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Seasonal and Size-Related Fish Microhabitat Use Upstream and Downstream from Small Hydropower Plants

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Abstract: Hydropower can have significant impacts on riverine ecosystems due to hydropeaking (i.e., artificial rapid and short-term fluctuations in water flow and water levels downstream and upstream of hydropower stations) that negatively affect downstream fish. However, when it comes to analyzing species habitat use and availability above and below small hydropower plants (SHPPs), studies conducted at the microhabitat scale are scarcer, particularly in Mediterranean rivers. The goal of this study is to assess the seasonal (early and late summer) and size-related (juveniles and adults) microhabitat use by native fish above and below SHPPs. Fish were sampled by a modified point electrofishing procedure, and a multivariate approach was used to analyze microhabitat use and availability data from sites located upstream (reference) and downstream (disturbed) from two SHPPs in northeast Portugal. Cover and water depth were the most influential variables in the use of microhabitat for all species at both the reference and disturbed sites, although some differences in the variable rankings were found. Leuciscids exhibited similar patterns of non-random (i.e., selective) microhabitat use between the reference and the disturbed sites. Overall, the seasonal and size-related patterns in species microhabitat use were similar, with the majority of species displaying seasonal patterns in microhabitat use from early summer to late summer. This study showed that differences in fish microhabitat use between downstream SHPP and upstream reference sites were negligible. Cover might have had a significant role in tempering the effects of detrimental environmental conditions, namely, peaking flows, by providing hydraulic shelter, highlighting the need to maintain riparian vegetation strips and mosaics of submerged aquatic macrophytes, as well as the provision of coarse substrata that can be critical for fish. Future studies are needed to better clarify how different size classes of fish select microhabitats when facing past and present hydropeaking conditions.

Keywords: hydropower; fish; habitat use; cover; mitigation measures; peaking rivers

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1. Introduction

Hydropower is one of the leading renewable energy sources, contributing two-thirds of the global electricity generation from all renewable sources combined [1]. This renewable source has also been highlighted for its potential role in reducing climate change impacts [2], making it integral to the EU's target of achieving at least 32 per cent of energy from renewables by 2030 and net zero emissions by 2050 [3]. However, hydropower projects and their associated infrastructures have been highlighted as emerging threats to riverine ecosystems, e.g., [4], causing severe declines in vertebrate populations, particularly migratory fish, as a result of river fragmentation, blockage of migratory routes and modification of the natural flow and thermal regimes, e.g., [5].

In contrast to large hydropower plants (LHPPs), which have been studied extensively [6] and for which their environmental sustainability and associated costs are the subject of debate [4,7], emphasis has been increasingly focused on the development of small-scale hydropower plants (SHPPs, i.e., plants with installed capacity < 10 MW, ref. [8]). Such facilities have been proliferating around the world since the 1990s as a response to governmental incentives in the form of competitive tariffs, as well as investments by the private sector to promote rural electrification in remote regions [9]. Although Europe's hydropower potential is highly exploited [10], more than 80k SHPPs are operating and new ones are still being built (11 SHPPs for every 1 large plant) [11] as a means to implement the transition to renewable energy production.

Small hydropower plants produce artificial flow fluctuations, i.e., significant variations in water velocity and depth, in downstream river segments. This phenomenon known as "hydropeaking" [12] can have serious negative impacts on river ecosystems, including fish stranding [13] and drift [14], obstruction to fish migration patterns [15], changes in food sources [16], impairment of flood intolerant river bank vegetation and macrophytes [17], sharp fluctuations in river temperature [18], and modifications of natural rates of sediment transport [19]. Knowledge of hydropeaking effects on Mediterranean rivers and on Leuciscidae, the main fish family represented in the present study, is much scarcer than for salmonids, e.g., [14,20], and includes drifting [21], egg detachment [22] and stranding [23].

One of the most persistent effects of hydropeaking is the alteration in the habitat use by aquatic species, particularly fish, which are subjected to significant variations in water velocity and depth, and are vulnerable to drifting and stranding, e.g., [24,25]. Therefore, to further improve the knowledge on how the presence of peak-operating SHPPs influences fish habitat use, it is important to investigate how individual fish occupy microhabitats on river reaches that are continuously subjected over time to such abrupt flow fluctuations. A microhabitat roughly corresponds to an "hydraulic unit", described by a combination of distinct hydraulic and physical factors such as flow velocity and depth, usually at a scale of 1 m^2 or less [26], comprising the actual position of a fish, particularly adequate for identifying drivers of biological responses to hydropeaking [27].

Nonetheless, contrarily to studies developed at larger scales (i.e., river segments or mesohabitats), e.g., [28,29], studies at the microhabitat level analyzing the fish species resource use and availability upstream and downstream from SHPPs are much scarcer. To the knowledge of the authors, very few, e.g., [30], studies have so far focused on both leuciscids and salmonids. In addition, such studies often neglect the effects of other key physical variables that are prone to be altered by peaking flows, i.e., the substratum and instream cover, as well as the role of season or ontogeny [31]. These variables (depth, velocity, substratum, and cover) are the most important ones that structure the spatial and temporal dynamics of habitats [32,33], affecting fish microhabitat use and energy budgets of different life stages as a result of shifting environmental conditions [34]. Thus, microhabitat assessments should encompass the joint effects of point physical variables in peaking rivers on species microhabitat use and availability, while integrating stratified sampling by season and ontogeny (i.e., size related).

The goal of this study is to assess fish microhabitat use at sites located upstream (i.e., reference) and downstream (i.e., disturbed) from peak-operating SHPPs, in particular searching for seasonal and size-related differences. This information can prove important to assist future conservation efforts and to inform possible mitigation measures that may serve as a model for other SHPP-regulated rivers. Specifically, we address the following questions: (i) Are the variables that drive species microhabitat use the same at reference (expected to be driven by depth and water velocity, ref. [35]) and at the peak-operating SHPP affected (henceforth, disturbed) river sites? (ii) Do species select different microhabitats (i.e., do species display non-random microhabitat use) at reference and disturbed river sites? (iii) Do species display seasonal or ontogenetic differences in microhabitat use at the reference and disturbed sites?

2. Materials and Methods

2.1. Study Area

The study area is located in the Couto and Avelames Rivers, tributaries of the Tâmega River (Douro River basin, Figure 1), northeast Portugal. These rivers present a low stream order (3) and small drainage basins (<100 km^2), with the riverbed being mainly composed of a mixture of boulders, cobbles, and sand. They typically run through a series of steep, narrow valleys and present a pluvial runoff regime, with both the riverbed and banks in natural conditions. Riparian vegetation consists of Pyrenean oak (*Quercus pyrenaica*), common alder (*Alnus glutinosa*) and poplar (*Populus* spp.). The climate is close to that of the Mediterranean with continental influence, characterized by warm and dry summers and concentrated precipitation from autumn to spring. There are no relevant pollution sources in these basins.

