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Multispecies fishways in a Mediterranean river: Contributions as migration corridors and compensatory habitat for fish

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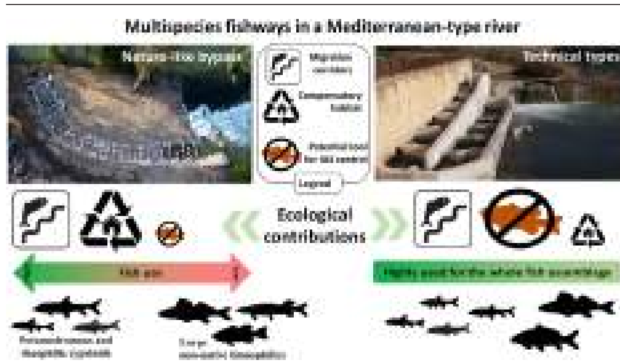
HIGHLIGHTS

- Connectivity is severely altered in rivers and has critical effects on fish persistence.
- Fishways have been postulated as relevant management tools to sustain fish populations.
- Dominant fish species used both nature-like and technical fishways.
- Fishways provided key compensatory habitats mainly for small and juvenile fish.
- Fishways should be considered for applying successful restoration in Mediterranean rivers.

GRAPHICAL ABSTRACT



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ABSTRACT

River connectivity is essential for the resilience of fish assemblages and populations and is a priority goal to reach good ecological status for river systems. Increasing knowledge on the functionality of restoration tools such as fishways is relevant for future management strategies. The present two-year assessment showed clear ecological contributions of different types of multispecies fishways in the fish assemblage of a strongly modified Mediterranean-type river. Just after their implementation, early and extended use by dominant river-resident fish of both naturelike and technical fishways were observed. All fishways were used in different seasons, especially during the migratory periods by potamodromous cyprinids, suggesting a possible use as migration corridors. Fishways also may provide compensatory habitats for small and juvenile individuals throughout the annual cycles, mostly for rheophilic fish inside nature-like bypasses and for limnophilics inside technical types. Fluvial habitat characteristics and lower flow variability inside the fishways could favour their role as a fish refuge, mainly to juveniles of cyprinids, in heavily regulated rivers where large flow fluctuations occurred. Nature-like fishways could be a better option to function as a compensatory habitat for rheophilic cyprinids in Mediterranean-type Rivers, even more because their use by large nonnative limnophilics seems to be very scarce. However, technical fishways could offer the opportunity to establish control traps of some nonnative fish, which could be of interest to reduce the risk of spreading invasive fish. Therefore, fish ecology and local hydrology should drive the decision between the types to implement. The obtained information on the ecological functionality of multispecies fishways should be considered for applying successful river restorations that are demanded by water and wildlife management schemes (e.g., the European Water Framework Directive).

1. Introduction

The loss of connectivity due to anthropogenic barriers within river systems is among the main emerging threats to freshwater biodiversity (Reid

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et al., 2018). These artificial barriers are built to meet human needs such as increased energy demand or the expansion of irrigated agriculture, causing severe ecological, hydrological and geomorphologic changes (Olden et al., 2010; Vitousek et al., 1997). Almost half of the global freshwater volume has already been altered by flow regulation, with the Iberian Peninsula being one of the world's most artificially water-regulated regions (Brink et al., 2018; Hermoso and Clavero, 2011). Fluvial connectivity is essential for river dynamics and for the resilience of freshwater biota (Pringle, 2003). As a consequence, artificial obstacles that impact on key environmental variables (e.g., water flow, temperature or substrate composition) may potentially induce changes in freshwater community composition and structure (Jones et al., 2020). The fish fauna is especially affected by artificial barriers such as dams and weirs that preclude population connectivity and migration (Branco et al., 2017; Silva et al., 2017). As a consequence, mitigating the effects of river fragmentation is a priority goal of the European Commission to achieve the good ecological status (based on chemical, hydrological and biological indicators) for river systems required by the EU's Water Framework Directive (European Commission, 2000).

Reducing the effects of river fragmentation is essential to restore freshwater ecosystem functioning (Pringle, 2003). However, the implementation of generalized solutions is difficult due to the specific characteristics of each river, its particular fish community and the effect of each obstacle on the complex dynamics of river systems, which requires a regional or even local approach for successful management (Nilsson et al., 2005; Kemp and O'Hanley, 2010; Terêncio et al., 2021). To mitigate the negative impact of non-passable barriers on fish populations, fishways have been implemented as a useful restoration tool when barrier removal is not feasible (Katopodis and Williams, 2012; Silva et al., 2017). In the past, work on the design of fishways has generally focused on species of high socioeconomic value, particularly salmonids, with limited success for other non-commercial fish species (Mallen-Cooper and Brand, 2007; Noonan et al., 2012; Roscoe and Hinch, 2010). However, in the last decades, a more holistic approach has led to the implementation of new designs focusing on a wider range of species to maintain the whole fish community (Ackerman et al., 2019; Stuart et al., 2008; Thiem et al., 2012; Tummers et al., 2016). These multispecies fishways have not only functioned as migration corridors, but have also been used as new compensatory habitats for both migratory and resident fish since they could offer resources which are declining in strongly altered river reaches (Calles and Greenberg, 2007; Pander and Geist, 2018; Pander et al., 2013).

