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Hydropeaking effects on movement patterns of brown trout (*Salmo trutta* L.)

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Running title: Hydropeaking effects on brown trout movements

Acknowledgements

Financial support was provided by the Biodiversity Conservation Plan of ENDESA, S.A. (ENEL Group). We want to thank Josep Maria Puigarnau, Miquel Arilla, Inmaculada Ordoñez, Fermí Sort and Josep Piqué for field assistance. All appropriate ethics and permissions required for the realization of this manuscript were obtained, previously, by the authors.

Abstract

Radio-telemetry was used to investigate seasonal movement and home range of brown trout *Salmo trutta* (size range 188–420 mm FL, $N = 30$) in two reaches of the Noguera Pallaresa River (Ebro Basin, northeast Spain) subjected to different flow regulation schemes. NP-1 reach is a by-passed section with near natural flow conditions whereas the downstream reach NP-2 is subjected to daily pulsed flow discharge (*i.e.* hydropeaking) from an upstream hydropower station. Significant differences in home range size (95 % kernel estimates) and seasonal movement pattern between study reaches were found. Mean home range size was ($\mu \pm SE$) 112.1 ± 11.5 m in the by-passed reach NP-1 and increased significantly in the hydropeaking reach NP-2 up to 237.9 ± 37.2 m. There was a large individual variability in fish home range size within reaches. Most of the seasonal differences in fish movement among reaches were associated with the spawning season. Pulsed discharge events in NP-2 during daytime in summer (lasting about 3 hours and increasing water flow from $1 \text{ m}^3 \text{ s}^{-1}$ to $20 \text{ m}^3 \text{ s}^{-1}$) did not cause significant displacements in either upstream or downstream direction during the duration of the event. Our results highlight the importance of habitat connectivity in hydropeaking streams due to the need of brown trout to move large distances among complementary habitats, necessary to complete their life cycle, compared to unregulated or more stable streams.

Keywords: *pulsed discharge; home range; diel cycle; river connectivity; radio-tracking; salmonids; management*

Introduction

Flow dynamics is a major determinant of physical habitat in streams and play a crucial role for aquatic organisms (Bunn & Arthington, 2002; Poff & Allan, 1995; Poff & Zimmerman, 2010). In regulated rivers, the natural flow regime has been greatly modified because of the impoundment and release of water according to variations in human demands (*e.g.* hydroelectric production, water supply for domestic, agricultural, and industrial activities). Hydropower-related pulsed flows (commonly designated by hydropeaking) are the periodic releases of water from reservoirs associated with on-demand hydroelectric generation (Moog, 1993) and result in significant hourly and diel fluctuations in magnitude, duration, and frequency of streamflow. Consequently, hydropeaking operations alter the riverine habitat, including the bank and channel morphology, water depth, wetted area, water velocity, substrate composition and temperature (Gore & Pett, 1989; Magilligan & Nislow, 2005; Olden & Naiman, 2010). Since flow fluctuations caused by hydropeaking exceed those observed naturally (Poff et al., 1997), negative impacts on riverine organisms such as benthic invertebrates and fish are expected. For example, the resulting rapid changes in river discharge affects the invertebrate drift (Bruno et al., 2013; Gibbins et al., 2007; Lauters et al., 1996; Rocaspana et al., 2016), and reduce both the quantity and quality of habitat available to fish (Liebig et al., 1999; Person, 2013; Young et al., 2011).

Fish movement is a critical behaviour that determines habitat selection, foraging efficiency, predator refuge or spawning (Jacobson & Peres-Neto, 2010; Kahler et al., 2001), and is a key factor in understanding how populations respond to rapid environmental change and perturbations. Fish may cope with short-term flow changes caused by hydropeaking by moving from an original habitat to a new suitable habitat (Taylor et al., 2014). The effects of hydropeaking on fishes vary among species and

river types. For example, Atlantic salmon (*Salmo salar* Linnaeus, 1758) shows contrasting patterns during hydropeaking events, while some individuals have high site fidelity other move large distances in response to flow pulses. The brook trout, *Salvelinus fontinalis* (Mitchill, 1814), exhibits higher movement rates during flow pulses (Scruton et al., 2003). This pattern is similar to the reported in the Iberian barbel (*Luciobarbus bocagei* Steindachner, 1864), fish inhabiting an hydropeaking river exhibit larger and more continuous home ranges than those individuals from an unregulated river (Alexandre et al., 2015). In the brown trout (*Salmo trutta* Linnaeus, 1758), previous studies have shown a weak influence of hydropeaking on its movement pattern. For instance, Bunt et al. (1999) reported a minimal influence of pulsed discharges, although there was a high inter-individual variation, while most of the individuals remained sedentary others showed a high degree of mobility. In other study, brown trout from a hydropeaking reach showed larger home ranges, but differences were not significant due to the large individual variation, and no short time effects on movement were observed during peak flow events, *i.e.* no fish were displaced downstream (Heggenes et al., 2007).

In the Iberian Peninsula there are more than 1300 hydroelectric power plants in operation (Espejo & García, 2010; Manzano-Agugliaro et al., 2017), most in headwater streams inhabited by the brown trout. The impact of river regulation and altered flow regimes, along with other factors such as overfishing and genetic introgression, have caused a marked decline both in the abundance and range of native brown trout populations (Almodóvar & Nicola, 2004, 1999; Aparicio et al., 2005; Benejam et al., 2016). Data on the influence of pulsed discharges from hydropower stations on movements and home range of brown trout in Iberian rivers are lacking, but such data are essential to enhance and implement of both management and conservation measures.

