies and of the trout diet was higher in the regulated reach.

Total invertebrates in the unregulated reach were larger in the column drift (*t*-test, $P < 0.001$) and the surface drift (*t*-test, $P < 0.001$) than in the regulated reach (Table V and Figure 3b and c). The average size differences of benthic invertebrates and prey consumed by brown trout between the two reaches was only 0.1 mm (Table V and Figure 3a and d) and was therefore within the error range of the measurements (we measured individuals to the nearest millimetre). In the two reaches, the size of total prey items was higher than the size of total invertebrates in each of the potential food supplies (*t*-test, $P < 0.001$).

In the unregulated reach, Orthocladiinae dominated the potential food supplies and were potentially highly vulnerable to predation (classification of Rader, 1997; Table V). Trout mainly consumed Chironomidae larvae (Orthocladiinae), pupae and pre-adults. However, the prey selection indices showed that trout tended to avoid Orthocladiinae (or this prey was less accessible to trout than predicted by its high abundance), and preferably selected Chironomidae pupae, although the latter were smaller than Orthocladiinae in each of the food supplies (*t*-test, $P < 0.001$).

In the regulated reach, Orthocladiinae, Simuliidae, Tanytarsini, Chironomidae pre-adults, *Baetis* and terrestrial invertebrates were the dominant taxa in one or more potential food supplies. Most of these taxa were potentially highly vulnerable to predation according to the classification of Rader (1997). Trout fed on *Baetis*, Simuliidae and terrestrial invertebrates. However, only Simuliidae were preferably selected by trout, although they were (i) less abundant than Orthocladiinae and both less abundant and potentially vulnerable than *Baetis* in each of the potential food supplies, and (ii) smaller than *Leuctra* in the total food supply (*t*-test, $P < 0.001$) and than Tanytarsini and *Serratella* in the water column (*t*-test, $P < 0.001$) and surface drift (*t*-test, $P < 0.001$).

Table IV. Mean size of captured trout for diet analysis, and main characteristics of food supplies and brown trout diets, in the reaches

		Unregulated reach		Regulated reach		P
		n	$\bar{x} \pm 1SE$	n	$\bar{x} \pm 1SE$	
Trout size (mm)		109	216.1 ± 7.5	115	201.9 ± 6.9	*
Total invertebrate						
Density (ind m ⁻²)	B	18	13 345 ± 2458	18	8283 ± 1210	*
Density (ind m ⁻³)	Dc	4	26.7 ± 2.2	4	4.3 ± 0.7	*
	Ds	4	16.2 ± 2.9	4	10.7 ± 4.3	ns
Density / trout density (ind trout ⁻¹)	B	18	115 178 ± 17 687	18	168 497 ± 28 204	ns
	Dc	4	15 268 ± 5180	4	3285 ± 1077	ns
	Ds	4	9011 ± 3629	4	6282 ± 3771	ns
Drift flow (ind m ⁻² s ⁻¹)	Dc	4	25.2 ± 3.1	4	1.6 ± 0.6	***
	Ds	4	16.0 ± 2.2	4	4.7 ± 1.9	***
CI (ind g ⁻¹)	Gc	109	3.08 ± 0.33	115	1.52 ± 0.18	***
FI (mg g ⁻¹)	Gc	109	5.60 ± 0.56	115	2.58 ± 0.23	***
Terrestrial invertebrates						
Density (ind m ⁻²)	B	18	107 ± 15	18	66 ± 17	*
Density (ind m ⁻³)	Dc	4	0.5 ± 0.1	4	0.3 ± 0.1	ns
	Ds	4	0.5 ± 0.1	4	2.7 ± 1.1	ns
Density / trout density (ind trout ⁻¹)	B	18	1095 ± 234	18	1050 ± 215	ns
	Dc	4	268 ± 87	4	203 ± 69	ns
	Ds	4	324 ± 145	4	1671 ± 1103	ns
Drift flow (ind m ⁻² s ⁻¹)	Dc	4	0.5 ± 0.1	4	0.1 ± 0.1	*
	Ds	4	0.5 ± 0.1	4	1.2 ± 0.5	ns
CI (ind g ⁻¹)	Gc	109	0.09 ± 0.01	115	0.41 ± 0.14	*
FI (mg g ⁻¹)	Gc	109	0.71 ± 0.28	115	0.47 ± 0.14	ns
Taxonomic diversity ^a	B	18	0.55 ± 0.03	18	0.84 ± 0.01	***
	Dc	4	0.45 ± 0.03	4	0.90 ± 0.00	***
	Ds	4	0.60 ± 0.04	4	0.76 ± 0.04	*
	Gc	109	0.63 ± 0.02	115	0.78 ± 0.02	***

Means ($\bar{x} \pm 1SE$) were compared using the Wilcoxon two-sample test. CI, capture index; FI, fullness index: B, benthos; Dc, column drift; Ds, surface drift; Gc, gut contents. See Table II for further details.

^a Simpson index for total invertebrates

Finally, high percentage occurrence of the prey predominantly consumed by trout displayed a low diet difference among trout individuals within each reach (Table V).

Analyses on the macrohabitat scale

Physical habitat characteristics. The two macrohabitats of the unregulated reach (m1 and m2) were deeper than m4, which in turn was deeper than m3 (Table VI). The grain size was larger in m2 than in m1, and in m3 than in m4, but was similar between m2 and m3. Therefore, the relative roughness was lower in m1 than in m2, m3 and m4. Current velocity, Froude and Reynolds numbers were higher in m1 and m2 than in m3 and m4. They were similar for m1 and m2, while m3 was faster flowing and had a higher Froude number than m4.