Despite the fact that most fish species are of low economic value, the implementation of fishways is currently focused on maintaining the entire fish community, since these engineering solutions contribute significantly to restoring fish movements and population connectivity (Kemp and O'Hanley, 2010; O'Hanley et al., 2013; Tummers et al., 2016). Taking into account the wide diversity of species with different biological requirements and strategies to deal with passage facilities, successful fishway design and implementation requires a multidisciplinary working group that involves experts in ecohydraulics, fish behaviour, policy and socioeconomics (Silva et al., 2017). However, just as important as the design process is assessment of the effectiveness of fishways once they are operative (Odeh, 1999; Roscoe and Hinch, 2010). In fact, monitoring programmes are essential to understand the response of fish assemblages to passage facilities, enabling us to maximize their performance and improve future fishway designs (Cooke and Hinch, 2013; Kemp, 2012). Furthermore, the selection of the appropriate fishway design to implement depends on various requirements (e.g. logistical limitations or economic resources) (DVWK, 2002; Travade and Porcher, 2002), and assessing the use of different types of fishway under similar environmental conditions enables comparisons and helps in the design of future successful implementations.

Although the construction of multispecies fishways has been increasing, there have been few studies concerning their use and effectiveness with regard to the entire fish assemblage in Mediterranean rivers, such as those of the Iberian Peninsula, where the scarcity of fish species of commercial value limits funding for assessment of the effectiveness of implemented fishways (Noonan et al., 2012). Most Iberian studies have focused on providing robust information on target species, mainly endemic cyprinids (see Hershey (2021), which positions the Iberian barbel (*Luciobarbus bocagei* Steindachner, 1865) as the fifth most studied species), addressing fish passage to improve fishway designs (e.g., Branco et al. (2013); Bravo-Córdoba et al. (2021); Romão et al. (2017, 2019)). The use and effectiveness of fish passages for whole fish assemblages has rarely been studied in this region (Aparicio et al., 2012; Ordeix, 2017), and comprehensive field assessments are usually limited to the reproductive periods of some target species (Sanz-Ronda et al., 2019, Sanz-Ronda et al., 2016; Silva et al., 2015). In sum, approaches focussing on basic ecological knowledge underpinning the need for effective fish passages within a fish assemblage (e.g., temporal patterns of fish passage use) remain scarce in the literature (Silva et al., 2017).

The present study was developed in the context of the fish-based monitoring of an extensive river restoration programme, the LIFE+ Segura-Riverlink project (Oliva-Paterna et al., 2016). Our main aim was to validate the implementation of multispecies fishways as a useful tool to restore fish population connectivity. We investigated the use of five fishways of different typologies (nature-like and technical) by the fish assemblage over two annual cycles in a middle section of a Mediterranean-type river (Segura River, southeastern Spain) by setting the following objectives: 1) to assess the differences between types of fishways on the basis of use by the whole fish assemblage; 2) to determine the ecological contributions of fishways for the dominant river-resident fish by assessing temporal patterns across ecological guilds (rheophilic and limnophilic), movement behaviour (potamodromous and non-migratory) and the main factors that explain the patterns of fishway use. On the basis of the ecological traits of the species, we hypothesized that the fishways would be especially used by dominant cyprinids during their movement period as migration corridors. But in addition, we also expect that due to the availability of new habitats inside the fishways, they could also be used by other species of the fish assemblage. The results may be relevant for future management strategies and may help decision-makers to deploy appropriate restoration measures in highly impacted rivers, since considering the features of Mediterranean river systems will enable us to achieve the goals proposed by the EU's Water Framework Directive.