In this context, the aim of this study is to assess the effect of hydropeaking on the seasonal movement patterns, diel cycle and home range of brown trout from late summer to winter, thus including the spawning season. We hypothesized that trout are not displaced downstream during peak flows because substrate heterogeneity, which may provide physical refuge reducing water (e.g. by obstruction). However, seasonal movements and home range may be influenced by repeated flow pulses in hydropeaking reaches.

Methods

Study area

Brown trout movements were monitored in two reaches of the Noguera Pallaresa River (140 km of length, $40.3 \text{ m}^3 \text{ s}^{-1}$ of average flow, and a catchment area of 2807 km^2), a tributary of the Segre River in the Ebro Basin, north-eastern Iberian Peninsula (Figure 1). Study river reaches had an unconstrained channel with stony streambed, and a well-developed riparian forest. The hydrology is influenced by snow melt in spring and increased rainfall in autumn, typical of the Mediterranean climate (Figure 2). The fish assemblage is mainly composed of native brown trout of the Mediterranean lineage (Aparicio et al., 2005), although the introduced rainbow trout, *Oncorhynchus mykiss* (Walbaum) and the European minnow (*Phoxinus* sp.) are occasionally recorded.

The Noguera Pallaresa River is regulated, within the study area, by the Esterri hydropower plant that uses water from the Borén Reservoir and Unarre stream (Figure 1). Two tagging reaches (NP-1 and NP-2 hereafter) were defined to study brown trout movement patterns under different flow regime scenarios (Figure 1; Table 1). NP-1 is a by-passed section located downstream of the Borén Reservoir and upstream of the Esterri hydropower plant outlet. This reach receives the inflow from the Bonaigua

stream, an unregulated tributary which restores a semi-natural flow regime in the study reach. NP-2 is located downstream of the Esterri plant and during the study period river discharge was characterized by daily-pulsed flows from hydroelectric peaking, increasing the base flow 10-30 times for about 3 h once or twice a day (Figure 2).

Fish tagging and tracking

Brown trout were captured by electrofishing (Hans-Grassl GmbH ELT60-IIH backpack electrofisher, DC pulsed, 1.3 KW) and radio transmitters were surgically implanted (Table 2). Tagging was performed in August 2012. Two sizes of radio tags (MST-720: Size 7 × 18 mm, weight in air 1.3 g; and MST-820: 8 × 20 mm, 2.1 g; Lotek Wireless Inc., Newmarket, Ontario, Canada), according to fish size. Transmitter weight in air ranged from 0.5 to 1.8 % of the fish's body weight. Before tag surgery, fish were individually anaesthetised (clove oil; 0.05 mL/L stream water) and placed on a V-shaped padded board for surgery. A maintenance dosage of anaesthetic was continuously pumped over the gills during surgery. Tags were implanted using a modified shielded-needle technique (Ross & Kleiner, 1982). Thus, a 1.0 cm incision was made with a scalpel on the mid-ventral line anterior to the pelvic girdle, the radio transmitter was inserted into the body cavity above the pelvic girdle, and whip antenna was exited through a different puncture using a hollow needle. The incision was closed with two or three independent silk sutures. Total handling time was usually < 5 minutes, never exceeding 10 minutes. After surgery, trout were held in keep-nets for approximately 2–4 hours and released within 50 m of the capture site when fully recovered. All fish were treated in compliance with the national regulations for the use of animals for scientific purposes.

Radio-tracking began one week after tagging to ensure full recovery and resumption of normal activity, and extended at *ca.* 10-day intervals from August to December, thus including trout spawning season, which in the study area occurs from early November to early December. Additionally, from August 29 to September 1 tagged individuals were radio-tracked during diel cycles. Fish positions were determined four times per day (sampling intervals: 06:00–08:00 h, 12:00–14:00 h, 17:00–19:00 h and 22:00–24:00 h) to track morning, afternoon, evening and night movements. In the hydropeaking site (NP-2), fish were also positioned three times during flow pulses (*i.e.* immediately before, after the start, and at the end) for measuring possible trout displacements caused by hydropeaking. The hydropeaking events took place in the morning and lasted three hours (from 10:00 to 13:00 h).

Fish were positioned with a manual tracking receiver (IC-R20, Icom America Inc., Kirkland, Washington, USA) connected to a three-element Yagi antenna by walking along the bank. Trout position was fixed either visually, signal strength or triangulation, and a GPS was used to log positions along the longitudinal axis of the stream. According to the GPS manufacturer's specifications, accuracy was estimated to be about 5 m. Fish status (*i.e.* alive or dead) was determined by direct observation, when possible, or by tracking upstream displacement. Fish displacement distance was measured with Geographic Information System software, QGIS 2.6.0 (<http://www.qgis.org>) as the linear distance between the initial and final position of an individual along the longitudinal axis of the stream. Positive values were assigned to upstream movements and negatives to downstream movements.

