Effects of pulsed discharges from a hydropower station on summer diel feeding activity and diet of brown trout (*Salmo trutta* Linnaeus, 1758) in an Iberian stream

Running head: Effects of pulsed discharges on feeding activity of brown trout

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Summary

The influence of pulsed discharges associated with hydroelectric power generation (i.e. hydropoeaking) on feeding activity and diet composition of adult brown trout (*Salmo trutta*) was studied during summer by comparing two sites: upstream (control site) and downstream from a power plant (hydropoeaking site). Twenty fish were captured from each study site by electrofishing at four-hour intervals for two consecutive days and stomach contents were collected with pulsed gastric lavage. Hydropoeaking events affected brown trout feeding behaviour as well as prey availability. Feeding intensity, measured by the stomach Fullness Index, showed pronounced variations with maximum values after flow pulses, which were linked to variations in prey availability because of increased drift rates of invertebrates. In contrast, brown trout living at the control site showed smoother variations of feeding activity not linked to invertebrate drift. Overall, brown trout at the hydropoeaking site had higher food consumption rates and a more generalist and heterogeneous diet than trout from the control site, indicating an opportunistic feeding behaviour during flow pulses. Therefore, the hydrological disturbance caused by hydropoeaking did not appear to cause direct negative impacts on feeding of adult brown trout. However, reduced trout density and imbalanced size structure in the hydropoeaking site were detected, requiring further research to clarify the spatial influence of hydropoeaking on other factors that could negatively affect brown trout populations.
Introduction

In regulated rivers, pulsed discharges from hydropower plants associated with temporal distribution of energy demands (known as hydropoeaking) result in significant hourly and diel fluctuations in streamflow, depth, and water velocity. This represents a challenging environment for biota, and negative effects on benthic invertebrates and fish populations have been reported (Moog, 1993; Liebig et al., 1999; Bruno et al., 2013). In the Iberian Peninsula, more than 1600 hydroelectric power plants are in operation (Montes et al., 2005), most of them in mountain rivers inhabited by the brown trout (*Salmo trutta* Linnaeus, 1758). There is an increasing need to conserve and enhance native brown trout populations in the Iberian Peninsula, which have declined due to several factors, such as overfishing (Almodóvar and Nicola, 2004), genetic introgression (Aparicio et al., 2005), river fragmentation (Gosset et al., 2006) and altered flow regimes caused by dams (Almodóvar and Nicola, 1999). In order to counteract these negative impacts, a better understanding of trout ecology in regulated riverine systems is required to implement better management decisions and contribute more effectively to fish and ecosystem conservation.

Brown trout in streams are visual foragers that mainly feed on invertebrate drift but also on benthos, and display high dietary plasticity (Elliott, 1973; Bachman, 1984). Flow pulses associated to hydropoeaking operations are reported to alter invertebrate drift patterns which could change the availability of food supply for brown trout (Céréghino et al., 2002; Lagarrigue et al., 2002). Since consumption rates and the level of energy intake influence growth and, ultimately, survival (Elliott, 1976), further knowledge on how trout populations would adapt their...
feeding patterns to these altered environments is important to clarify the factors that could have an impact on such populations.

The aim of the study was to examine the influence of hydropeaking operations on prey availability, feeding activity, diet composition and feeding strategy of adult brown trout in an upper reach of the river Noguera Pallaresa, a Pyrenean stream of the Mediterranean basin.

**Materials and methods**

**Study area**

The river Noguera Pallaresa (NE Iberian Peninsula) is a tributary of the river Segre (Ebro basin). The study area (940-970 m a.s.l.; drainage area: 321 km²) had a stony substrate with a mean slope of 1.1% and a mean stream width of 13.2 m (range 5.1-18.5 m). The area has a fully developed riparian forest. The fish assemblage is composed by native brown trout of Mediterranean lineage (Aparicio et al., 2005), introduced rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) and minnow *Phoxinus sp.*, the latter species with a very low abundance.

The river Noguera Pallaresa supplies the Esterri-Unarre hydropower plant, which uses waters from Boren reservoir (1098 m a.s.l) and the Unarre stream (left tributary, mean discharge < 0.2 m³·s⁻¹). Between the Boren dam and the hydropower plant, the unregulated river Bonaigua (mean discharge ca. 2 m³·s⁻¹) meets the Noguera Pallaresa and restores a near-natural flow pattern downstream from the confluence (Fig.1).