Structure of brown trout populations. Trout collections in 1998 yielded the following abundance and biomass: unregulated reach, 655 ind ha⁻¹ and 29 kg ha⁻¹ in m1 and 2261 ind ha⁻¹ and 131 kg ha⁻¹ in m2; regulated reach, 889 ind ha⁻¹ and 49 kg ha⁻¹ in m3 and 316 ind ha⁻¹ and 24 kg ha⁻¹ in m4.

Potential food and trout diet. The size of trout captured for diet analysis only differed between m1 and m4 (Table VII).

Table V. Invertebrate vulnerability to salmonids: scores (functional classification of Rader, 1997). Brown trout diet and characteristics of invertebrates on the reach scale

Reach	Taxan	Invertebrate vulnerability	Gut contents			Benthos			Column drift			Surface drift		
			%occ	%abund	size	%abund	size	V	%abund	size	V	%abund	size	V
Unregulated	Diptera													
	Orthocladinae	70.5	98.2	40.9 ± 2.3	5.0 ± 0.5	59.6 ± 3.8	3.3 ± 0.4	73.5 ± 2.2	3.9 ± 0.4	51.6 ± 7.0	3.5 ± 0.4	—	—	
	Simuliidae	79.5	78.9	5.8 ± 1.3	4.2 ± 0.5	16.3 ± 4.7	3.2 ± 0.5	6.5 ± 1.1	2.8 ± 0.5	3.6 ± 0.3	2.6 ± 0.4	0	0	
	pChironomidae	57.6	98.2	15.6 ± 1.0	3.4 ± 0.3	4.3 ± 0.6	3.1 ± 0.4	8.1 ± 0.5	3.3 ± 0.4	7.0 ± 0.7	3.1 ± 0.4	+	+	
	paChironomidae	70.5	78.9	17.6 ± 1.8	2.9 ± 0.3	0.7 ± 0.1	2.4 ± 0.5	3.7 ± 0.8	2.6 ± 0.4	30.7 ± 7.0	3.0 ± 0.4	+	—	
	Oligochaeta	12	5.5	0.4 ± 0.3	13.1 ± 6.5	6.9 ± 1.9	2.6 ± 0.6	0.6 ± 0.2	1.7 ± 0.2	0.4 ± 0.2	1.8 ± 0.3	—	—	
Total				4.4 ± 0.5	3.2 ± 0.5			3.6 ± 0.4		3.3 ± 0.4				
Regulated	Diptera													
	Orthocladinae	70.5	79.1	5.3 ± 2.2	3.6 ± 0.4	20.9 ± 2.7	2.7 ± 0.3	18.7 ± 1.3	2.8 ± 0.4	14.9 ± 3.8	2.8 ± 0.4	—	—	
	Simuliidae	79.5	92.2	20.9 ± 9.6	5.0 ± 0.4	10.7 ± 3.4	4.0 ± 0.6	10.2 ± 0.4	3.5 ± 0.6	2.6 ± 0.5	3.3 ± 0.6	++	++	
	Tanytopodinae	57.6	55.7	2.5 ± 1.8	5.7 ± 0.4	2.8 ± 2.4	3.2 ± 0.4	5.8 ± 0.4	4.0 ± 0.4	4.2 ± 1.8	3.9 ± 0.4	0	0	
	Tanytarsini	70.5	53.9	2.6 ± 2.1	3.9 ± 0.4	12.8 ± 2.4	3.0 ± 0.4	5.1 ± 0.9	2.9 ± 0.4	2.9 ± 1.3	3.0 ± 0.3	0	0	
	pChironomidae	57.6	60.0	2.2 ± 1.4	2.8 ± 0.3	3.6 ± 0.5	2.9 ± 0.3	7.0 ± 0.6	2.4 ± 0.3	7.3 ± 0.9	2.5 ± 0.3	—	—	
paChironomidae	70.5	0.0	0.0 ± 0.0	—	0.3 ± 0.1	2.5 ± 0.4	8.7 ± 1.8	2.2 ± 0.4	31.6 ± 5.5	2.4 ± 0.3	—	—		
Ephemeroptera														
<i>Baetis</i>	93	98.3	24.5 ± 6.6	5.1 ± 0.5	12.0 ± 2.3	2.6 ± 0.5	19.2 ± 0.8	2.8 ± 0.7	7.0 ± 0.7	3.3 ± 0.6	+	+		
<i>Serratella</i>	61.2	88.7	8.9 ± 4.3	5.8 ± 0.5	4.2 ± 0.9	3.9 ± 0.6	0.9 ± 0.1	3.8 ± 0.6	0.6 ± 0.3	3.5 ± 0.7	+	+		
Plecoptera														
<i>Leuctra</i>	30	36.5	0.9 ± 0.8	4.8 ± 0.4	6.5 ± 1.3	4.2 ± 0.4	0.4 ± 0.0	4.7 ± 0.4	0.1 ± 0.0	4.0 ± 0.7	0	0		
Hydracarina	NA	11.3	0.3 ± 0.6	0.6 ± 0.1	3.1 ± 0.8	0.7 ± 0.2	6.5 ± 0.2	0.8 ± 0.3	1.3 ± 0.3	0.9 ± 0.3	0	0		
Terrestrial inv.	NA	88.7	16.8 ± 8.5	3.6 ± 0.6	1.1 ± 0.3	2.1 ± 0.4	6.6 ± 0.6	2.2 ± 0.4	21.0 ± 2.0	2.3 ± 0.4	0	0		
Total				4.5 ± 0.6	3.1 ± 0.5			2.6 ± 0.5		2.5 ± 0.4				

Prey-selection indices (V) were derived from number of invertebrates in the trout gut contents and in the benthos, the column drift and the surface drift: ++, $V \geq 0.25$ strong preference; +, $0.10 \leq V < 0.25$ moderate preference; 0, $-0.10 < V < 0.10$ indifference; -, $-0.25 < V \leq -0.10$ moderate avoidance or inaccessibility; ---, $-0.50 < V \leq -0.25$ strong avoidance or inaccessibility; ---, $-0.50 > V$ very strong avoidance or inaccessibility. Blanks indicate not significant behaviour ($P > 0.01$) or no data. %occ, percentage occurrence; %abund, mean relative abundance ($\bar{x} \pm 1SE$); size, mean size ($\bar{x} \pm 1SE$) of invertebrates in mm; inv, invertebrates; p, pupa; pa, pre-adult; NA, data not available.