2. Material and methods

2.1. Study area and fishways

This study was conducted in the Segura River basin, which is located in the south-eastern Iberian Peninsula, a semiarid region characterized by warm summer temperatures (mean annual temperature = 18 °C) and scarce rainfall (300 mm/year approx.) (Fig. 1). This Mediterranean basin drains an area of 18,870 km^2 and is distinguished by a marked climatic gradient and severe annual and interannual variations in the natural flow regime, from extreme droughts to torrential floods (Hooke, 2006; Miró et al., 2018). Agricultural practices account for 80% of the total water demands and involve the construction of a large number of different types of flow regulation structures (Aldaya et al., 2019; Bruno et al., 2014). Overall, free water flow is constrained by a total of 33 dams (>10 m height and > 1 hm^3 of reservoir capacity) and 170 smaller obstacles along the longitudinal gradient. This basin accounts for approximately 1200 hm^3 of storage capacity, and additional water resources (approx. 350 hm^3 $year^{-1}$) are supplied from interbasin water transfer from the Tagus Basin (Grindlay et al., 2011). Consequently, the Segura River basin is considered one of the most human-impacted Mediterranean basins, with a high level of flow alteration (Aldaya et al., 2019; Grindlay et al., 2011). Flow regulation in this area leads to an increase in base flow throughout the year as well as more stable flow regime (Amat-Trigo et al., 2021; Sánchez-Pérez et al., 2020). This strong modification of the natural flow regime, operating in combination with the channelization and pollution derived from agricultural and urban activities (CHS, 2015), causes a severe degradation of fluvial and riverine habitats with a loss of lentic areas and resources such as refuge for rheophilic species (Belmar et al., 2013; Bruno et al., 2014).