The study compared a site with a daily pattern of hydropeaking, located 1000 m downstream from the power plant (42°36’58” N; 1°7’41” E), with a control site
located 800 m upstream from the discharge point (42°37'52" N; 1°7'24" E) (Fig. 1). Monitoring was conducted in summer during low flow conditions. According to the seasonal distribution of energy demand and the snowy river regime in the study area, the highest differences between the natural and peaking flows are in winter, but middle summer also shows notable variations in flow due to hydropoeaking; in addition, brown trout activity is higher than in winter and, hence, feeding patterns of brown trout could be mostly influenced by hydropoeaking operations. During the field works (August 22-24, 2011), base-flows at the control and hydropoeaking sites were about 0.4 m$^3$.s$^{-1}$, and they were increased up to 8-10 m$^3$.s$^{-1}$ during power plant operations for about 2-3 h, twice a day. Except for these hydrological operational conditions, other stream features were similar between the two considered sites. Water temperature regimes were also similar during the course of this study between control (mean: 13.6 ± 1.2 ºC) and hydropoeaking (mean: 15.2 ± 2.1 ºC) sites.

**Brown trout sampling**

Previously to the feeding behaviour sampling, the density, biomass and size structure of brown trout populations were estimated with two-pass depletion electrofishing (Pulsed DC) at two 100–m-long river sections at the control site (surface area 872 and 985 m$^2$; mean depth 0.30 and 0.32 m, respectively) and at two sections 100–m-long at hydropoeaking site (surface area 740 and 1317 m$^2$; mean depth 0.41 and 0.38 m, respectively).

To assess the daily feeding patterns of brown trout, ten samples of 20 fish specimens were collected from each study site by electrofishing at about four-hour intervals for two consecutive days. Repeated fish samplings at each site
were always performed at different sections (range 30-60 m long) to minimize fish stress and disturbance. After collection, fish specimens were anesthetized with MS-222 (50 mg L$^{-1}$), measured (fork length FL, mm) and weighed (g). Stomach contents were collected by pulsed gastric lavage (Meehan and Miller, 1978) and were preserved in formaldehyde (4%) for later identification. After recovering, fish were released at the river section from which they were caught.

**Invertebrate sampling**

To assess the food resources available to fish and their prey selection, invertebrate drift and benthos samples were collected at the control and hydropeaking sites. Drift nets (250-$\mu$m mesh size, 1 m length and 30 cm mouth diameter) were set in the current at least 2 m away from the shore, and were always positioned at the same place at the upstream end of each study site, so that all electrofishing operations were performed downstream from the drift nets. Nets remained in place for the entire period between fish collections (4 h) and, thus, ten samples were obtained. Benthos was sampled once at midday at each study site by randomly taking four Surber samples per site using a 250-$\mu$m mesh size net with an area of 0.18 m$^2$. Special attention was paid to perform this sampling in central areas of the river channel, permanently submerged. All captured organisms were preserved in formaldehyde (4%) for later taxonomic identification and enumeration.

**Data analysis**
Brown trout density (individuals·ha$^{-1}$) and biomass (kg·ha$^{-1}$) were estimated based on catch rates from two passes (Seber and Le Cren, 1967). Length-frequency distributions were used to analyze the size structure of populations.

The stomach contents of individual fish were weighed (to 0.01 g accuracy) in the laboratory. Prey items and drift and benthic samples were enumerated and generally identified at the taxonomic family level. Density of organisms present in the benthic and drift samples were expressed as individuals·m$^{-2}$ and individuals·m$^{-2}$·min$^{-1}$, respectively.

Stomach Fullness Index (FI) was used to determine diel-feeding intensity (Hyslop, 1980). For each fish specimen, FI was calculated by dividing the weight of fresh stomach content (SW, mg) by fish weight (FW, g) [FI=SW/FW (mg·g$^{-1}$)].