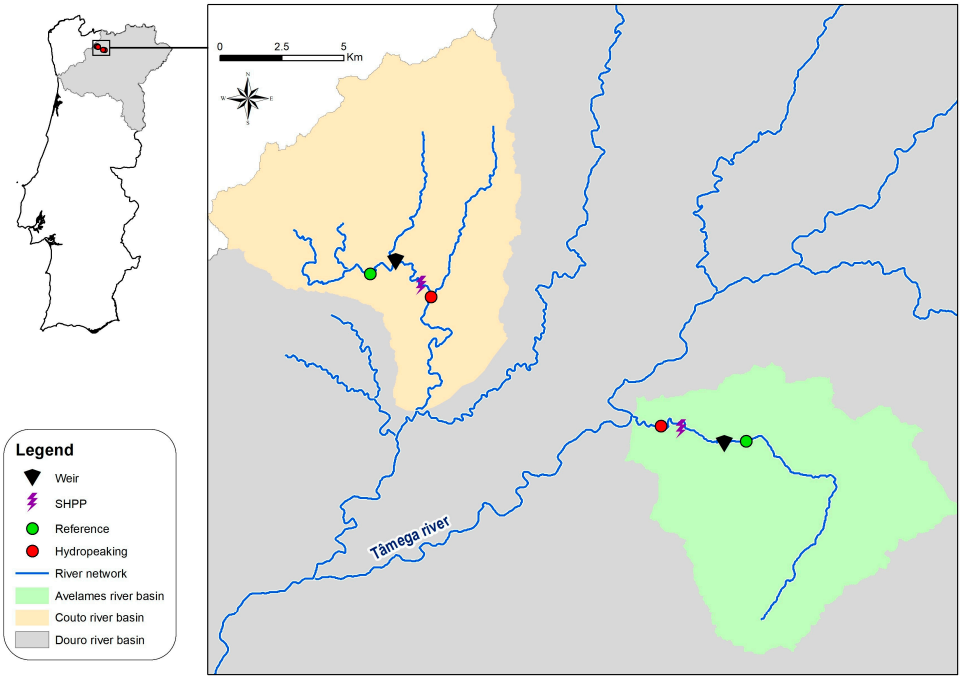


Figure 1. Study area (Avelames and Couto river basins), showing the location of the reference (upstream) and disturbed (downstream) sites sampled in early and late summer 2021, as well as those of each SHPP.

Both Couto and Avelames Rivers are regulated by SHPPs, namely, Covas do Barroso (41°37.830′ N; 7°47.696′ W) and Bragado (41°34.894′ N; 7°40.805′ W), respectively. The case studies are of run-of-river type [11], although they are able to store the portion of daily inflows smaller than the minimum design discharges, particularly during low flow periods (late spring to early autumn). This type of operation induces sudden variations in the river discharges downstream from the powerhouses' tailraces (Figure 2), which portrait a hydropeaking exploitation mode on fluvial segments downstream [34]. The diversion structures, located at steep and narrow valleys, have reduced storage capacities and transport water in canals to a distant forebay and then through a penstock to a powerhouse (Covas do Barroso = 3.0 km; Bragado = 3.6 km) and operate under a hydropeaking regime whenever there is sufficient water available (Figure 2). The mean annual flow and the design discharge at Covas do Barroso SHPP is 3.33 and 5.70 m^3/s, respectively. The equivalent values for Bragado SHPP are 1.28 and 2.20 m^3/s. The discharge assigned to ecological and irrigation purposes is 0.170 m^3/s at Covas do Barroso SHPP and 0.114 m^3/s at Bragado SHPP, which are released whenever SHPPs are not operating to maintain the longitudinal connectivity of habitats.

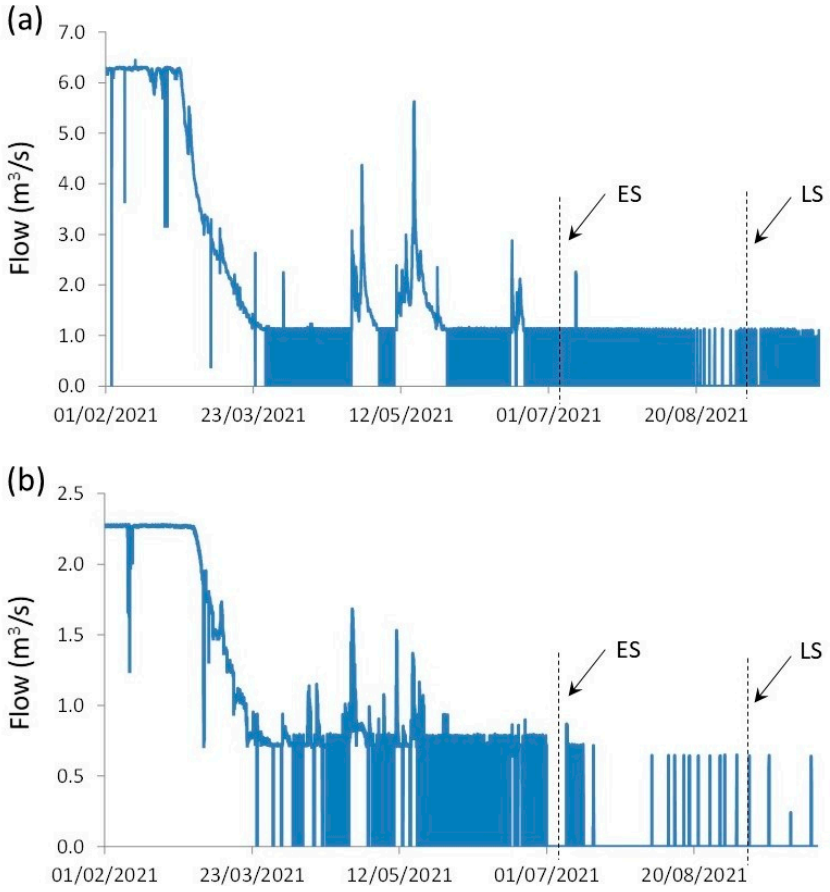


Figure 2. Hydrographs of (**a**) Couto and (**b**) Avelames rivers, downstream from Covas do Barroso and Bragado SHPPs, respectively. Both hydrographs present the turbined flow released by SHPP in the period from 1 February 2021 to 30 September 2021. Whenever the SHPPs are not operating (turbined flow = 0 m^3/s), the discharges assigned to ecological and irrigation purposes are released to maintain rivers' connectivity. The timing of fish sampling campaigns in early (ES) and late summer (LS) is marked with an arrow.

Four study sites, each 150 m long and 4–5 m wide—2 representing disturbed river segments located downstream of both SHPPs and 2 representing the corresponding reference conditions (i.e., without the occurrence of hydropeaking) located on the lotic river segments upstream of SHPPs—were selected. Because river barriers, such as SHPP weirs, can affect fishes in the free-flowing sections above their impoundment (e.g., by migratory blockage), the upstream river segments may not serve as the best reference sites for the fish community structure. Instead, reference sites selected in similar, but unregulated streams in the region, when available, can be more adequate candidates. As this was not the case, we treated the upstream lotic river segments as the best reference sites, in the sense that they are not affected by hydropeaking and lack any other human pressures, such as channelization, water abstraction, nutrient enrichment or agricultural/urban runoff. Such an approach has also been employed elsewhere, e.g., [7,36]. Riffles, runs and pools are the main mesohabitats found at both reference and disturbed sites, with similar proportions at both types of sites, i.e., 30%, 55% and 15%, respectively.

The rheophilic and lithophilic leuciscids Northern straight mouth nase (*Pseudochondrostoma duriense*, hereafter "nase") and Northern Iberian chub (*Squalius carolitertii*, hereafter "chub") are the dominant species in the study sites [37]. The former is a medium-sized fish that undergoes potamodromous migrations, whereas the latter is smaller in size (maximum recorded sizes are approximately 25 cm) [38]. Other species that occur in the study area are the calandino *Squalius alburnoides* (present in Avelames River, but not in Couto River), a

small-sized resident leuciscids, and the brown trout *Salmo trutta* (hereafter "trout"), present in Couto River only. Both are water-column and insectivorous species [39]. Previous studies conducted in the same river basin did not report competition for food and space between the studied species [35,40]. In addition to their intrinsic conservation value, these species are considered environmental sentinels due to their consistent frequency and abundance in well-preserved northern-Iberian rivers [35].