Statistical analyses

Differences in fish fork length among reaches were analysed with analysis of variance (one-way ANOVA). Individual home range was calculated using the kernel-density estimation, which is considered preferable to linear range because it reveals the internal structure of the home range and is also indicated for small sample sizes (Seaman & Powell, 1996). Kernel density estimations with barriers were computed in R through the `adehabitatHR` package (Calenge, 2006). This approach uses the shortest distance between points without intersecting a defined barrier, in this case the river banks. The area that incorporates 95 % of the utilization distribution (*i.e.* the minimum area on which the probability to relocate the animal is 0.95) was calculated as an estimate of individual home range (Worton, 1989). The bandwidth is a smoothing value that determines the width of the kernel and was set to $h = 25$ by iterative visual inspection of outputs and evaluating the results (Gitzen *et al.*, 2006). Mixed Model Analysis of covariance (Mixed Model ANCOVA) was used to compare movement variables, such as home range and displacement distances, among study reaches, sampling dates, diel periods and between hydropeaking events, using fish fork length as the covariate. Following the methods described in Rogers and White (2007) individual fish were included as the sampling unit to avoid pseudoreplication issues. We started with the most complex model, introducing all possible sources of variation, including interactions of covariates \times factors, following García-Berthou & Moreno-Amich (1993). Then, we simplified the model by removing non-significant interactions (*i.e.* $P > 0.10$) to increase statistical power, and when the covariate was not significant (*i.e.* $P > 0.10$) it was also deleted from the model (so a Mixed Model ANOVA was used). Estimated marginal means were also used to describe the differences between factor levels. Estimated marginal (or size-adjusted) means of a dependent variable are the means for each level of the factor after adjusting for fish fork length (see Alcaraz & García-

Berthou, 2007; García-Berthou & Moreno-Amich, 1993; Rovira *et al.*, 2016).

Preference for movement direction (*i.e.* the proportion of upstream and downstream movements) was assessed with a *G*-test of independence, and a Student's *t*-test was used to test whether mean signed movement significantly deviated from zero.

Correlation between trout home range and fish fork length were analysed using Pearson's correlation coefficient. All quantitative variables were log-transformed for the analyses because homoscedasticity and linearity were clearly improved. All data analyses were performed with SPSS 23.0.

Results

Of the 34 brown trout initially tagged in the two study reaches, 30 individuals were tracked for the duration of the study: 15 in NP-1 and 15 in NP-2. Four trout disappeared rapidly after tagging, probably because of predation, angling or transmitter failure.

Mean size of radio-tagged brown trout did not significantly differed between reaches (ANOVA; $F_{1, 29} = 0.370$, $P = 0.55$) (Table 1).

Mean fish displacement between successive locations were lower in the by-passed reach (NP-1, $\mu = 16.27$ m \pm SE = 2.85) than in the hydropeaking reach (NP-2: $\mu = 125.36$ m \pm SE = 23.56). Maximum displacement tracked was 132 m in NP-1 and 1355 m in NP-2. The analysis of the overall displacement pattern showed that after accounting for fish length (Mixed-Model ANCOVA; $F_{1, 31.53} = 7.03$, $P = 0.012$) the total distance moved by brown trout differed significantly between sampling reaches ($F_{1, 24.19} = 14.614$, $P < 0.001$), being larger in NP-2. ANCOVA size-adjusted estimated marginal means ($\mu \pm$ SE) were 0.751 ± 0.109 and 1.328 ± 0.105 in NP-1 and NP-2. No interaction effects were detected ($P = 0.32$), and reach was a more important factor than fish fork length (power analysis) in explaining such differences. The direction pattern,

for fish movement > 5 m (GPS estimated accuracy), did not differ between reaches ($G = 0.074$, $df = 1$, $P = 0.79$), and there was the same proportion of upstream and downstream movements ($G = 0.36$, $df = 1$, $P = 0.55$).

The temporal distribution of movements varied between study reaches (Figure 3). In the control reach (NP-1) movement distance significantly varied among sampling dates (Mixed Model ANCOVA, $F_{11, 75.17} = 2.63$, $P = 0.007$) and was positively related (Pearson's $r = 0.38$, $N = 100$, $P < 0.0001$) to fish fork length ($F_{1, 34.25} = 5.11$, $P = 0.030$). Differences among sampling dates were explained by an increase in upstream movements of some individuals before the spawning period and downstream movements after the spawning (Figure 3). A similar pattern was observed in NP-2, but observed differences were not statistically significant (Mixed Model ANOVA, $F_{11, 101.74} = 1.47$, $P = 0.16$). Movement was not significantly related to fish length in the hydropeaking reach ($P > 0.28$). Most of the differences in mean movement distance among sampling dates were generally due to a few individuals with medium or long movements, thus, the upstream : downstream movement ratio did not show significant differences per sampling date ($P > 0.46$ in both reaches).

Mean 95 % kernel home range size was ($\mu \pm SE$) 112.1 ± 11.49 m (ranging from 73.2 to 224.5 m) in NP-1 and 237.9 ± 37.22 m (ranging between 82.5 and 568.9 m) in NP-2 (Figure 4). Trout home range size (95 % kernel estimate) showed significant differences between study reaches (Mixed Model ANCOVA, $F_{1, 30} = 13.53$, $P = 0.001$), after accounting for fish fork length ($F_{1, 30} = 4.32$, $P = 0.046$). Reach was a more important factor than fish fork length (power analysis) in explaining such differences. Home range was shorter in NP-1 reach, ANCOVA size-adjusted estimated marginal means ($\mu \pm SE$) were 2.027 ± 0.052 , 2.295 ± 0.051 in NP-1 and NP-2, respectively. Home range overall increased with fish fork length (Pearson's $r = 0.39$, $N = 30$, $P =$

0.033), but there was a large individual variability in fish home range within reaches, thus, while some individuals showed a sedentary behaviour others exhibited a large degree of mobility. This variability was particularly pronounced in hydropeaking reach, NP-2 (Figure 4).