Table VI. Physical characteristics of the macrohabitats

	Unregulated reach				Regulated reach				P
	m1 (a)		m2 (b)		m3 (c)		m4 (d)		
	n	$\bar{x} \pm \text{ISE}$	n	$\bar{x} \pm \text{ISE}$	n	$\bar{x} \pm \text{ISE}$	n	$\bar{x} \pm \text{ISE}$	
Width (m) ^a	9	19.2 ± 1.2	12	12.4 ± 1.3	17	13.2 ± 0.9	15	13.6 ± 0.7	(ac), (ad), (bc), (bd)**
Depth (cm) ^a	89	54.1 ± 1.8	88	58.2 ± 1.7	98	25.5 ± 0.8	93	32.6 ± 1.1	(ac), (ad), (bc), (bd), (cd)***
Grain size (cm) ^a	472	23.3 ± 2.6	490	19.1 ± 0.9	535	21.3 ± 1.1	520	16.5 ± 0.9	(cd)**; (ab), (ac), (ad), (bd)***
Relative roughness (%)	96	15.0 ± 1.6	98	30.1 ± 4.9	107	34.3 ± 2.8	104	29.7 ± 2.7	(ab), (ac), (ad)***
Velocity (cm s ⁻¹) ^a	89	93.9 ± 4.2	88	87.3 ± 3.8	98	35.1 ± 2.4	93	27.0 ± 1.7	(ac), (ad), (bc), (bd)*** (cd)*
Froude number	89	0.43 ± 0.02	88	0.38 ± 0.02	98	0.23 ± 0.02	93	0.16 ± 0.01	(ac), (ad), (bc), (bd), (cd)***
Reynolds number (× 10 ⁶)	89	0.37 ± 0.02	88	0.37 ± 0.02	98	0.07 ± 0.01	93	0.07 ± 0.00	(ac), (ad), (bc), (bd)***

Means ($\bar{x} \pm \text{ISE}$) were compared between each pairs of macrohabitats (in brackets) using the Wilcoxon two-sample test (taking into account the Bonferroni correction). See Table II for further details.

^a Measured in July 1998

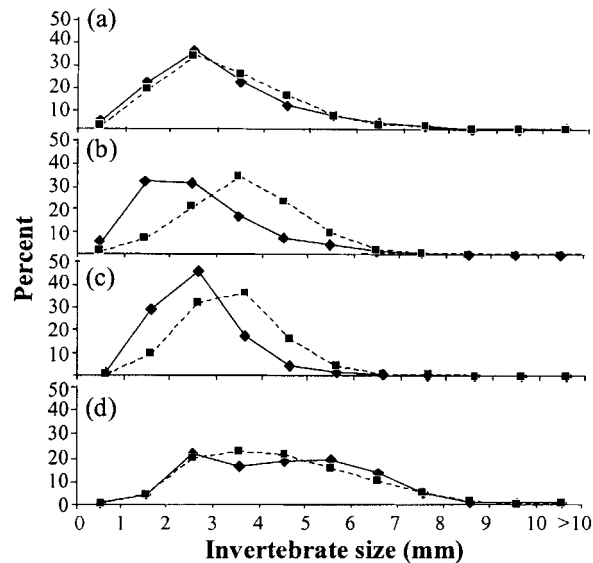


Figure 3. Size class distribution of total invertebrates in (a) the benthos, (b) the column drift, (c) the surface drift and (d) the gut contents. - - - , unregulated reach; —, regulated reach

The density of the total invertebrates in the benthos was similar for the four macrohabitats. However, the total benthic invertebrate density per trout individual was lower in m2 than in m4. In the column drift, total invertebrate density, density per trout individual and drift flow tended to be higher in m1 and m2 than in m3 and m4, while they tended to be similar in the surface drift. The density of terrestrial invertebrates in the benthos was similar in m1, m2 and m3 but lower in m4 than in m1. Their density per trout individual was similar in m2, m3 and m4 but higher in m1 than in m2.

The indices of capture and fullness of total invertebrates were higher in the two macrohabitats of the unregulated reach, but were similar for m1 and m2 and for m3 and m4. Concerning terrestrial invertebrates, the capture index was highest in m4 and the fullness index was higher in m1 and m4 than in m3.

The mean taxonomic diversity of the total benthic invertebrates was higher in the two macrohabitats of the regulated reach, but was similar between the macrohabitats of each reach. Similarly for water column and surface drift, the total invertebrate diversity tended to be higher in the regulated reach, and was similar between the macrohabitats of each reach. The total invertebrate diversity in trout gut contents was highest in m4, followed in decreasing order by m3, m1 and m2.

Total invertebrates in the water column and surface drift were smaller in m3 and m4 than in m1 (t -test: $P < 0.001$) and m2 (t -test: $P < 0.001$) (Table VIII and Figure 4b and c). The average size differences of benthic invertebrates and prey consumed by brown trout between the macrohabitats varied from 0.1 to 0.6 mm (Table VIII and Figure 4a and d) and were within the error range of the measurements.