2.2. Fish Sampling

Fish sampling took place in early summer (6–8 July, hereafter "ES") and late summer (7–9 September, hereafter "LS") of 2021, when the powerhouses were operating discontinuously, potentially generating the greatest impacts associated with hydropeaking. Early- and late-summer periods are recognized as critical for Iberian stream fish, as they are associated with the spawning period of most native leuciscids species [41], when fish are expected to move upstream to spawning grounds, and the rearing and growth period, when fish abundance is expected to be at its highest in Mediterranean rivers [42]. In addition, these two seasons are the ones when hydropeaking is most likely to occur in the studied hydropower plants. Sampling was not conducted from winter to spring due to the high flows in the study area, which prevented access to the river in safe conditions. More specifically, sampling was conducted during daylight and under base-flow conditions at the reference sites and immediately after the turbine's shutdown at the disturbed sites, as it was technically impossible to sample the disturbed sites while the powerhouse plants were operating due to safety reason, because of the high-water depth and flow velocity. However, this shortcoming should not be sufficient to affect the representativeness of the results, as the study leuciscids [37] and a sister species of brown trout, the brook trout *S. fontinalis* [43], have been shown to present very small movement ranges (up to a few meters) upon facing hydropeaking conditions, thus presenting a strong site fidelity. Sampling was conducted in 150-m-long river segments selected from each site, chosen based on representativeness of the main habitat types (i.e., riffles, runs and pools) and accessibility. Streams' water temperatures during both sampling campaigns ranged between 15 °C and 17 °C (early summer) and between 17 °C and 19 °C (late summer), as measured by a multiparametric probe (HANNA, model HI 9812-5).

Fish capture methodology consisted of characterizing microhabitat use conditions (as defined by a set of physical variables—see Section 2.3 below) at the exact locations where an individual or a shoal of fish was captured. Different methods are available to assess microhabitat use by fish: electrofishing, underwater (i.e., snorkeling) and surface observations. As underwater and surface observations work better in slow-flowing habitats with fine substrata and minimum turbulence [44], capture was performed using wadable electrofishing (Hans Grassl IG-200), closely following the protocols adopted by the European Committee for Standardization [45]. However, the study followed a modified point electrofishing procedure (Hans Grassl IG-200, Schönau am Königsee, Germany) [46],to prevent pushing the anode forward in the water and avoid causing fish displacements from their original positions. Three operators—one gently maneuvering the anode and the others catching stunned fish with dip nets—moved upstream in zigzags to cover all mesohabitats. Upon the capture of a fish or a shoal of fishes, a numbered location marker was anchored to the streambed for the subsequent microhabitat use measurements [35]. Captured fish were then transferred to a separate dip net held by another operator and promptly measured for total length (TL) before being placed in buckets with portable aerators (ELITE, Holm, Germany) to avoid repeated counting. After the fish sampling, all fish were returned alive to the river. To further account for ontogenetic differences in microhabitat use, fish were stratified into size classes based on length-at-age differences reported in the literature, roughly corresponding to juveniles and adults, respectively: $\leq$11 and >11 cm TL for nase [47], $\leq$7 and >7 cm TL for chub [48]; <5 and $\geq$5 cm TL for calandino [33], and <12 and $\geq$12 cm TL for trout [49].

2.3. Microhabitat Use and Availability Measurements

2.3.1. Microhabitat Use

Following fish sampling, a set of microhabitat variables—water depth, mean water velocity, substratum composition (dominant size) and percent cover—were measured at the previously marked fish locations. Depth (cm) was measured with a graduated dipnet pole. Velocity measurements (cm/s) were taken with a flow probe (model FP101, Global Water Instrumentation, Inc., Sacramento, CA, USA) at 60% of the distance from the surface to the substratum if depth was less than 80 cm; otherwise, it was the mean of measurements recorded at 20% and 80% of depth. Both dominant substratum size and percent cover were determined visually in 0.8 × 0.8 m quadrats directly below the location of the captured fish. Substratum was measured according to a modified Wentworth scale [50] in eight size classes ((1) organic detritus; (2) silt (1–2 mm); (3) sand (2–5 mm); (4) gravel (5–25 mm); (5) pebble (25–50 mm); (6) cobble (50–150 mm); (7) boulder (>150 mm) and (8) bedrock). Cover was defined as any natural structure present in the riverbed (e.g., logs, tree roots, dead branches, submerged and emergent macrophytes <50 cm above water surface) that could confer protection to fish. It was estimated at each fish location in 10% increments, by the same operator to minimize potential errors.

2.3.2. Microhabitat Availability

Habitat selection studies have been widely used to quantify fish–habitat relationships, to assess and predict differential space use, and to identify habitat variables that are most important to fish, e.g., [51]. Quantifying habitat selection involves the statistical comparison of samples of microhabitat use and availability. Selection is therefore contingent upon both of these samples and results from the ratio between proportional use and availability [52]. Therefore, after microhabitat use measurements at each sampling site, the microhabitat availabilities for the same variables (i.e., depth, velocity, substratum and cover) were measured every 0.50 m at 15–25 equidistant transects perpendicular to the flow and placed along representative mesohabitat units (i.e., runs, riffles and pool) encompassing site length to enable comparisons with microhabitat use and to search for non-random patterns.

2.4. Data Analysis

Data analysis followed the procedures from Santos et al. [33,35]. Differences in microhabitats available to and used by fish between the reference and the disturbed sites were first assessed either with an analysis of variance (ANOVA) for continuous variables (depth and water velocity) or a Kruskal–Wallis test for the ordinal variables (substratum and percent cover) [33]. For this, data were previously combined within each type of site, as a previous ANOVA and Kruskal–Wallis tests revealed no significant differences in microhabitat availability variables between them. However, as fish do not select physical habitat attributes independently of one another, but instead, choose specific habitats based on distinct combinations of variables (e.g., depth and velocity) [53], a multivariate approach was also performed to prevent misinterpretation of results. In addition, to evaluate the non-randomness (i.e., selection) of a species, spatial distribution requires contrasting microhabitats used with those available, taking into consideration that use can be modified according to resource availability [54]. Therefore, principal component analysis (PCA) with varimax rotation [55] employing availability and use data for reference and disturbed sites were employed separately for both types of sites to search for non-random (i.e., selective) microhabitat use by fish and to search for possible seasonal and size-related microhabitat use patterns [33,35]. Non-random microhabitat use occurs when median PCA scores of measurements taken to determine the microhabitat use by fish are significantly different ($p < 0.05$) than those taken to determine the available habitat. The analysis was conducted using transformed values to approach normality (log(x + 1) for all variables, except for percent cover, which was arcsin square root transformed) using the package STATISTICA v.10 (StatSoft, Inc., Tulsa, OK, USA). Only species size classes with sample sizes ≥ 10 were considered [35]. The components with eigenvalues > 1 and variables with loadings $\geq |0.70|$

were retained for interpretation, e.g., [33]. Mann–Whitney U-tests were conducted on the PCA scores to search for seasonal (i.e., from ES to LS) and size-related (i.e., from juveniles to adults) differences in species microhabitat use.

3. Results

3.1. Microhabitat Availability and Use

In total, 494 nase (mean TL ± SD: 82 ± 25 mm), 174 chub (76 ± 27 mm), 105 trout (124 ± 78 mm) and 60 calandino (67 ± 12 mm) were captured during the sampling program (Table 1). Nase accounted for most of the individuals (n = 427, 72.7%) in the disturbed sites, while chub (n = 97, 39.4%) represented the most captured species in the reference sites. Altogether, the sampled individuals from the four species accounted for 98.8% of the total captures.

Overall, and considering both seasons, the available water depth ranged from 4 to 150 cm and from 4 to 106 cm at the reference and disturbed sites, respectively, with no significant differences in the mean values (mean ± SD: reference = 39.9 ± 24.8 cm, disturbed = 38.8 ± 17.7 cm; ANOVA, F = 0.43, $p > 0.05$). Despite a similar range of water velocity experienced by both the reference and disturbed sites (0–106 cm/s), the mean values were significantly higher for the latter (13.3 ± 19.6 cm/s) than for the former (8.4 ± 17.2 cm/s) (ANOVA, F = 11.01, $p < 0.01$). The substrata at both types of sites were similar (Kruskal–Wallis test, $p > 0.05$) and mainly consisted of boulder and bedrock (median (range): class 7 (3–8)), with sand and gravel characterizing the deeper (pool) habitats. A similar finding was noted for instream cover, as its availability to fish was similar for the reference (median (range): 30% (0–100%)) and disturbed (30% (0–90%)) sites (Kruskal–Wallis test, $p > 0.05$), and was mainly in the form of patches of aquatic macrophytes, logs and submerged roots of riparian galleries.