The detailed analysis of the diel movement patterns of the brown trout (Mixed Model ANCOVA) showed that diel activity was not significantly related to fish fork length ($F_{1, 22.25} = 2.10$, $P = 0.16$) or FL \times factors interactions ($P > 0.12$), and therefore was not included in further analysis (*i.e.* a Mixed Model ANOVA was used). After excluding fish length, there were no differences in diel activity ($F_{3, 177.16} = 0.421$, $P = 0.74$), although it was observed an increase in diel activity at night in NP-1 and both at night and morning in NP-2 (Table 2). Trout displacements were larger in the hydropeaking reach than in the by-passed reach ($F_{1, 21.96} = 5.13$, $P = 0.034$), ANOVA size-adjusted estimated marginal means ($\mu \pm SE$) were 0.438 ± 0.103 in NP-1 and 0.765 ± 0.101 in NP-2. The movement ratio (*i.e.* upstream : downstream movement ratio) did not show significant differences between study reaches (G -test, $P = 0.86$), among diel events ($P = 0.92$) or among diel events within reaches ($P = 0.86$ in NP-1, and $P = 0.77$ in NP-2). Furthermore, the movement ratio did not differ from 1 : 1 in any diel period in both study reaches ($P > 0.24$, and $P > 0.16$ in NP-1 and NP-2, respectively).

We also analysed the movement behaviour of brown trout in relation to hydropeaking events by comparing displacements of the “before-mid” period (measured as the distance moved by a given individual from before the start of the hydropeaking to the mid hydropeaking event) and “mid-end” period (from the mid hydropeaking to immediately after the finish) (see Table 2). Mean fish displacement between hydropeaking periods were not significantly related to fish fork length (Mixed Model ANCOVA, $P = 0.99$) or to the fork length \times hydropeaking period interaction ($P = 0.29$).

“Mid-end” fish displacements was slightly larger than “before-mid” displacement (Table 2), but not statistically significant (Mixed Model ANOVA, $P = 0.27$). The net movement after hydropeaking events did not differ significantly from zero (Student’s t -test, $t_{25} = 1.68$, $P = 0.11$), but there was a higher proportion of upstream movements at the beginning of hydropeaking events (“before-mid”) (G -test, $G = 9.26$, $df = 1$, $P = 0.002$) compared to “mid-end” periods (Table 2). The net movement direction between hydropeaking events was marginally upstream ($P = 0.083$), see Table 2 & Figure 5).

Discussion

Movement patterns of brown trout were influenced by pulsed flow discharges, with trout increasing home range size in the hydropeaking reach (NP-2) when compared to the by-passed reach (NP-1). Our results are comparable to those reported by previous studies which showed that brown trout were more sedentary in rivers with more hydrologically stable conditions (Bachman, 1984; Heggenes, 1988a; Knouft & Spotila, 2002; Young, 1994), increasing home range size in hydropeaking rivers (Bunt et al., 1999; Heggenes et al., 2007; Scruton et al., 2005). Similar results have been reported for other fish species exposed to hydropeaking, such as the cyprinid *Luciobarbus bocagei* (Alexandre et al. 2015). These contrasting results on home range size between reaches might be due to differences in availability of complementary habitats necessary to complete their life cycle (Fausch et al., 2002). In concordance with that, movement pattern in the by-passed reach was similar to brown trout populations from unregulated Mediterranean streams, characterized by restricted home range size due to the close availability of suitable habitats for shelter, feeding and spawning (Aparicio et al. 2018). However, repeated flow pulses change substrate composition and distribution by altering the erosion and sedimentation patterns (Vericat et al., 2008), thus reducing the

heterogeneity of the river bed and causing shifts in key habitats for fish, such as gravel beds reduction and changes in channel morphology (Gibbins et al., 2007; Vericat et al., 2006). Consequently, the distance between complementary habitat types increase under hydropeaking conditions, forcing fish to move longer distances to seek the best-suited habitats for their optimum living requirements (Albanese et al., 2004; Bunt et al., 1999). There was a clear effect of hydropeaking regimes on the movement pattern of brown trout, but with a marked variability among individuals. This individual variability in movement patterns has been frequently observed in stream salmonids (Bunnell et al., 1998; Clapp et al., 1990; Heggenes et al., 2007; Ovidio et al., 2002; Quinn and Kwak, 2011), partly due to ontogenetic differences related to different life history strategies between larger and smaller individuals (Ayllón et al., 2010). Thus, some studies have shown a positive relation between movement distance and fish length (Clapp et al., 1990; Meyers et al., 1992; Quinn & Kwak, 2011; Young, 1994). Our results also show a positive relationship between home range size and fish length. Other possible source of individual variation could be related to behavioural phenotypes, for instance Höjesjö et al. (2007) showed that dominant brown trout individuals had larger home ranges than subordinates.