In m1 and m2, the benthos and the column drift were mainly composed of Orthocladiinae, and the surface drift of both Orthocladiinae and Chironomidae pre-adults (Table VIII). In these two macrohabitats, trout mainly consumed Orthocladiinae and Chironomidae pupae and pre-adults. The Chironomidae pupae were predominantly selected in m1 only, although this taxon was smaller than Orthocladiinae in the total food supplies (t -test, $P < 0.001$). In m3, Simuliidae, *Baetis* and Orthocladiinae dominated the benthos, while in m4 the benthos mainly included Orthocladiinae, Tanytarsini and *Leuctra*. In these two macrohabitats, *Baetis*, Orthocladiinae, Chironomidae pre-adults and terrestrial invertebrates dominated the drift. In m3, trout fed on *Baetis* as encountered, and preferred Simuliidae and *Serratella* which were both potentially highly vulnerable to drift-feeders. In m4, trout consumed *Baetis*, terrestrial invertebrates and *Serratella* as encountered.

Finally, the high percentage occurrence of these dominant prey items displayed a low diet difference among trout individuals within each macrohabitat.

Table VII. Mean size of captured trout for diet analysis, and main characteristics of food supplies and brown trout diets in the macrohabitats

	m1 (a)		m2 (b)		m3 (c)		m4 (d)		P
	n	$\bar{x} \pm \text{ISE}$	n	$\bar{x} \pm \text{ISE}$	n	$\bar{x} \pm \text{ISE}$	n	$\bar{x} \pm \text{ISE}$	
Trout size (mm)	59	218.7 ± 6.0	50	213.9 ± 6.6	55	205.01 ± 5.1	60	199.8 ± 4.8	(ad)*
Total invertebrates									
Density (ind m ⁻²)	B	10 357 ± 1385	9	16 333 ± 4641	9	9 181 ± 2060	9	7 386 ± 1333	ns
Density (ind m ⁻³)	Dc	(27.0–32.1)	2	(21.5–26.4)	2	(3.2–5.3)	2	(2.0–5.7)	–
	Ds	(10.2–23.9)	2	(14.5–16.2)	2	(14.2–19.0)	2	(0.3–19.6)	–
Density/trout density(ind trout ⁻¹)	B	158 117 ± 21 151	9	72 239 ± 20 524	9	103 275 ± 23 172	9	233 720 ± 42 193	(bd)*
	Dc	(22 022–26 189)	2	(5767–7094)	2	(941–1569)	2	(2159–6000)	–
	Ds	(8335–19479)	2	(3886–4345)	2	(4161–5588)	2	(352–20 804)	–
Drift flow (ind m ⁻² s ⁻¹)	Dc	(27.1–30.1)	2	(16.0–27.5)	2	(1.1–3.8)	2	(0.5–1.6)	–
	Ds	(10.3–21.0)	2	(15.7–16.9)	2	(8.1–8.2)	2	(0.1–6.9)	–
CI (ind g ⁻¹)	Gc	3.13 ± 0.53	50	3.02 ± 0.38	55	1.42 ± 0.16	60	1.60 ± 0.30	(ac), (ad)*; (bc), (bd)***
FI (mg g ⁻¹)	Gc	5.46 ± 0.76	50	5.78 ± 0.82	55	2.68 ± 0.33	60	2.50 ± 0.33	(ac), (ad), (bc), (bd)*
Terrestrial invertebrates									
Density (ind m ⁻²)	B	114 ± 22	9	100 ± 22	9	102 ± 27	9	30 ± 10	(ad)*
Density (ind m ⁻³)	Dc	(0.5–0.5)	2	(0.3–0.6)	2	(0.3–0.5)	2	(0.1–0.4)	–
	Ds	(0.5–0.9)	2	(0.3–0.5)	2	(3.8–3.9)	2	(0.0–5.6)	–
Density/trout density (ind m ⁻²)	B	1747 ± 342	9	442 ± 96	9	1150 ± 306	9	949 ± 316	(ab)*
	Dc	(392–459)	2	(83–157)	2	(76–149)	2	(61–401)	–
	Ds	(395–702)	2	(70–127)	2	(1118–1140)	2	(48–5878)	–
Drift flow (ind m ⁻² s ⁻¹)	Dc	(0.5–0.5)	2	(0.2–0.6)	2	(0.1–0.4)	2	(0.0–0.1)	–
	Ds	(0.5–0.8)	2	(0.3–0.5)	2	(1.7–2.2)	2	(0.0–2.0)	–
CI (ind g ⁻¹)	Gc	0.08 ± 0.01	50	0.11 ± 0.03	55	0.14 ± 0.04	60	0.66 ± 0.27	(ad), (bd), (cd)*
FI (mg g ⁻¹)	Gc	0.49 ± 0.14	50	0.97 ± 0.58	55	0.29 ± 0.15	60	0.64 ± 0.22	(ac), (cd)*
Taxonomic diversity	B	0.57 ± 0.04	9	0.53 ± 0.04	9	0.85 ± 0.02	9	0.83 ± 0.02	(ad), (bd)**; (ac), (bc): ***
	Dc	(0.35–0.41)	2	(0.45–0.50)	2	(0.89–0.91)	2	(0.88–0.91)	–
	Ds	(0.63–0.66)	2	(0.47–0.62)	2	(0.73–0.75)	2	(0.65–0.85)	–
	Gc	0.67 ± 0.02	50	0.59 ± 0.02	55	0.75 ± 0.02	60	0.81 ± 0.02	(ac)*; (ab)**; (ad), (bc), (bd), (cd)***

Means ($\bar{x} \pm \text{ISE}$) were compared between each pairs of macrohabitats (in brackets) using the Wilcoxon two-sample test (taking into account the Bonferroni correction). For $n = 2$, we give the minimum and maximum values (in brackets), and did not apply the two-sample test. See Tables II and IV for further details.