Significant differences in depth use between the reference and disturbed sites were found for all species (ANOVAs, $p < 0.05$), with individuals at the disturbed sites using on average deeper microhabitats (nase: 50.2 ± 14.8 cm; chub: 47.5 ± 18.3 cm; trout: 53.4 ± 13.3 cm; calandino: 43.0 ± 15.2) than the ones found at the reference sites (nase: 44.5 ± 20.9 cm; chub: 39.8 ± 14.6 cm; trout: 11 ± 25 cm/s; calandino: 35.3 ± 10.7 cm/s). On the contrary, no significant differences (ANOVAs, $p > 0.05$) were detected regarding species velocity use between the reference (nase: 5.6 ± 10.3 cm/s; chub: 3.9 ± 11.5 cm/s; trout: 10.7 ± 24.9 cm/s; calandino: 2.7 ± 5.1 cm/s) and disturbed sites (nase: 3.8 ± 9.9 cm/s; chub: 5.4 ± 9.0 cm/s; trout: 13.6 ± 20.0 cm/s; calandino: 2.6 ± 4.9 cm/s). Except for the calandino (reference: median = class 8, bedrock; hydropeaking: median = class 7, boulder; Kruskal–Wallis test, $H = 6.51$, $p < 0.05$), the other species did not differ in their substratum use in the reference and disturbed sites (median = 7, range 3–8; Kruska–Wallis tests, $p > 0.05$). A similar pattern was observed for cover, in which the calandino was the only species showing significant differences (Kruskal–Wallis test, $H = 5.50$, $p < 0.05$), as individuals from the reference sites favored microhabitats with a higher percentage of cover (median (range): 70% (10–100%)) relative to the ones from the disturbed sites (40% (10–90%)).

Table 1. Seasonal microhabitat available to, and used by, native leuciscids (nase, chub and calandino) and salmonids (trout) in Avelames and Couto River basins (Tâmega River, Douro basin, NE Portugal). Ref.—reference sites; Dis.—disturbed sites. Mean total length (TL) and range of individuals is also shown.

Season			Mean TL (Range) (cm)		Depth (cm)		Water Velocity (cm/s)		Substratum (Class)		Cover		N	
			Ref.	Dis.	Ref.	Dis.	Ref.	Dis.	Ref.	Dis.	Ref.	Dis.	Ref.	Dis.
Early summer	Availability				47.7 (5–150)	46.5 (4–106)	13.9 (0–106)	21.7 (0–106)	8 (3–8)	8 (3–8)	30 (0–90)	30 (0–90)	177	118
	Use													
		Nase												
		juvenile	6.7 (5.0–10.0)	8.0 (3.0–11.0)	54.6 (5.5)	45.8 (1.2)	14.4 (3.3)	9.6 (1.5)	8 (3–8)	8 (3–8)	35 (10–80)	30 (0–90)	20	103
		adult	-	-	-	-	-	-	-	-	-	-	0	7
		Chub												
		juvenile	5.8 (4.5–7.0)	5.2 (4.0–7.0)	38.6 (2.7)	57.1 (5.8)	3.7 (1.9)	6.5 (2.3)	8 (3–8)	8 (6–8)	20 (0–90)	50 (20–80)	27	20
		adult	10.8 (8.0–15.0)	10.0 (8.0–13.0)	46 (3.5)	47.6 (2.6)	11.1 (5.9)	9.7 (2.0)	8 (3–8)	8 (3–8)	35 (20–80)	40 (10–80)	16	27
		Calandino												
		juvenile	-	-	-	-	-	-	-	-	-	-	1	1
		adult	6.7 (6.0–8.0)	6.5 (6.0–7.5)	35.3 (1.3)	43.3 (2.7)	4.9 (1.8)	4.8 (1.5)	8 (8–8)	6 (3–8)	40 (10–50)	30 (20–60)	12	12
		Trout												
		juvenile	5.4 (4.0–7.0)	6.3 (5.0–8.0)	21.5 (1.2)	57.9 (3.6)	42.1 (10.3)	31.8 (6.6)	8 (6–8)	8 (3–8)	30 (20–50)	50 (30–50)	13	16
		adult	-	-	-	-	-	-	-	-	-	-	0	6
Late summer	Availability				32.6 (4–79)	32.7 (4–84)	3.3 (0–67)	6.7 (0–81)	7 (3–8)	7 (3–8)	30 (10–100)	30 (10–90)	189	150
	Use													
		Nase												
		juvenile	7.5 (4.0–11.0)	7.7 (3.0–11.0)	36.9 (3.3)	51.5 (0.9)	2.6 (0.8)	1.8 (0.4)	7 (3–8)	7 (3–7)	60 (20–100)	70 (10–100)	35	299
		adult	17.3 (12.0–25.0)	12.4 (11.5–15.0)	49.6 (0.4)	51.1 (3.5)	0 (0.0)	1.9 (0.9)	7 (6–7)	7 (7–7)	85 (50–100)	65 (20–100)	12	18
		Chub												
		juvenile	5.7 (3.0–7.0)	5.9 (2.5–7.0)	38.1 (2.1)	39.1 (3.6)	0.9 (0.4)	0.6 (0.6)	7 (3–8)	7 (3–7)	50 (10–100)	55 (20–70)	34	14
		adult	9.9 (7.5–16.0)	9.5 (7.5–12.5)	39.2 (4.2)	42.9 (3.3)	3.2 (1.1)	1.2 (0.8)	7 (3–8)	7 (3–7)	65 (40–100)	50 (30–100)	20	16
		Calandino												
		juvenile	-	-	-	-	-	-	-	-	-	-	0	2
		adult	7.2 (5.0–9.0)	6.9 (6.0–8.5)	34.9 (3.9)	45.6 (4.0)	0 (0.0)	1.6 (1.1)	5.5 (3–8)	7 (3–7)	90 (70–100)	70 (10–90)	14	18

Table 1. *Cont.*

Season			Mean TL (Range) (cm)		Depth (cm)		Water Velocity (cm/s)		Substratum (Class)		Cover		N	
			Ref.	**Dis.**	**Ref.**	**Dis.**	**Ref.**	**Dis.**	**Ref.**	**Dis.**	**Ref.**	**Dis.**	**Ref.**	**Dis.**
Late summer	Availability				32.6 (4–79)	32.7 (4–84)	3.3 (0–67)	6.7 (0–81)	7 (3–8)	7 (3–8)	30 (10–100)	30 (10–90)	189	150
		Trout												
		juvenile	7.4 (3.0–9.5)	8.3 (7.0–10.0)	30.7 (2.5)	49.0 (3.9)	1.4 (0.7)	1.8 (0.8)	7 (3–7)	7 (7–8)	40 (20–70)	50 (20–60)	23	14
		adult	18.7 (12.0–26.0)	26.1 (22.0–31.0)	45.7 (1.8)	53.4 (1.8)	0.6 (0.3)	4.4 (1.0)	7 (6–7)	7 (3–8)	70 (20–90)	75 (20–100)	19	14

Notes: Mean values are given for depth and water velocity, followed by standard error or range (in parentheses), for use and availability data, respectively. Median values (with range in parentheses) are given for dominant substratum size (1—organic detritus; 2—silt; 3—sand; 4—gravel; 5—pebble; 6—cobble; 7—boulder; 8—bedrock) and cover (in 10% increments). Statistics are only given for sample sizes $\geq$ 10. Species have been partitioned on the following size classes roughly corresponding to juveniles and adults, respectively: $\leq$11 and >11 cm TL for nase [55]; $\leq$7 and >7 cm TL for chub [56]; <5 and $\geq$5 cm TL for calandino [40]; and <12 and $\geq$12 cm TL for trout [57].