For the description of the trout diet, the following calculations were made according to Hyslop (1980): (i) relative abundance of a prey ($A_i = (\Sigma S_i / \Sigma S_t) \times 100$, where $S_i$ is the number of prey-type $i$ and $S_t$ the total number of preys in the entire sample); (ii) frequency of occurrence of a given prey ($O_i = (J_i / P) \times 100$, where $J_i$ is the number of fishes containing prey-type $i$ in their stomach and $P$ is the total number of fishes, omitting empty stomachs). Prey selection was assessed using the Vanderploeg and Scavia’s (1979) relativized electivity index ($E_i^*$): 

$$E_i^* = \frac{W_i - (1/n)}{W_i + (1/n)}, \quad \text{where} \quad W_i = \frac{r_i/p_i}{\Sigma r_i/p_i},$$

where $r_i$ is the relative abundance of prey $i$ in the diet, $p_i$ is the relative abundance of prey $i$ in the environment and $n$ is the number of prey types included in the analysis. The relative abundances of preys in the environment ($p_i$) were computed as the average of the proportions in the drift and benthos samples. This index
ranges from -1 (complete avoidance) to +1 (strong selection) and values near zero indicate neutral selectivity. The Tokeshi analysis (Tokeshi, 1991) was performed to describe the feeding strategy of brown trout (specialized vs. generalized). This graphical method consists in plotting mean individual feeding diversity \[ D_i = \frac{-\sum P_{ij} \ln P_{ij}}{N}, \] where \( P_{ij} \) is the proportion of prey-type \( i \) in the \( j \)th fish and \( N \) the total number of fish], against population feeding diversity \[ D_P = \sum P_i \ln P_i, \] where \( P_i \) is the proportion of prey-type \( i \) in the entire fish population]. In order to identify tendencies towards a particular feeding mode (i.e., drift feeding vs. benthic feeding), the similarity between trout diet and invertebrate samples (drift and benthos) was assessed by the Renkonen’s percent similarity index (Wolda, 1981). This index is calculated as the sum of the lowest percent value of a prey-type between samples \[ PS_{jk} = \sum \min (P_{ij}, P_{ik}), \] where \( P_{ij} \) and \( P_{ik} \) are the proportions of prey-type \( i \) in assemblages \( j \) and \( k \), respectively, and \( \min \) indicates that the smallest proportion is used in the summation]. The similarity index is expressed as a percentage, ranging from 0 % (no overlap between samples) to 100 % (complete similarity).

**Statistical analyses**

The nonparametric Kolmogorov–Smirnov (K-S) test was used to compare length-frequency distributions between sites. To compare fish body condition, we performed an ANCOVA on length-weight relationships with FL as the covariate (García-Berthou and Moreno-Amich, 1993). Data for FL and weight were log\(_{10}\) transformed for analyses. Relationships between FI and drift were analysed using Spearman’s correlation coefficient. For each site, FI values among samples collected over the diel cycle were compared using one-way Kruskal-Wallis tests.
Between-site differences concerning FI, invertebrate densities and taxonomic richness in diet were assessed using Mann-Whitney U-tests.

Results

Brown trout and invertebrate populations

At the control site, mean trout density (6320 ind·ha⁻¹) was threefold higher than at the hydropeaking site (2050 ind·ha⁻¹). Mean biomass at both sites was less contrasting, being 13% higher at the control site (133 kg·ha⁻¹) as compared to the hydropeaking site (117 kg·ha⁻¹). Length-frequency distributions were significantly different between the two sites (K-S test: D = 0.34, P < 0.001), mainly due to an increased relative abundance of younger fish at the control site (Fig. 2). No significant differences in length-weight relationships of the individuals used for feeding analysis were found between the control and hydropeaking sites (ANCOVA: F = 0.00, d.f. = 1, P = 0.998), suggesting similar body condition.

Benthic invertebrate densities were similar between sites (Mann-Whitney U-test: U = 15, P = 0.93), ranging from 2550 to 4760 ind·m⁻² (mean: 2990 ± 1330 ind·m⁻²) at the control site and from 1210 to 4140 ind·m⁻² (mean: 3120 ± 1130 ind·m⁻²) at the hydropeaking site. Overall, differences in mean drift densities between the hydropeaking site (mean: 6.2 ± 6.8 ind·m⁻²·min⁻¹; range: 0.3-22.8) and control site (mean: 2.6 ± 2.3 ind·m⁻²·min⁻¹; range: 0.2-8.2) were not significant (Mann-Whitney U-test: U = 34, P = 0.24). However, drift densities after flow pulses (mean: 11.9 ± 7.5 ind·m⁻²·min⁻¹; range: 6.4-22.8) were significantly higher than drift densities between pulses (mean: 2.4 ± 2.4 ind·m⁻²·min⁻¹; range: 0.3-6.9; Mann-Whitney U-test: U = 1, P < 0.05), and also higher than drift densities at the control site (Mann-Whitney U-test: U = 2, P < 0.05). Based on the relative
abundances of taxa in the invertebrate samples (Table 1), Ephemeroptera dominated the drift (mainly Baetidae) whereas Chironomidae and Baetidae dominated the benthos at the control site. At the hydropeaking site, Ephemeroptera and adults of Limnephilidae recently emerged showed the highest relative abundance in the drift, whereas the benthos was dominated by Chironomidae and Baetidae.