Table VIII. Brown trout diet and characteristics of invertebrates on the macrohabitat scale

Habitat	Taxon	Gut contents			Benthos			Column drift			Surface drift		
		%occ	%abund	size	%abund	size	V	%abund (min-max)	size	V	%abund (min-max)	size	V
m1	Diptera												
	Orthocladinae	96.6	34.5 ± 2.9	5.2 ± 0.5	61.8 ± 4.2	3.3 ± 0.4	--	(75.0–78.9)	3.9 ± 0.4	--	(38.2–45.0)	3.6 ± 0.4	0
	Simuliidae	72.9	4.5 ± 1.5	4.1 ± 0.4	11.8 ± 3.6	2.9 ± 0.4	--	(4.3–6.0)	3.0 ± 0.4	--	(2.7–4.2)	2.7 ± 0.4	0
	pChironomidae	98.3	18.4 ± 1.6	3.7 ± 0.3	5.0 ± 0.8	2.9 ± 0.3	+	(6.7–8.7)	3.6 ± 0.4	+	(5.0–8.3)	3.1 ± 0.4	+
	paChironomidae	86.4	19.5 ± 2.4	2.9 ± 0.3	0.7 ± 0.1	2.4 ± 0.4	++	(2.0–4.9)	2.7 ± 0.4	++	(34.6–46.1)	3.0 ± 0.4	--
	Oligochaeta	3.4	0.5 ± 0.5	20.3 ± 7.2	8.5 ± 3.4	3.6 ± 0.6	--	(0.2–0.2)	1.7 ± 0.3	0	(0.3–0.8)	1.8 ± 0.3	--
Total			4.5 ± 0.6		3.3 ± 0.5			3.8 ± 0.4			3.3 ± 0.4		
m2	Diptera												
	Orthocladinae	100.0	48.4 ± 3.4	4.8 ± 0.5	57.4 ± 6.6	3.4 ± 0.5	0	(68.4–71.9)	3.8 ± 0.4	--	(52.7–70.6)	3.5 ± 0.4	--
	Simuliidae	86.0	7.4 ± 2.1	4.2 ± 0.5	20.9 ± 8.8	3.3 ± 0.5	--	(6.0–9.6)	2.7 ± 0.4	--	(3.7–3.7)	2.9 ± 0.5	0
	pChironomidae	98.0	12.3 ± 1.1	3.4 ± 0.3	3.6 ± 0.8	3.1 ± 0.3	+	(7.9–8.9)	3.1 ± 0.3	0	(7.2–7.7)	3.1 ± 0.4	0
	paChironomidae	70.0	15.4 ± 2.8	3.0 ± 0.3	0.8 ± 0.2	2.4 ± 0.5	++	(2.8–5.3)	2.5 ± 0.3	+	(12.3–29.9)	3.0 ± 0.3	--
	Oligochaeta	8.0	0.3 ± 0.2	2.3 ± 0.3	5.3 ± 1.6	1.9 ± 0.3	--	(0.9–0.9)	1.7 ± 0.2	0	(0.1–0.4)	2.0 ± 0.4	--
Total			4.3 ± 0.5		3.2 ± 0.5			3.5 ± 0.4			3.3 ± 0.4		
m3	Diptera												
	Orthocladinae	87.3	6.4 ± 0.7	3.8 ± 0.5	17.9 ± 1.6	3.0 ± 0.4	--	(12.3–17.2)	3.0 ± 0.3	--	(5.4–5.7)	2.9 ± 0.3	0
	Simuliidae	94.5	34.1 ± 3.3	5.0 ± 0.4	21.0 ± 5.4	4.0 ± 0.6	+	(7.9–12.8)	3.6 ± 0.6	++	(2.2–2.6)	3.3 ± 0.7	++
	Tanytopodinae	36.4	1.1 ± 0.3	5.6 ± 0.4	1.8 ± 0.3	3.7 ± 0.4	0	(3.6–7.2)	4.2 ± 0.4	--	(1.3–1.8)	4.1 ± 0.4	0
	Tanytarsini	41.8	1.1 ± 0.3	3.7 ± 0.3	6.1 ± 1.9	3.1 ± 0.4	--	(1.8–3.6)	3.2 ± 0.5	0	(0.3–1.6)	3.1 ± 0.4	--
	pChironomidae	49.1	1.5 ± 0.4	2.5 ± 0.2	2.7 ± 0.5	2.5 ± 0.2	0	(8.5–10.3)	2.4 ± 0.2	--	(4.8–9.9)	2.5 ± 0.3	--
paChironomidae	0.0	--	--	0.5 ± 0.1	2.6 ± 0.4	0	(11.4–20.9)	2.1 ± 0.4	--	(43.9–44.0)	2.6 ± 0.3	--	