3.2. Non-Random (Selective) Microhabitat Use

Principal component analysis of the microhabitat availability and use by nase at the reference sites extracted two principal components (PCs) with eigenvalues > 1, which explained 65.6% of the variance in the data (Figure 3a). Depth (0.83) and cover (0.85) were positively loaded on the first principal component (PC1). Nase were found to select specific microhabitats, as this species showed non-random microhabitat use for this component, i.e., being overrepresented in deeper and sheltered positions (Mann–Whitney U-test on PCA scores, $Z = -5.10$, $p < 0.001$). PC2 loaded high on substratum (0.78), but no indication of non-random microhabitat use was found ($Z = 1.18$, $p > 0.05$). At the disturbed sites, PCA yielded two PCs with eigenvalues > 1, which explained 68.7% of the variance in the data (Figure 3b). Similar to the reference sites, depth (0.79) and cover (0.89) loaded high on PC1, with non-random microhabitat use being detected ($Z = -13.01$, $p < 0.001$).

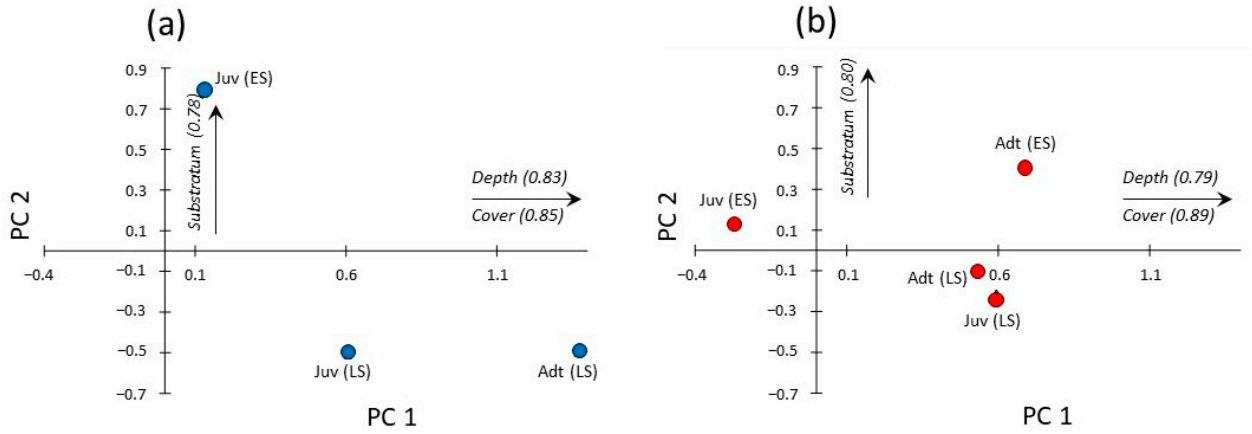


Figure 3. Principal component analysis (PCA) of seasonal and size-related microhabitat use by nase (*Pseudochondrostoma duriense*) at (**a**) reference river sites and at (**b**) river sites affected by peak-operating SHPPs. Mean PCA scores are shown for species size classes (Juv—juveniles; Adt—adults), in early summer (ES) and late summer (LS). Variables with loadings $\geq |0.70|$ are also shown. Only species size classes with sample sizes ≥ 10 were considered (see Table 1 for details).

Substratum (0.80) was the single variable that positively loaded on PC2. Non-random habitat use was found in this component, i.e., with nase being overrepresented in finer substrata ($Z = 2.75$, $p < 0.01$).

Principal component analysis of microhabitat availability and use by chub at the reference sites produced two PCs with eigenvalues > 1, accounting for 65.0% of the variance in the data (Figure 4a). Depth (0.84) and cover (0.85) loaded high on the first PC, with chub showing non-random microhabitat use ($Z = -4.23$, $p < 0.001$) similar to that of nase for this component. Substratum (0.77) was the single variable that loaded high on PC2, with chub being overrepresented on finer substrata ($Z = 3.45$, $p < 0.001$). PCA on availability and use data by chub at the disturbed sites extracted two PCs with eigenvalues > 1, which accounted for 65.0% of variation in the data (Figure 4b). Again, depth (0.87) and cover (0.83) were positively loaded on PC1, with chub being overrepresented at deeper and sheltered positions ($Z = -5.28$, $p < 0.001$). PC2 loaded high on substratum (0.82), but non-random microhabitat was not found for this component ($Z = 1.06$, $p > 0.05$).

Principal component analysis of microhabitat availability and use by calandino at the reference sites extracted two PCs with eigenvalues > 1, which explained 63.7% of the variance in the data (Figure 5a). PC1 loaded high on cover (−0.71) and velocity (0.89), with calandino being overrepresented in slow-flowing areas with high cover ($Z = 4.66$, $p < 0.001$). For PC2, depth was selected as the most important variable (0.89), with this species selecting deeper habitats ($Z = -2.75$, $p < 0.01$). PCA conducted on data from the disturbed sites revealed two PCs that accounted for 67.9% of data variance (Figure 5b). PC1 loaded high on depth (0.80) and cover (0.91), with calandino being overrepresented in

deeper and more covered habitats ($Z = -2.86$, $p < 0.01$). PC2 loaded high on velocity (0.91), with calandino selecting slower-flowing areas ($Z = 3.19$, $p < 0.01$).

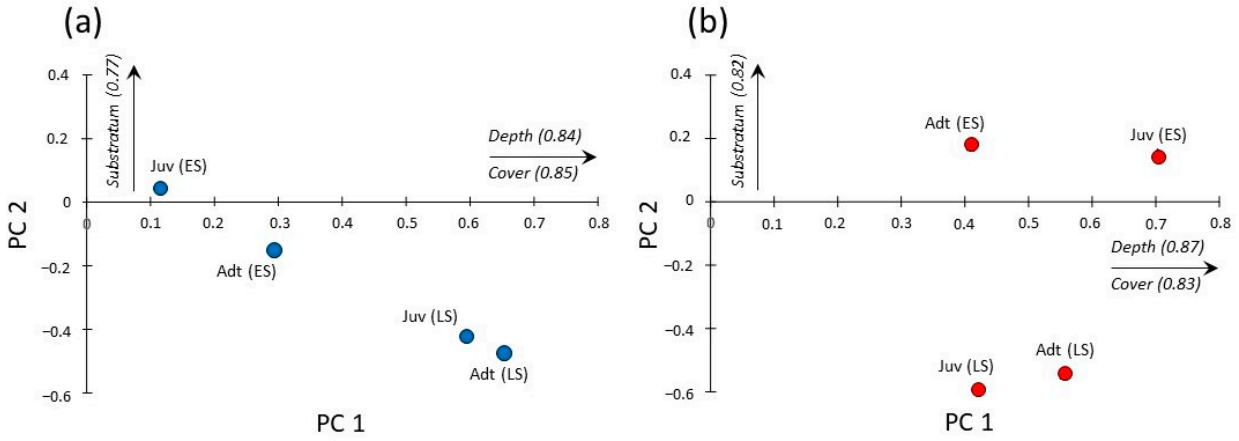


Figure 4. Principal component analysis (PCA) of seasonal and size-related microhabitat use by chub (*Squalius carolitertii*) at (**a**) reference river sites and at (**b**) river sites affected by peak-operating SHPPs. Mean PCA scores are shown for species size classes (Juv—juveniles; Adt—adults) in early summer (ES) and late summer (LS). Variables with loadings $\geq |0.70|$ are also shown.