**Feeding activity**

In total, 200 individuals from the control site (mean FL: 154 ± 22 mm; range: 118-229 mm) and 200 from the hydropeaking site (mean FL: 165 ± 31 mm; range: 115-275 mm) were captured and used for feeding analyses. These fish corresponded to adult individuals of age 2+ and older. Plots of the FI against fish length showed that the index was not size-dependent; therefore, it was considered appropriate for comparisons among samples irrespective of differences in fish sizes.

FI values and invertebrate drift rates followed contrasted patterns between sites (Fig. 3). Overall, FI was significantly higher at the hydropeaking site (mean FI = 6.8 ± 6.5 mg·g⁻¹) than at the control site (mean FI = 4.1 ± 3.5 mg·g⁻¹) (Mann-Whitney U-test: U = 15390, P < 0.001). Mean FI values at the control site did not show any significant variation among samples over the diel cycle (Kruskal Wallis test: H = 12.36, P = 0.19), although they were slightly higher at dusk, and during the night until dawn (Fig. 3). Conversely, mean FI values the hydropeaking site were significantly different among samples over the diel cycle (Kruskal Wallis test: H = 41.15, P < 0.001), being highest after flow pulses (Mann-Whitney U-test: U = 2599, P < 0.001) (Fig. 3). Spearman rank correlations showed that mean
FI was significantly correlated with invertebrate drift density at the hydropeaking site ($r_s = 0.77$, $n = 10$, $P < 0.05$) but not at the control site ($r_s = 0.27$, $n = 10$, $P = 0.44$).

**Dietary analysis**

From the total number of fish examined, the overall proportion of empty stomachs was low at both control (n = 7; 3.5%) and hydropeaking (n = 1; 0.5%) sites. Brown trout from both sites ingested a wide variety of prey taxa, predominantly aquatic stages of insects (Table 1). Taxonomic richness in individual stomachs was significantly higher (Mann-Whitney $U$-test: $U = 10410$, $P < 0.001$) at the hydropeaking site (mean: 4.9 ± 2.6; range: 1-12) than at the control site (mean: 2.9 ± 1.8; range: 1-9). The most important prey types in terms of occurrence and relative abundance were Chironomidae and Baetidae at the control site, and Baetidae and Limnephilidae adults at the hydropeaking site (Table 1). Consumption of terrestrial invertebrates was rare (<2%), and piscivory was not detected. The Vanderploeg and Scavia’s electivity index (Fig.4) showed a negative electivity for most prey classes at both control and hydropeaking sites, indicating that most potential preys were consumed at lower proportion than their relative abundance in the environment. The most notable difference in prey electivity between sites concerned the Chironomidae, which were actively selected at the control site but avoided at the hydropeaking site. Based on the plot of Tokeshi’s method of dietary analysis (Fig. 5), most samples tended to cluster in the lower right region, which indicates an overall generalist feeding pattern and a heterogeneous diet. Differences between study sites were low, but trout exhibited a slightly more homogenous and generalist feeding pattern at the hydropeaking site as compared to the control site, where some samples could be described as
specialist feeding. Renkonen Similarity Indices showed that diet similarity at the control site was higher for benthos (56.6%) than for drift samples (47.2%), whereas at the hydropeaking site the diet was more similar to drift (67.8%) than to benthos (51.1%) composition.