Ephemeroptera	98.2	25.6 ± 2.0	5.0 ± 0.5	18.2 ± 3.8	2.4 ± 0.5	0	(15.0–17.7)	2.9 ± 0.7	+	(8.3–8.5)	3.4 ± 0.6	++
<i>Baetis</i>	85.5	5.9 ± 0.7	5.7 ± 0.5	1.8 ± 0.7	3.5 ± 0.6	+	(1.2–1.6)	3.8 ± 0.5	+	(0.1–0.4)	3.8 ± 0.6	+
Plecoptera	25.5	0.6 ± 0.2	4.7 ± 0.3	4.0 ± 1.7	3.9 ± 0.4	–	(0.2–0.2)	4.3 ± 0.3	0	(0.1–0.1)	4.5 ± 0.9	0
<i>Leuctra</i>	7.3	0.3 ± 0.2	0.5 ± 0.0	1.3 ± 0.4	0.8 ± 0.3	0	(5.4–6.7)	0.8 ± 0.3	–	(1.7–1.8)	0.9 ± 0.3	0
Hydracarina	85.5	9.9 ± 1.6	4.1 ± 0.7	1.9 ± 0.6	2.2 ± 0.4	+	(8.1–9.5)	2.3 ± 0.4	0	(20.4–26.9)	2.4 ± 0.4	–
Terrestrial inv.			4.8 ± 0.5		3.2 ± 0.5			2.6 ± 0.5			2.6 ± 0.4	
Total												
Diptera	71.7	4.4 ± 0.6	3.4 ± 0.3	24.0 ± 5.5	2.5 ± 0.3	--	(15.2–26.0)	2.6 ± 0.4	--	(17.8–27.8)	2.7 ± 0.4	--
Orthocladinae	90.0	8.9 ± 1.1	4.8 ± 0.4	0.4 ± 0.2	2.7 ± 0.4	+	(9.4–10.6)	3.5 ± 0.6	0	(1.4–5.6)	3.0 ± 0.6	+
Simuliidae	73.3	3.8 ± 0.7	5.7 ± 0.4	3.8 ± 0.7	3.1 ± 0.4		(5.0–7.1)	3.8 ± 0.4	0	(0.4–8.5)	3.4 ± 0.4	0
Tanypodinae	65.0	4.1 ± 0.8	4.0 ± 0.4	19.5 ± 3.8	3.0 ± 0.4	–	(2.9–11.4)	2.7 ± 0.4	0	(0.0–6.3)	2.9 ± 0.4	
Tanytarsini	70.0	3.0 ± 0.4	3.0 ± 0.3	4.5 ± 0.8	2.5 ± 0.2	0	(3.9–7.0)	2.3 ± 0.3	0	(6.8–8.3)	2.6 ± 0.3	–
pChironomidae	0.0	0.0 ± 0.0	—	0.1 ± 0.1	2.2 ± 0.4	0	(3.0–5.2)	2.2 ± 0.3	–	(19.4–25.4)	2.2 ± 0.3	--
paChironomidae												
Ephemeroptera	98.3	23.5 ± 2.0	5.3 ± 0.4	5.8 ± 1.1	3.0 ± 0.6	++	(18.4–24.1)	2.7 ± 0.7	0	(5.6–6.4)	3.1 ± 0.8	++
<i>Baetis</i>	91.7	11.7 ± 1.6	5.8 ± 0.5	6.6 ± 1.6	4.0 ± 0.6	0	(0.3–1.0)	3.9 ± 0.8	+	(0.0–1.2)	–	+
<i>Serratella</i>												
Plecoptera	46.7	1.1 ± 0.2	4.8 ± 0.4	9.0 ± 2.0	4.3 ± 0.4	–	(0.2–0.6)	5.0 ± 0.6	0	(0.0–0.1)	3.5 ± 0.9	0
<i>Leuctra</i>	15.0	0.3 ± 0.1	0.8 ± 0.3	5.0 ± 1.5	0.7 ± 0.2	–	(5.7–7.5)	0.7 ± 0.2	–	(0.0–1.4)	0.9 ± 0.3	0
Hydracarina	91.7	23.1 ± 3.0	3.5 ± 0.6	0.3 ± 0.1	2.0 ± 0.4	++	(2.8–7.0)	1.8 ± 0.4	++	(19.1–19.4)	2.2 ± 0.4	0
Terrestrial inv.												
Total												

See Tables V and VII for vulnerability scores of taxa and further details.

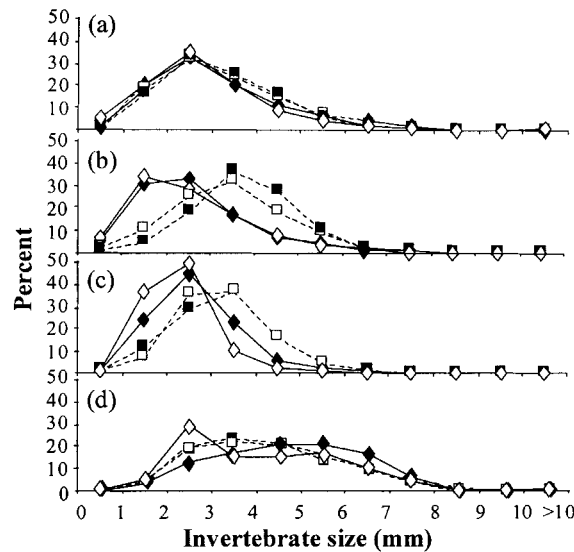


Figure 4. Size class distribution of total invertebrates in (a) the benthos, (b) the column drift, (c) the surface drift and (d) the gut contents. - - - , unregulated reach; □, m2; ■, m1; —, regulated reach; ◆, m3; ◊, m4

DISCUSSION

Analyses on the reach scale

In the unregulated reach, trout grew faster than in the regulated reach. Fish growth depends on both biotic (fish competition, food availability) and abiotic factors (water chemistry and temperature, availability of suitable habitats for feeding and hiding; Jobling, 1994). In the Neste d'Aure, differences in trout growth appeared to be independent of fish competition, water chemistry and temperature because (i) trout density and biomass were lower in the regulated than in the unregulated reach; (ii) water chemistry was similar for the two reaches; and (iii) temperature-independent trout growth, measured by the ecological growth coefficient (*EGC*), was lower in the regulated reach. Thus, the lower trout growth in the regulated reach may have resulted from a lack of suitable habitat for feeding and hiding (Baran *et al.*, 1995), and/or from alteration in food availability or potential vulnerability. However, as field surveys were carried out at two different periods (trout growth in 1995; trophic patterns of trout in 1998), we cannot evaluate how trout growth varied relative to food supply.