The movement pattern of brown trout varied temporally, particularly associated with the spawning season, such as upstream movements of some individuals in October and downstream movements in December. Increased brown trout movement is often observed in preparation for spawning (Bettinger and Bettoli, 2004; Burrell et al., 2000; Ovidio, 1999) followed by fast downstream movement after spawning (Burrell et al., 2000; Meyers et al., 1992; Ovidio, 1999). Differences among study reaches in the range extension of the spawning-related movements may be due to different availability of suitable spawning substrates. The by-passed reach (NP-1) offers a wide range of gravel

beds, which are the necessary spawning grounds for the brown trout, thereby implying no need for long displacements. However, spawning habitat (*i.e.* gravel beds) was more limited in the hydropeaking affected reach NP-2 (see Table 1). The highest movement activity of brown trout coincided with the onset of spawning period around the beginning of November when most of the individuals performed longer movements and settled in areas with abundant gravel beds where spawning fish were later observed (personal observations of the authors). There were no significant differences in trout diel activity, thus suggesting that brown trout individuals were active during the day and night. These results agree with a recent study showing an absence of diel cycling in the summer feeding activity of brown trout in the study area (Rocaspana et al., 2016), and other works reporting that brown trout individuals are active during the day and night in summer (Clapp et al., 1990; Young et al., 1997).

Trout individuals exhibited a higher proportion of upstream movements in NP-2 at the beginning of hydropeaking events. Positive rheotaxis responses of fish to the increase in water velocity may confer benefits, for instance, by increasing the interception of drifting prey or to remain in the same position under high flow conditions (Arnold, 1974). Trout individuals may be susceptible to being displaced downstream during flow pulses due to high water velocities. However, our results did not show marked downstream displacements in relation to hydropeaking events and are similar to those reported by previous works that did not find effects of peaking flows on downstream movements by adult trout (Bunt et al., 1999; Cocherell et al., 2010; Gido et al., 2000; Heggenes et al., 2007). In the hydropeaking reach NP-2 streambed substrate was dominated by coarser substrates (boulders and cobble) that provide sheltered areas with reduced water velocities, and thus preventing downstream displacement (Bunt et al., 1999; Heggenes, 1988b; Taylor et al., 2014). Resistance to downstream

displacement is also mediated by fish length. Radio-tagged trout in the present study corresponded to adult individuals (mean FL range: 235.5 – 283.7 mm), which are characterized by a superior swimming performance than smaller trout, which are more likely to be displaced downstream by high flows (Crisp & Hurley, 1991; Heggenes & Traaen, 1988; Thompson et al., 2011).

In summary, our results highlight that in the hydropeaking reach the range of movements of the brown trout increases, which has marked implications for the species management. Connectivity between hydropeaking reaches and contiguous upstream sections should have a higher priority in streams subjected to hydropeaking. Otherwise, limitation of fish movements, hindering or impeding access to complementary habitats, can lead to a reduction of the fitness of brown trout populations and may affect their productivity and long-term persistence. Alternatively, if connectivity cannot be restored or guaranteed, habitat improvement projects should also be taken into account in compensating potential losses in the availability of important stream features such as coarse substrates for velocity shelters or gravel substrates for spawning grounds.

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Table 1. Reach features during the sampling period, and brown trout radio-tracking data. Mean \pm standard error, when necessary, is shown.

| Variable | Reach code | |
|--|------------------------------|-----------------------------|
| | NP-1 | NP-2 |
| Tagging coordinates | 42° 37' 48" N 1° 7' 26" E | 42° 37' 5" N 1° 7' 44" E |
| Hydropeaking regime | No | Yes |
| Elevation range (m a.s.l.) | 951 – 968 | 930 – 951 |
| Mean slope (%) | 1.46 | 0.76 |
| Mean stream width (m) | 13.2 \pm 0.6 | 13.0 \pm 0.5 |
| Flow range (m ³ s ⁻¹) | 0.4 – 3.5 | 0.5 – 15.0 |
| Mesohabitat units (%) | | |
| Pool | 13 | 16 |
| Run | 30 | 32 |
| Riffle | 59 | 53 |
| Substrate composition (%) | | |
| Boulder | 62 | 76 |
| Cobble | 21 | 21 |
| Gravel | 17 | 3 |
| Sand/Silt | 2 | 0 |
| Number of fish tagged | 16 | 18 |
| Fork length (mm) | 235.5 \pm 14.0 | 242.9 \pm 10.2 |
| Observations (N) | 201 | 243 |
| Home range (m) | 112.1 \pm 11.5 | 237.9 \pm 37.2 |
| Home range (m) - median | 98.1 | 223.7 |

Table 2. Mean movement (m) and proportion of upstream displacements of radio-tagged brown trout per reach, diel periods and during hydropeaking events (Before-mid: distance moved from before the start of the flow pulse to the mid of the event; Mid-end: distance moved from the mid of the event to immediately after the finish; Net movement: distance moved from before the flow pulse to immediately after the finish). Only fish with displacements > 5 m (GPS accuracy) were included in direction analysis. Hydropeaking occurred from about 10:00 to 12:00 hours, thus hydropeaking movements in NP-2 are included in the morning diel movements.