**Discussion**

Population parameters of brown trout observed in the present study were consistent with the hydrological disturbance caused by pulsed discharges. Brown trout density and, to a lesser extent, biomass at the hydropeaking site were markedly lower than at the control site (upstream), mainly due to a lower proportion of young of the year fish (age 0+) below the hydropower plant. This pattern has been frequently reported in river sections subjected to sudden flow pulses, in which high water velocities during the critical period of emergence from nests caused entrainment of trout fry, resulting in lowered densities of 0+ individuals (Liebig et al., 1999; Nislow and Armstrong, 2012). Hydropeaking has also been noted to decrease the density of benthic invertebrates downstream from hydropower plants (Moog, 1993). However, this was not observed in the present study, where benthic invertebrate densities downstream from the hydropower plant were similar to those found at the control site. If hydropower stations release cold hypolimnetic waters from a reservoir then they can modify the thermal regime below the outlet (known as thermopeaking; Zolezzi et al., 2011). When both hydropeaking and thermopeaking occur simultaneously, a stronger response in drift rates and considerable losses among benthic populations (Bruno et al., 2013) can occur. In the study area of the Noguera Pallaresa, the reservoir that supplies the power plant has a low volume (<1 Hm³) and a high turnover of the water volume, thus preventing the formation of a thermocline. Therefore,
hydropeaking is not coupled with thermopeaking, and this may have limited the reduction in density of benthic invertebrates.

Pulsed water releases from the hydropower plant altered patterns of trout feeding intensity, with increased food consumption during flow pulses. This pattern contrasted with the feeding activity of brown trout upstream from the hydropower plant, where feeding activity rhythms were smoother. Brown trout are flexible foragers and can modify their predation rates depending on the daily or seasonal availability of forage resources (Giroux et al., 2000). Thus, the higher feeding intensity during flow peaks is likely to occur in response to greater encounter rate with prey due to an increased drifting of invertebrates (Crespin de Billy et al., 2002; Lagarrigue et al., 2002). Additionally, the fact that hydropeaking occurred during daylight hours could also have favoured foraging because invertebrates may be more visible and therefore more vulnerable to brown trout predation (Elliott, 2011). Many studies have found a positive correlation between discharge and invertebrate drift (e.g. Imbert and Perry, 2000; Gibbins et al., 2007). In contrast, stream sections with stable flows may have limited effects on drift rate because benthic disturbance is minimal. Under these conditions, invertebrate drift would be more influenced by behavioural factors to minimize predation risk, such as drifting mostly at night-time (Huhta et al., 1999). This pattern was observed at the control site of the present study, where drift density peaked at dusk and remained relatively high throughout the night until dawn.

Downstream from the hydropower plant, the highest food consumption was observed among samples collected immediately after hydropeaking and it decreased afterwards, which suggests that hydraulic conditions during flow pulses...
did not hinder trout feeding. Probably this was due to the complex structural habitat of this river, with high availability of water current shelters for fish. A different linkage between the hydropeaking and feeding activity periods was reported by Lagarrigue et al. (2002) in the Oriège river, where the highest levels of food consumption were found 2-4 h after peak flows ceased, and they concluded that trout did not feed during peak flows, possibly because of trouble in finding energetically favourable positions and/or because the drop of water temperatures (up to 8°C) slows down the activity level of fish. Thus, in the river Oriège, fish apparently took advantage of increased behavioural drift in response to thermopeaking, after peak flows ceased and water temperatures recovered (Lagarrigue et al., 2002). In absence of thermopeaking, drift rates in the Noguera Pallaresa dropped shortly after flow pulses, as did food consumption. Overall higher ingestion rates by trout downstream from the hydropower plant would determine a higher energy intake which should be reflected in higher body condition as well (Fausch, 1984). However, no differences were detected in the condition of individuals between sites. Although the present study was performed only in summer and additional data would be needed, we hypothesize that the energy gain obtained by trout at the hydropoeaking site due to greater prey ingestion may be counteracted by higher energy expenditure when exposed to higher water velocities (Fausch, 1984; Rincón and Lobón-Cerviá, 1993).