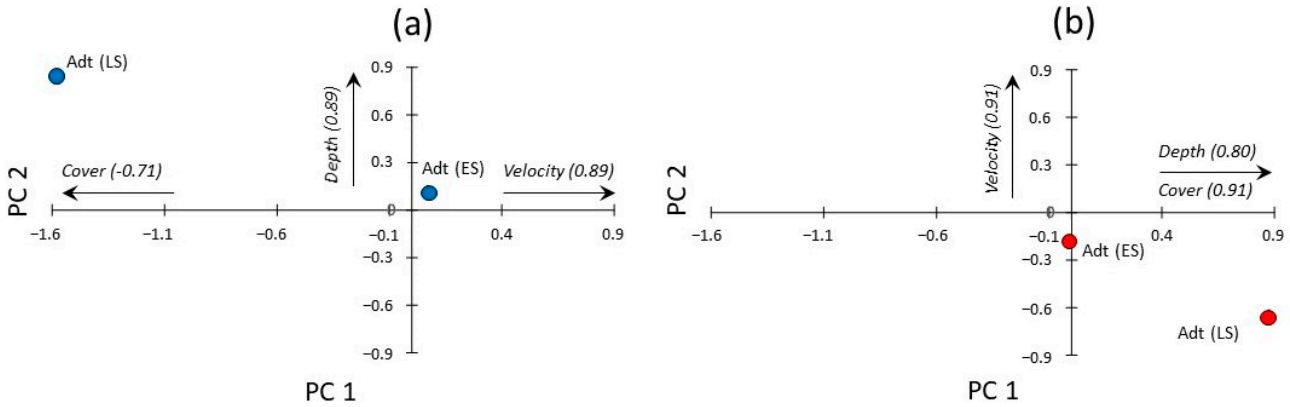


Figure 5. Principal component analysis (PCA) of seasonal and size-related microhabitat use by calandino (*Squalius alburnoides*) at (**a**) reference river sites and at (**b**) river sites affected by peak-operating SHPPs. Mean PCA scores are shown for adult fish (no sufficient number of samples for juveniles were obtained), in early summer (ES) and late summer (LS). Variables with loadings $\geq |0.70|$ are also shown. Only species size classes with sample sizes ≥ 10 were considered (see Table 1 for details).

Principal component analysis of availability and use by trout at the reference sites yielded two components with eigenvalues > 1, which explained 73.4% of the variation (Figure 6a). PC1 had high loadings on depth (0.87) and cover (0.88), whereas velocity (0.81) was the single variable that loaded on PC2. No indication of non-random microhabitat use was found for either PC ($p > 0.05$). At the disturbed sites, PCA produced two PCs that explained 64.9% of the variance in the data (Figure 6b). Again, PC1 loaded high on depth (0.82) and cover (0.84), with trout being overrepresented in deeper and more covered areas ($Z = -5.92$, $p < 0.001$). PC2 loaded high on substratum (-0.80) and there was no evidence of non-random microhabitat use for this component ($Z = 1.33$, $p > 0.05$).

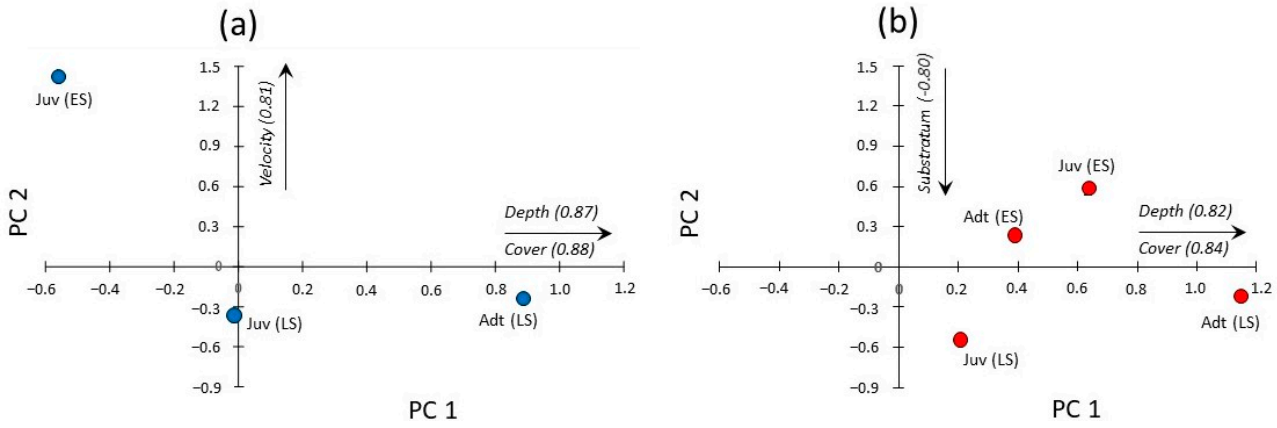


Figure 6. Principal component analysis (PCA) of seasonal and size-related microhabitat use by trout (*Salmo trutta*) at (**a**) reference river sites and at (**b**) river sites affected by peak-operating SHPPs. Mean PCA scores are shown for species size classes (Juv—juveniles; Adt—adults) in early summer (ES) and late summer (LS). Variables with loadings $\geq |0.70|$ are also shown. Only species size classes with sample sizes ≥ 10 were considered (see Table 1 for details).

3.3. Seasonal and Size-Related Variations in Microhabitat Use

Mann–Whitney tests on the PCA scores of PC1 showed a significant effect of season on microhabitat use by nase at both the reference ($Z = -2.93$, $p < 0.01$) and disturbed ($Z = -8.09$, $p < 0.001$) sites (Table 2, Figure 3a,b), with individuals shifting to deeper and more covered habitats from ES to LS. Microhabitat use for this component was also size related but only for the reference sites ($Z = -3.83$, $p < 0.001$) (Figure 3a), where adults used deeper and more covered areas than juveniles. A significant effect of season was also reported at PC2, with individuals shifting to finer substrata from ES to LS, both at the reference ($Z = 4.67$, $p < 0.001$) (Figure 3a) and disturbed ($Z = 4.82$, $p < 0.001$) (Figure 3b) sites. The effect of size class was not significant for either type of site ($p > 0.05$).

Table 2. Results of the Mann–Whitney U-tests on principal component analysis (PCA) scores addressing the effect of season and size class on microhabitat use of native leuciscids (nase, chub and calandino) and salmonids (trout) in reference and disturbed sites, in relation to the extracted principal components (PCs).

Species	PC	Source of Variation	Reference		Disturbed	
			Z	*p*	Z	*p*
Nase	1	Season	−2.93	<0.01	−8.09	<0.001
		Size-class	−3.83	<0.001	−0.72	0.471
	2	Season	4.67	<0.001	4.82	<0.001
		Size-class	1.82	0.070	0.71	0.478
Chub	1	Season	−2.27	<0.05	0.06	0.950
		Size-class	−1.22	0.222	0.59	0.552
	2	Season	4.07	<0.001	4.35	<0.001
		Size-class	0.29	0.774	−0.58	0.559
Calandino	1	Season	4.32	<0.001	−2.62	0.01
		Size-class	--	--	--	--
	2	Season	−1.85	0.064	1.41	0.059
		Size-class	--	--	--	--
Trout	1	Season	−3.76	<0.001	−1.17	0.241
		Size-class	−4.86	<0.001	−2.75	<0.01
	2	Season	4.58	<0.001	2.99	<0.01
		Size-class	1.08	0.063	0.89	0.373

A significant seasonal effect ($Z = -2.27$, $p < 0.01$) was detected on PC1 of the chub data, as individuals shifted to deeper and more covered areas from ES to LS at the reference sites (Table 2, Figure 4a). In contrast, the season was not significant for this component for the disturbed sites ($Z = 0.06$, $p > 0.05$) (Figure 4b). The effect of size class was also insignificant for this component for both types of sites ($p > 0.05$). As with nase, the season was found to have a significant effect on microhabitat use by chub on PC2 at both the reference ($Z = 4.07$, $p < 0.001$) (Figure 4a) and disturbed ($Z = 4.35$, $p < 0.001$) (Figure 4b) sites, as individuals shifted to finer substrata from ES to LS. Again, size class was not significant for this component for either type of site ($p > 0.05$).