| Period | NP-1 | | | NP-2 | | |
|-------------------------------|-------|------|--------------------------|-------|-------|--------------------------|
| | Mean | SE | % Upstream displacements | Mean | SE | % Upstream displacements |
| <i>Diel movements</i> | | | | | | |
| Night | 11.77 | 3.96 | 66.7 | 24.86 | 11.68 | 52.9 |
| Morning | 4.97 | 1.57 | 60.0 | 43.63 | 16.82 | 69.2 |
| Afternoon | 8.20 | 4.85 | 75.0 | 10.62 | 2.80 | 50.0 |
| Evening | 7.00 | 2.34 | 50.0 | 15.05 | 6.44 | 60.0 |
| <i>Hydropeaking movements</i> | | | | | | |
| Before-mid | | | | 21.27 | 7.16 | 92.3 |
| Mid-end | | | | 26.28 | 9.37 | 40.0 |
| Net movement | | | | 31.15 | 11.68 | 75.0 |

Figure 1. Location of the study area in the Noguera Pallaresa River (Ebro River basin). NP-1 reach is a by-passed section upstream from the Esterri hydropower plant (A); NP-2 reach is downstream from the outlet of the Esterri hydropower plant. Red dashed lines are the channels connecting the river to hydroelectric plant. The arrow indicates the direction of water flow. Photographs by Enric Aparicio.

Figure 2. Top: Flow regime (monthly averages per study reach for the period 2001-2012). Bottom: Flow regime in NP-2 during the 48 h radiotracking cycle. Black triangles are the tracking times.

Figure 3. Left: Box-plots of brown trout movement (m) per sampling occasion (from August to December) in the study reaches. Upstream and downstream movements are indicated as positive and negative. Each box corresponds to the 25th and 75th percentiles, the dark line inside the box represents the median, error bars are the minimum and maximum values, and the filled circle is the mean. Note different y-axis scale. Right: Relationship of sampling date with estimated marginal means of distance displacements for brown trout.

Figure 4. Ranked home ranges (95 % kernel estimates) of brown trout per study reach. NP-1 ($N = 15$) and NP-2 ($N = 15$) sampled from August to December 2012.

Figure 5. Box-plots of brown trout movement (m) in the hydropeaking reach (NP-2) during flow pulses. Upstream and downstream movements are indicated as positive and negative. See Fig. 3 for statistics given. Open circles are individual movement observations.

Figure 1. Rocaspana et al.

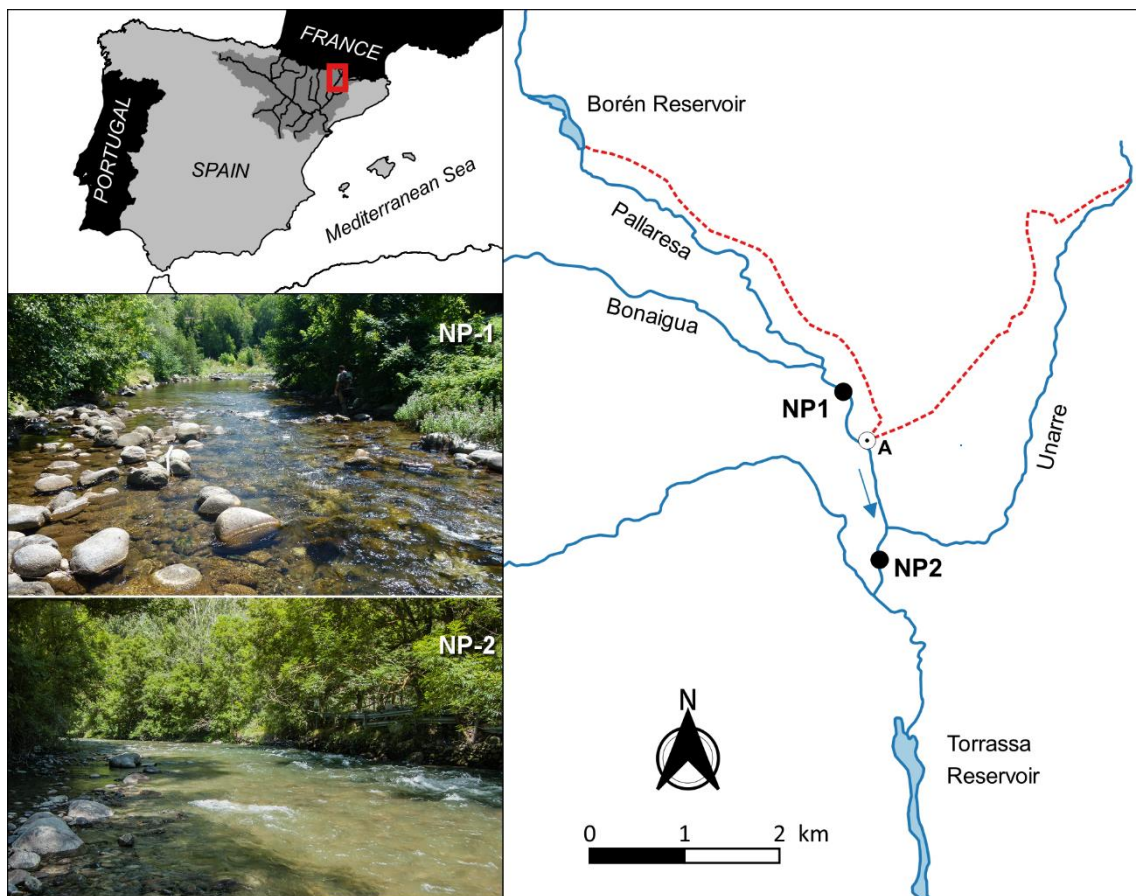


Figure 2. Rocaspana et al.