In the regulated reach, we found a decrease in total prey consumption by trout (i.e. capture and fullness indices), and an increase in the use of terrestrial items (i.e. capture index) and in the diet diversity. Hunt (1975) stated that a high contribution of terrestrial invertebrates to trout diet indicates a shortage of food of aquatic origin. Moreover, optimal foraging theory predicts that at low food availability, predators should use items of lower value and diversify their diets (Krebs and McCleery, 1984). Hence, trout appeared to be more food-limited in the regulated than in the unregulated reach. In the latter, the availability of food supplies (i.e. the overall abundance of invertebrates in the benthos and in the drift) was higher. However, because trout density was also higher in the unregulated reach, the availability of food supplies per trout individual was similar for the two reaches. Thus, trout prey consumption appeared to vary independently of the availability of potential food supplies per trout individual, suggesting that differences in invertebrate vulnerability (i.e. accessibility, conspicuousness and ease of handling) were also involved.

Analyses on both habitat and invertebrate characteristics suggest that food supply was potentially more vulnerable in the unregulated reach. In the latter reach, we observed that (i) the lower structural habitat complexity (i.e. lower relative roughness; Table II) may have favoured the accessibility of suitable feeding microhabitat or trout foraging efficiency (Wilzbach *et al.*, 1986; Braaten *et al.*, 1997); (ii) the higher current velocity and invertebrate drift flow may have increased the encounter rate of trout with potential prey (Nislow

et al., 1999); (iii) the larger sizes of potential prey in the water column drift (1 mm; Table V) and at surface (0.8 mm) may have facilitated size-selective feeding by trout; and (iv) other invertebrate traits (e.g. habitat, flow exposure) may have promoted prey capture efficiency by trout, the proportion of potentially highly vulnerable invertebrates (e.g. Orthocladiinae, Chironomidae pre-adults and pupae, Simuliidae, *Baetis*, *Serratella*, Heptageniidae; cf. Rader, 1997) being higher than in the regulated reach (84.6% versus 60.8%, respectively).

However, according to the classification of Rader (1997), Orthocladiinae should be vulnerable because of their high abundance, but have a low potential vulnerability to drift-feeders because of a low tendency to drift, to move and to be exposed at the surface of the bottom substrate. In the unregulated and regulated reaches, trout avoided this taxon despite its high availability in the total food supply and its large size. Instead, trout preferred (i) Chironomidae pupae, which were preferably selected in the unregulated reach, and (ii) *Baetis* and terrestrial invertebrates, which constituted the dominant prey used in the regulated reach. Hence, particular traits of Orthocladiinae may have made them less vulnerable than predicted by Rader's classification (1997). If Orthocladiinae are excluded, the proportion of potentially highly vulnerable taxa becomes higher in the regulated than in the unregulated reach (39.9% and 25.0%, respectively).

Hence, the differences in trout prey consumption may be due to changes in the availability of large-sized invertebrates and in their vulnerability due to habitat characteristics. Correspondingly, the potential food availability was less relevant than the potential invertebrate accessibility for explaining differences in trout growth (Greenberg and Dahl, 1998), foraging efficiency and habitat use (Hill and Grossman, 1993). In the unregulated reach, the low proportion of potentially highly vulnerable taxa (as indicated by their habitat, mobility and exposure on the substrate) may have been balanced by their high availability in the total food supply, and their high vulnerability due to both their large sizes and their accessibility on the bottom substrate and in the full drift (low structural habitat complexity and high invertebrate drift flow). In contrast, in the regulated reach, the higher proportion of potentially highly vulnerable taxa may not have balanced their low availability in the total food supply, and their low vulnerability due to both their small sizes and low potential accessibility and conspicuousness on the bottom substrate and in the full drift (high structural habitat complexity and low invertebrate drift flow).

Analyses on the macrohabitat scale

The gut contents we have analysed in this study should have represented the macrohabitat where individuals were captured, because diel movements of trout tend to be restricted in summer (Bunnell *et al.*, 1998), and trout occupy a particular location from which short trips (<2 m) are made to capture drifting invertebrates (Bachman, 1984). In both macrohabitats of the regulated reach (i.e. m3 and m4), we found a decrease in total prey consumption by trout (i.e. capture and fullness indices) and an increase in trout diet diversity if compared to the two macrohabitats of the unregulated reach (i.e. m1 and m2) (Table VII). Within each reach, we observed no effect of macrohabitat on total prey consumption by brown trout, confirming results of Magoulick and Wilzbach (1998). However, in pools (m4), trout diet was more diversified and consumption of terrestrial invertebrates was higher than in the three other macrohabitats. These results corresponded with those obtained on the reach scale and suggested that (i) there were no macrohabitat-specific differences in the total prey consumption; and (ii) trout appeared to be more food-limited in pools than in riffles.

Frankiewicz *et al.* (1993) stated that on a local scale, trout feeding habits were more influenced by intra-specific competition in slow-flowing areas and by current velocity in fast-flowing areas. Our results suggest that changes in habitat characteristics within reaches led to differences in both food availability per trout individual and potential invertebrate vulnerability, which in turn may have affected trout diet, foraging efficiency and strategy.