Season had a significant effect on the microhabitat use of calandino at both types of sites, as shown by the Mann–Whitney test on the PC1 scores. Accordingly, at the reference sites (Table 2, Figure 5a), individuals were found to shift to more covered and slow-flowing areas from ES to LS ($Z = 4.32$, $p < 0.001$), whereas at the disturbed ones (Figure 5b), fish shifted to deeper and more covered habitats during LS ($Z = -2.62$, $p < 0.01$). No significant seasonal effects were found for PC2 at either type of site ($p > 0.05$).

For trout, the Mann–Whitney tests on the PC1 scores highlighted a significant effect of both season ($Z = -3.76$, $p < 0.001$)—with individuals shifting to deeper and more covered areas in LS—and size class ($Z = -4.86$, $p < 0.001$)—with adults using deeper and more covered habitats than juveniles—at the reference sites (Table 2, Figure 6a). However, for the disturbed sites, a significant effect on this component was only noted for size class ($Z = -2.75$, $p < 0.01$), with adults using deeper and more covered positions than juveniles (Figure 6b). Regarding PC2, significant effects were only reported for season for both types of sites: indeed, at the reference sites, individuals shifted to slower-flowing areas from ES to LS ($Z = 4.58$, $p < 0.001$) (Figure 6a), whereas at the disturbed sites (Figure 6b), substratum was the key variable, with fish shifting to coarser substrata from ES to LS ($Z = 2.99$, $p < 0.01$).

4. Discussion

As with LHPPs, SHPPs are known to have multiple impacts on the health of river ecosystems, in particular the loss of longitudinal connectivity and the consequent fragmentation of critical habitats, the disruption of the natural flow regime and the inundation of former flowing habitats into homogenous lentic ones (i.e., reservoir) that stand as behavioral barriers [9,11]. Fishes are particularly sensitive to such effects, as the most immediate consequence caused by SHPP installation is the blockage of their movements to upstream spawning and feeding habitats, or to downstream floodplains for refuging [7]. In the downstream affected river segments, changes in habitat use can also arise due to suppression or alteration of the natural flow regime, as well as to the trapping of organic matter and sediments in the upstream reservoirs. Nonetheless, due to their geographic location—typically in low- to medium-sized rivers, still encompassing a high degree of riparian vegetation coverage and habitat patchiness—their smaller size and diverse modes of operation (that often do not store flows, sensu [11]), as well as a lower detectable effect of the impoundments (10–300 m) they create, the magnitude of such impacts can be much smaller than those created by LHPPs [7,11].

4.1. Driving Variables of Microhabitat Use

One of the most prominent results of this study was that the variables that structured microhabitat use for fish species at the reference and disturbed sites were cover and depth, as shown by the high loadings on PC1, which explained most of the variation for all the species studied. This partially agrees with our initial expectation that depth and water velocity should be the most important variables for habitat selection, particularly at the reference sites. Reference sites are not subjected to human-induced abrupt flow variations, e.g., [35], and hence, fish should not be dependent on the use of cover against potentially harsh environmental conditions, such as those experienced under hydropeaking [14,56]. Some studies reported different rankings of habitat variables in leuciscid microhabitat

use, where substratum, e.g., [57,58], or depth [59] were appointed as the primary factors affecting microhabitat use. In undisturbed or minimally disturbed river segments, several other factors, such as microhabitat availability, may affect the ranking of microhabitat variables, as well as factors not accounted for in the present study, such as time of day, food resources, or species interactions [60]. The inclusion of these variables in habitat-use models has been recommended [25] and should be considered in future research. It is also possible that different habitat factors may be limiting in different streams [61].

The importance of cover for fish microhabitat use and for fish assemblage structure has been highlighted in several studies, e.g., [62]. Cover provides (i) protection against predators, (ii) visual isolation, reducing competition risk, and (iii) hydraulic shelter against detrimental environmental conditions, such as those imposed during hydropeaking. Therefore, cover is a critical factor in most fish lifecycle stages, including spawning or growth and diel life activities, including foraging, resting, or avoiding predators. A field study designed to assess the effect of induced hydropeaking on habitat use by trout showed that individuals were not displaced by peak flows, provided that a coarse substratum supplying cover was present [63]. Under experimental hydropeaking conditions, ref. [64] highlighted the role of an overhead cover consisting of a plywood structure, which acted as an effective hydropeaking flow–refuge mitigation measure. In the present study, additional forms of cover could have also been provided by the well-structured and continuous riparian vegetation galleries. Besides offering cover, vegetation also has important functions in terms of ecological structure and river functioning, namely, by providing structural protection for instream habitats, regulation of the river flow, as well as substratum fixation for algae and periphyton [65]. On the other hand, in contrast to lowland streams, the role of cover is higher where there is a more acute contact of riparian vegetation with the aquatic stream, i.e., in rivers with narrow channels and where the water volume is relatively low [66], as it was at the sites of the present study.

Depth and substratum were selected as key variables for nase and chub, the most abundant species in the study area, as shown by the high loadings displayed on PC1 and PC2, respectively, at both the reference and disturbed sites. Such variables have been previously determined to be important correlates of fish assemblage organization [67]. Deeper habitats, such as pools, can offer refuge during summer drying or provide increased protection for larger fish against visual predators [68]. Pools may also be utilized by fish in an attempt to seek shelter during and following abrupt hydropeaking flow variations, as they are considered more 'stable' environments. Though we could not find in the literature evidence of microhabitat shifts to deeper areas (pools) by fish in areas influenced by peak flows, it is clear that this is an issue that deserves future attention, as creating "nature-like" pools, using native woody debris [69] in peaking rivers could be a possible mitigation measure to "dampen" hydropeaking impacts further downstream, e.g., [70]. The availability of coarse substratum, as in the present study, where boulders and cobbles dominated, is important to provide hydraulic shelter against excessive current velocities [7], hindering fish from being washed away by sudden discharges. Some differences on the importance of variables were, however, reported between the reference and disturbed sites, particularly for trout. Though, once again, depth and cover were found to be the most influential variables at both types of sites; velocity was more important at the reference sites, whereas substratum was found to be key at the disturbed ones. The association of water velocity to trout microhabitat use in natural streams is widely reported in the literature, e.g., [53,71], as this species typically inhabits areas with low to moderate velocities [72], often choosing velocity shelters close to fast-flowing areas, as they are the most energetically profitable positions [73]. At the disturbed sites, we believe that, due to the occurrence of abrupt daily flow variations (Figure 2), that are expected to impose higher energetic costs to sustain positions [74], it is possible that the effect of the substratum overtakes that of the velocity, e.g., [75,76].

4.2. Non-Random (Selective) Microhabitat Use

The results demonstrated that all species exhibited similar patterns of non-random microhabitat use at the reference and disturbed sites, i.e., preferring the same types of habitats. At both types of sites, nase and chub occupied non-randomly deeper and sheltered microhabitats than those available, as shown by the PC1 high loadings. Both species also showed non-random microhabitat use on PC2, which was substratum-related, being overrepresented in habitats with finer substrata. Taken together, these patterns seem to suggest an association of both species with pool habitats. Similar results—mainly snapshot studies based on a single season (usually summer)—have been reported by other authors in Iberian rivers, e.g., [39], suggesting that both species mainly adopt pool-dwelling behavior to both counteract the effects of water shortages in warmer seasons and also the effects of floods and peaking events in the wet ones [37]. However, an association to water velocity (but not to substratum) at the reference sites would be expected, at least for nase, which is often described to inhabit fast-flowing areas of running waters [35,47], whereas chub is more generalist in terms of habitat preference [38]. It is possible that this lack of association could be the result of the impossibility of sampling in the winter and spring seasons (see Section 2.2), when the dependence of summer refugia is expected to be lowest [77], and fish habitat use is mainly driven by water velocity, following concurrent microhabitat availability [35]. It is clear that future studies should be conducted all year round, including during the flooding season, when sampling with electrofishing is often constrained by river inaccessibility due to the occurrence of high flows. This could be performed using fish-marking techniques, such as radio telemetry [78], to better clarify microhabitat use patterns between low and high flows, including the shift between habitat patches as they change over time [34].