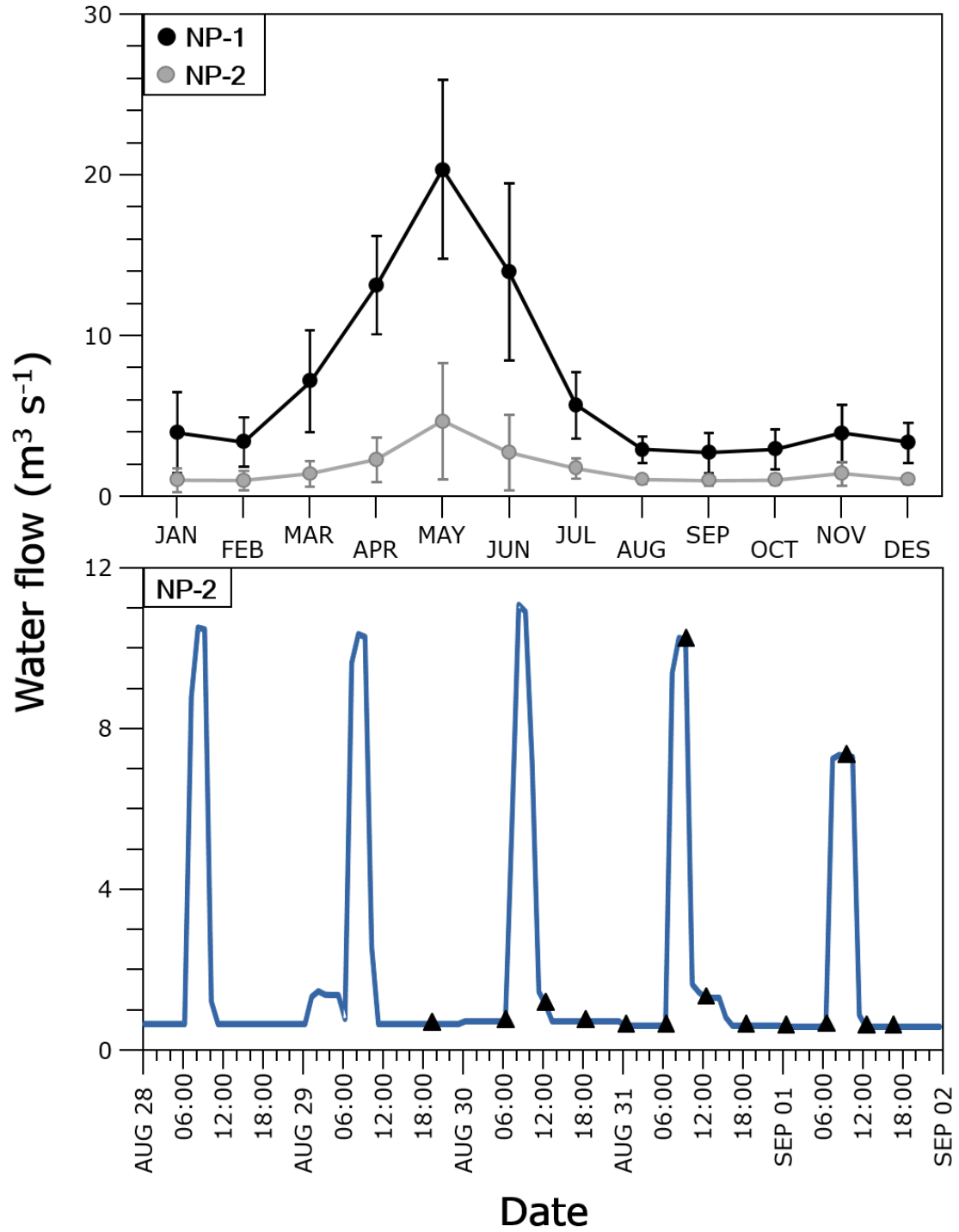


Figure 3. Rocaspana et al.