In m1, trout preferably selected Chironomidae pupae, while in m2, they did not consistently select any of the prey items. Neither flow characteristics nor the composition of invertebrate communities could explain these differences as they were quite similar for the two macrohabitats (Tables VI and VIII). However, in m2, the lower availability of benthic food supply per trout individual and the higher structural habitat complexity may have altered the invertebrate accessibility, conspicuousness and ease of handling on the bottom substrate and in the drift, and may explain the differences in brown trout selective behaviour.

In m3, trout preferably selected Simuliidae and *Serratella*, while in m4 they used more terrestrial items but did not consistently select any of the prey items. This shift in brown trout diet and selective behaviour confirmed that the use of terrestrial invertebrates was inversely correlated with current velocity (Heinimaa and Erkinaro, 1999), and suggested differences in food vulnerability between the two macrohabitats. Invertebrate vulnerability as indicated by their measured size was similar between m3 and m4, and cannot therefore explain differences in brown trout diets. In contrast, both habitat and invertebrate characteristics varied between the two macrohabitats.

In m3, the high velocities should have created suitable microhabitats for feeding, especially for the larger fish (Bachman, 1984), involving a high accessibility of drifting invertebrates. However, the low depth may have reduced the accessibility of suitable microhabitats for feeding (Braaten *et al.*, 1997). In this fast-flowing area, most of the benthic invertebrates were potentially highly vulnerable to predation (72.6% and 56.5% without Orthoclaadiinae), because of their active drift behaviour and/or their high exposure to the flow. This may have balanced the low availability and accessibility of drifting invertebrates, leading trout to specialize on potentially highly accessible and conspicuous amphibiotic invertebrates on the bottom substrate (Simuliidae and *Serratella*).

In m4, the low food accessibility in the drift due to the low velocities, could have been balanced by the higher availability of food supply per trout individual than in m3, but may have been out of balance because of the low vulnerability of the food supply. In this slow-flowing area, potentially highly vulnerable benthic invertebrates were in the minority (43.9% and 18.8% without Orthoclaadiinae). Most of the organisms were potentially poorly accessible and conspicuous because of their hyporheic habitat (*Leuctra*), their low tendency to drift and/or their low mobility (Tanytarsini). Thus, particular traits of these large-sized and abundant taxa in the benthos may have led trout to use either less abundant taxa having traits making them more vulnerable (*Serratella*), or small-sized energetically less profitable taxa (*Baetis*, terrestrial invertebrates) but more available and accessible in the drift.

CONCLUSION AND PERSPECTIVES

Although the growth model of Elliott *et al.* (1995) predicts growth for fish fed to satiation, it could be successfully applied to our two trout populations. Thus, as food supply alters fish growth patterns (Cada *et al.*, 1987), the model may be useful for comparing trophic conditions for lotic salmonids among stream reaches. In addition, our results suggest that the estimate of availability of suitable microhabitats for feeding (see Baran *et al.*, 1995), combined with the analysis of invertebrate drift flow and vulnerability, illustrates the trophic conditions for trout better than the overall abundance of potential food supplies. Similarly, Sagar and Glova (1995) showed that the abundance and biomass of drifting invertebrates described potential prey availability better than the abundance and biomass of benthic invertebrates, and Nislow *et al.* (1999) used prey encounter rates to model habitat suitability for Atlantic salmon. Therefore, invertebrate drift and vulnerability should be relevant ecological descriptors of salmonid habitat suitability.

Our two-scale approach gave a complementary picture of trophic patterns and processes. On the reach scale, invertebrate drift flow explained how changes in food accessibility for brown trout may have affected their prey consumption in the regulated reach, despite the fact that the composition of invertebrate communities and brown trout feeding habits depend on local habitat patterns (Frankiewicz *et al.*, 1993). However, considering the macrohabitat scale provided a finer and more realistic analysis of trout feeding habits and came closer to a functional habitat approach.

The analysis of relative invertebrate abundance, real invertebrate sizes and particular traits (e.g. habitat use, drift behaviour) showed the relevance of the ecological, behavioural or morphological traits of prey for estimating their potential vulnerability to predators, and for explaining switches in brown trout diets. According to several authors, prey abundance and size are traits that predominantly affect prey choice by brown trout (e.g. Bannon and Ringler, 1986). Our results confirmed that whatever the food availability, brown trout were size-selective and fed on the most abundant taxa. However, the analysis of prey selection by trout at the taxon level showed that trout preferences were not always related to prey size or abundance, as in

previous observations (Bryan and Larkin, 1972; Sagar and Glova, 1995). These preferences may also depend on invertebrate habitat use, mobility and other traits, confirming that an estimate of the potential vulnerability of food supply to fish predators has to address multiple invertebrate traits.

In this context, the functional classification of Rader (1997) was helpful for understanding differences in brown trout diet and foraging strategy between the slower and faster flowing macrohabitats of the regulated reach. Nevertheless, we observed some contradictions among the invertebrate scores and prey preferences by trout, suggesting that traits other than those already used may have affected prey vulnerability. For instance, the potential vulnerability of a given taxon may have also depended on its development stages (e.g. Chironomidae pupae were more selected than larvae and pre-adults), and on habitat patterns (e.g. Simuliidae were only selected in the regulated reach). Thus, to improve the estimate of the vulnerability of food supply, (i) more traits such as invertebrate development stages and/or anti-predator strategies should be taken into account; and (ii) the relative importance of physical habitat features and prey traits on the invertebrate vulnerability should be analysed in different habitat types. Moreover, brown trout habitat use and diet vary according to trout size, suggesting that the relative importance of traits that make prey vulnerable may also vary according to trout size. Thus, the analysis of prey traits predominantly used by small, medium and large trout should enable to better determine factors that may affect trout foraging behaviour and to improve estimates of trout habitat suitability.

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