The diet of the trout in the river Noguera Pallaresa was composed of a high spectrum of aquatic invertebrates, but a few types of prey constituted the majority of stomach contents, as reported in other feeding studies of brown trout in the Iberian Peninsula (Montori et al., 2006; Teixeira and Cortes, 2006). Similarity indices between the diet of brown trout and invertebrate abundance were
relatively weak, but some trends were observed. At the hydropeaking site, trout
diet was more similar to drift than to benthos composition, which seems
consistent with the high drift rates observed. Conversely, trout diet at the control
site appeared to be more similar to benthos than to drift composition. Drift rates in
this site were relatively low, as often reported in unregulated or semi-natural
rivers during periods of low flows (e.g. James et al., 2009), which could have
encouraged trout towards a greater use of benthic resources (Tippetts and Moyle,
1978). According to the Vanderploeg and Scavia’s electivity index, the most
noteworthy result is the antagonistic electivity of Chironomidae between sites.
This prey type was strongly selected at the control site, but trout avoided feeding
on Chironomidae at the hydropeaking site, despite their higher relative abundance
in this latter site, in both drift and benthos. A possible explanation for this
behaviour could be related to the difficulty of detecting Chironomidae larvae
during conditions of high water velocities due to their small size (Rader, 1997;
Piccolo et al., 2008). The fact that, both at control and hydropeaking sites, most
prey types were not positively selected, along with the low percentage of empty
stomachs found, suggests that brown trout showed a high feeding flexibility and
an opportunistic behaviour. This is confirmed by the Tokeshi’s (1991) graphical
model, which indicates that, overall, the trout feeding strategy in the Noguera
Pallaresa was one of a generalist heterogeneous type. The trend for a generalist
feeding strategy among salmonids has been noted elsewhere (e.g. Bridcut and
Giller, 1995; Montori et al., 2006; Oscoz et al., 2008). This strategy was more
marked at the hydropeaking site as compared to the control site, in which, at
certain times, fish may have a more specialized diet. This behaviour is consistent
with the trend towards greater resource specialization in hydrologically stable habitats (Poff and Allan, 1995).

In conclusion, the hydrological disturbance caused by hydropoeaking led to brown trout higher food consumption rates as an opportunistic response to increased prey availability. Therefore, regarding feeding activity in summer, there is no evidence of direct negative effects on adult brown trout caused by hydropoeaking. However, some signs of disturbance on brown trout populations were detected, such as reduced trout density and imbalanced size structure, which demands further research to clarify the role of other factors (e.g. habitat suitability for different age classes, availability of spawning grounds, movement patterns, hydropoeaking regime, spatial variation of the effects downstream from hydropower plant, etc.) in regulating brown trout production in hydropoeaking river reaches.

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(Oncorhynchus kisutch) and steelhead (Oncorhynchus mykiss irideus).


Table 1. Diet composition of brown trout and macroinvertebrate composition (in drift and benthos samples) at the control and hydropeaking sites in summer 2011. Data on fish and drift are based on a total of ten samples taken at four-hour intervals for two consecutive days at each site. Data on benthos are based on a total of four samples per site. Values of relative abundance (A, %) and frequency of occurrence (O, %) of major prey types are shown. Category ‘Other’ pooled prey-types with a relative abundance in the trout diet A <1%.

<table>
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<th>Taxa</th>
<th>Control Diet A (%)</th>
<th>Drift O (%)</th>
<th>Benthos A (%)</th>
<th>Hydrominimally Diet A (%)</th>
<th>Drift O (%)</th>
<th>Benthos A (%)</th>
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FIGURES

Figure 1. Study area and sampling sites in the river Noguera Pallaresa (river Ebro basin). Control site (A) is 800 m upstream from the hydropower plant and hydropeaking site (B) is 1000 m downstream from the outlet of the hydropower plant.

Figure 2. Length-frequency distributions of brown trout collected by electrofishing at the (a) control and (b) hydropeaking sites in summer 2011.

Figure 3. Diel variations of mean Fullness Index (FI) and drift density at the (a) control and (b) hydropeaking sites in summer 2011. Grey solid area indicates periods of increased flows due to power generation (hydropeaking). Each point represents a brown trout (filled circles) or drift (open circles) sample taken at four-hour intervals for two consecutive days in each site (solid and dashed lines are drawn by hand).

Figure 4. Electivity (Vanderploeg and Scavia’s index, $E^*$) by brown trout on main prey items (numerical abundance of drift and benthic samples combined) at the control and hydropeaking sites in summer 2011.

Figure 5. Feeding strategy based on Tokeshi’s (1991) plot. Each point represents a brown trout sample taken at four-hour intervals for two consecutive days at the control (open circles) and hydropeaking (filled circles) sites.