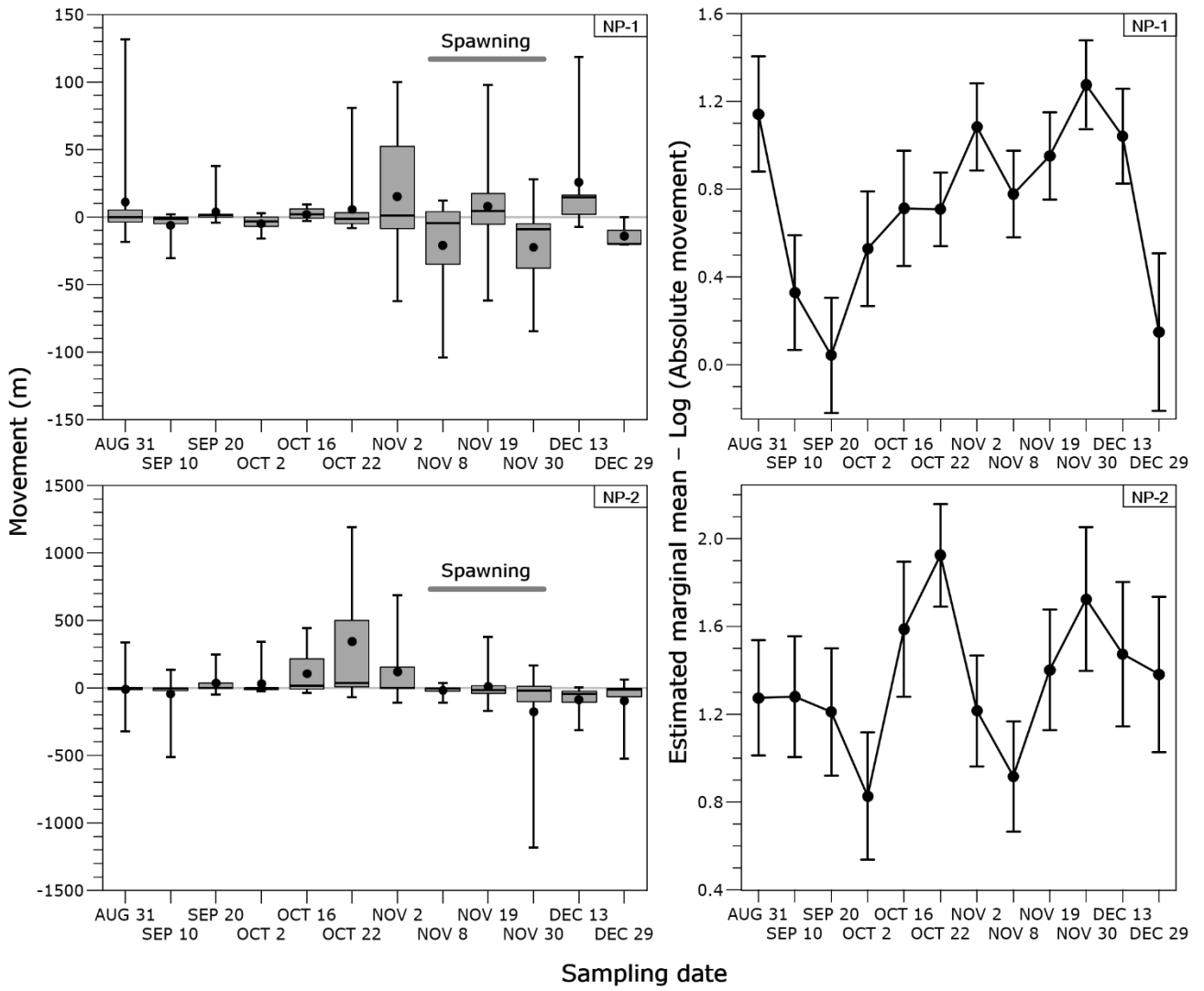


Figure 4. Rocaspana et al.

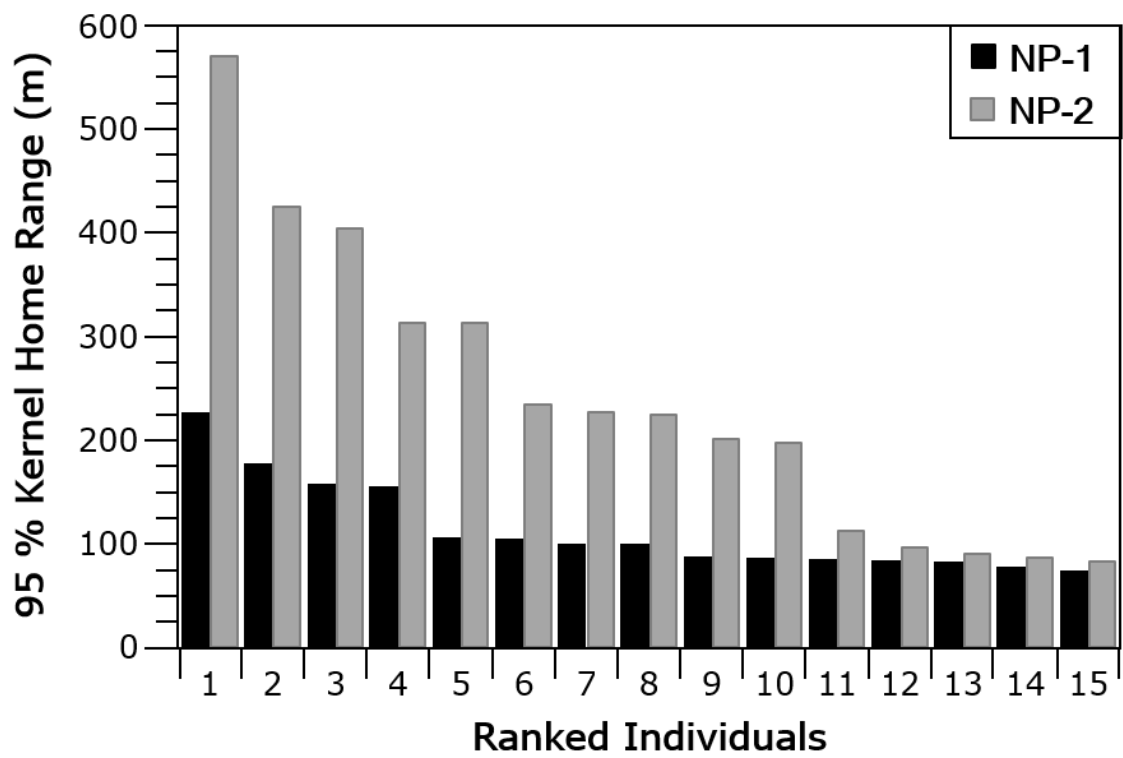


Figure 5. Rocaspana et al.