Like nase and chub, calandino showed evidence of non-random microhabitat use at the reference and disturbed sites. Though the ranking of variables selected by each PC was different for the two types of sites, the overall microhabitat use of this species at both types of sites was structured based on the same variables, i.e., cover, depth, and velocity, with individuals from both sites occupying deeper and slow-flowing areas with higher amounts of cover than those available. Such similarity regarding microhabitat use of the studied peaking rivers appears once again to be related to the high amount of cover habitat, the maintenance of well-developed riparian galleries, and the availability of undisturbed large-sized substrata, such as boulders and rocks. These, coupled with the smaller size and lower flow magnitudes when compared to large hydropower plants, may not be sufficient to exceed the environmental range needed to alter the role of key variables structuring species microhabitat use [7]. Stranding, a common phenomenon observed in many hydropeaking rivers [13], was never detected throughout the sampling period, though its occurrence should be minimal, as this phenomenon is mainly driven by (i) the substratum particle size, with stranding being higher in the presence of finer substrata such as sand or gravel, e.g., [79] and (ii) riverbank slope [80], with stranding being higher in the presence of flat riverbanks and very low in cases of steep banks, as is the case in our study area. Future studies encompassing long-term periods would be needed to clarify these issues and explore any possible effects on species recruitment and fitness and to further clarify the effects of peaking flows on species microhabitat use.

In contrast to leuciscids, we found no evidence of non-random microhabitat use by trout at the reference streams, confirming their plasticity in habitat selection that has been already described, e.g., [53]. This species can flexibly change selection behavior as a function of habitat features, which is, in turn, determined by the interaction of the structural features of the channel and the hydrological regime [53]. In rivers characterized by a Mediterranean regime of high intra- and interannual flow variability, as in the study area, river hydrology can be a relevant driving force for trout dynamics [81], as this species may display higher habitat plasticity in such variable environments [71]. However, following hydropeaking conditions, trout were found to display non-random microhabitat use, occupying deeper and sheltered positions than those available. As habitat use by trout is highly based on the

profitability of territory in terms of the potential net energy intake rate [82] and, thus, on the tradeoff between energy gain and risk [83], we believe that the selection of deeper and sheltered positions provided increased protection against peaking flows, making them able to cope with excessive current velocity and drifting [84].

4.3. Seasonal and Size-Related Variation in Microhabitat Use

Overall, the seasonal and size-related patterns in species microhabitat use were similar for the reference and the disturbed sites, with the majority of species displaying seasonal patterns in microhabitat use from ES to LS (though such shifts were more expressive at the reference sites) but, in most of the cases, revealing no size-related differences between the two types of sites. The most common species showed a shift to deeper and more covered areas from ES to LS, along with the selection of areas with finer substrata. This would be naturally expected, particularly in rivers that seasonally experience water shortages due to their Mediterranean regime, and where fish need to find deep and sheltered positions in late summer to increase their survival chances during this season, e.g., [85]. As with nase and chub, both cover and depth primarily structured microhabitat use of trout at the reference and the disturbed sites. However significant seasonal variation was only found for the former, with individuals shifting to deeper and sheltered positions from ES to LS. It is possible that the lack of seasonal differences in habitat use at the disturbed sites can be related to the release of peak flows, which change with seasonal environmental variability, bringing no advantage for trout to shelter in deep pools in late summer, as this species has a strong swimming capability [86], making it able to withstand fast-flowing velocities associated with small-scale artificial peak-flow events [87]. The similarity in seasonal microhabitat use patterns between the reference and disturbed sites was also evident for the calandino, as microhabitat use by this species at both types of sites was also cover related, with this species shifting to more covered areas from ES to LS. This result agrees with others from other Mediterranean rivers, in which this species could be classified as a shelter-oriented eurytopic species, as cover was the most important variable [33].

Unlike seasonal patterns, significant size-related differences in microhabitat use by species were barely noted, either at the reference or disturbed sites. A few exceptions were noted for the nase at the reference sites and for trout at both types of sites, in which adults used deeper and more covered habitats than juveniles. This is in accordance with the frequently documented larger fish—deeper habitat association, either for leuciscids [33,35] or salmonids [71]. In the present study, such patterns could result from an antipredator response (i) to shallower areas of smaller fish, avoiding non-gape-limited predators, such as the otter (*Lutra lutra*), and water snakes (*Natrix natrix* and *Natrix maura*), which feed in deeper areas [37], and (ii) to deeper areas of larger fish, avoiding visual predators, such as birds [88]. It should be noted, however, that the observed size-related differences could also be due to other factors, such as time of day, presence of competitors, water temperature or river flow [60], as due to operational and safety limitations it was not possible to sample during the high-flow periods of turbine operation, a limitation of the study that deserves further attention in future investigations. Once again, the absence of differences—in this case, in size-related habitat use patterns—between the reference and disturbed sites seems to indicate the effect of habitat heterogeneity and the availability of highly undisturbed coarse substratum and cover in overcoming the effects of peak flows.

5. Conclusions

This study showed that differences in fish microhabitat use between sites downstream of SHPPs and upstream of reference sites were negligible. Cover and depth were found to be the most important variables structuring habitat use, both at the reference and disturbed sites, being therefore critical, as they also elicited non-random responses for all species, as shown by the PCA results. For nase and chub, by far the two most abundant species in the study area, substratum was secondarily important, as it always loaded high on PC2. We suggest that these variables have created rich and heterogeneous

habitats at the disturbed sites, thereby providing satisfactory resources and favorable conditions required by fish to cope with hydropeaking. Cover was provided by a diversity of forms, such as well-structured and continuous riparian vegetation galleries, as well as patches of aquatic macrophytes, logs and submerged roots, and indirectly by the availability of coarse undisturbed substrata (mainly boulders). Such diversity and availability might therefore have had a significant role in tempering the effects of time-persistent fluctuating flow conditions. It could be argued that the impossibility of sampling the fish at the disturbed sites during hydropeaking events could bias the results, particularly regarding the species microhabitat use. Nonetheless, we believe it should not be sufficient to change the representativeness of the results, as the target leuciscid species [45] and a sister species of brown trout, *S. fontinalis* [51], have been shown to have very small movement ranges (up to a few meters) upon facing hydropeaking conditions, thus presenting strong site fidelity.

Potential mitigation measures should consider maintaining riparian vegetation strips and mosaics of submerged aquatic macrophytes downstream from SHPPs that are critical for fish, in particular during unfavorable flow conditions such as those imposed by peak flows. The provision of large coarse substrata (e.g., boulders) to the river channel may provide hydraulic shelter against excessive current velocities [7,62], hindering fish from being washed away by sudden discharges. Nonetheless, finer-scale studies, both in the field and experimental (e.g., in indoor flumes or mesocosms) using fish tagging techniques (e.g., electromyogram telemetry, PIT tagging) will be needed to better clarify how different size classes of fish select microhabitats when facing past and present hydropeaking conditions [20,27].

Finally, it should be noted that the present study focused on the assessment of microhabitat use in small-sized river segments affected by a single pressure (i.e., hydropeaking). However, hydropeaking by SHPPs may interact with other stressors, such as hydromorphological ones [89], or climate change and land cover alterations [90], for which the effects remain unclear. Future studies are thus needed to better understand multiple potential impacts.

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Data Availability Statement: The data presented in this study are available upon request from the corresponding author. The data are not publicly available due to potential use in future works.

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