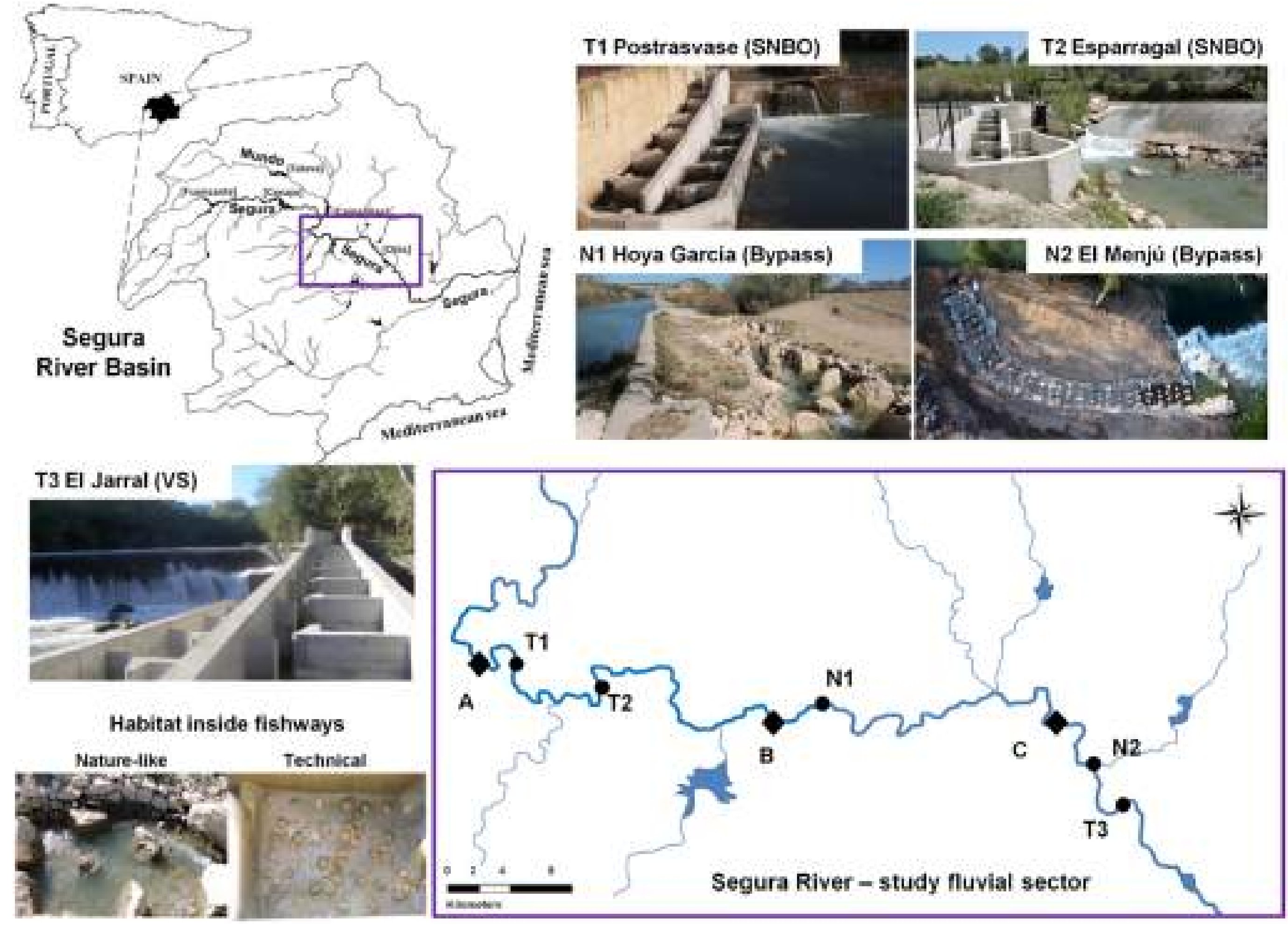

Fig. 1. Location of sampling sites (●) and gauging/weather stations (A Bayo, B Almadenes and C Menjú) in the Segura River basin and its location in the southeastern Iberian Peninsula. (N) nature-like fishways; (T) technical fishways: (SNBO) submerged notch with bottom orifice type and (VS) vertical slot type.

This study was carried out at five sampling sites distributed along a fluvial sector 54 km long, 5–15 m width in the middle part of the Segura River basin, with a mean gradient of 2.2 m/Km (Fig. 1). This river reach is a succession of irrigation and hydropower small dams (height < 8 m), that means an obstacle every 4 km of river and therefore, the main mesohabitat type in the river reach are dammed pools, with some scarce runs and glides, whereas rapid, riffle and plunge pool areas are unusual.

The most abundant fish were four cyprinids: the limnophilic *Alburnus alburnus* (Linnaeus, 1758), which is nonnative and has invaded large areas in the Iberian Peninsula, and three rheophilic species; the single native fish in the study area *Luciobarbus sclateri* (Günther, 1868); and two nonnatives: *Pseudochondrostoma polylepis* (Steindachner, 1865) and *Gobio lozanoi* Doadrio & Madeira, 2004. Other nonnative and limnophilic fish are locally present, such as *Gambusia holbrooki* (Agassiz, 1859), *Cyprinus carpio* Linnaeus, 1758 and *Lepomis gibbosus* (Linnaeus, 1758), and some alien piscivore fish occur at low densities (i.e., *Micropterus salmoides* (Lacépède, 1802), *Sander lucioperca* (Linnaeus, 1758) and *Esox lucius* Linnaeus, 1758). Nonnative fish species represent 90% of the total richness of the fish assemblage in the studied fluvial sector (Oliva-Paterna et al., 2019, Oliva-Paterna et al., 2014).

Each sampling site included a multispecies fishway and a 100-m long river reach just downstream (Fig. 1). All the fishways were designed and built in the context of an extensive river restoration programme following standard guidelines (DVWK, 2002; Travade and Porcher, 2002) and taking into account hydraulic recommendations for cyprinids (Sanz-Ronda et al., 2019). In all fishways, the fish entrance was at the most upstream end of the weir, there was an auxiliary flow to improve fish attraction, and the depth downstream the entrance was enough to ensure a suitable fish entrance. They started to operate in autumn 2015 (see Oliva-Paterna et al. (2016)), and the fish assemblage use of different types of fishways was evaluated over two annual cycles since January 2016. Two nature-like (N) fishways of rocky bypass type (N1 Hoya García and N2 El Menjú) and three technical (T) stepped fishways, two of them of SNBO type (Submerged Notch with Bottom Orifice; T1 Post-trasvase and T2 Esparragal) and one of VS type (Vertical Slot; T3 El Jarral), were monitored (Fig. 1; Table 1). Bypass types were nature-oriented constructions with variable current speed, water depth and natural bottoms originally composed of rocks. Substrates of both natural and technical fishways were quickly naturalized through sandy and muddy materials deposited from the river over a few months of fishway operation. Flow discharge inside the fishways was individually measured (Table 1) and regulated by a sluice gate placed in the flow entrance. More descriptive variables of the five monitored fishways and the downstream reaches sampled are presented in Table 1.

2.2. Sampling design and fishway monitoring

The five studied fishways were monitored during two complete annual cycles (from January 2016 to December 2017); with the beginning of the sampling period being approximately three months from the operation start date (see sampling details in Table S1). Each fishway was sampled twice per season during autumn and winter, but twice a month during spring and summer. We quantified the use of each fishway by the whole

Table 1
Sampling site descriptive variables for nature-like (N1,N2) and technical (T1, T2, T3) fishways; SNBO is a submerged notch with bottom orifice type and VS is a vertical-slot type. Location (UTM30 ETRS 89) with coordinates is provided as Universal Transverse Mercator. Downstream reach just below each fishway included the presence of a pool directly connecting river and fishway.

Sampling site	Name	Location	Fishway characteristics						Downstream pool characteristics		
			Typology	Slope (%)	Discharge design ($m^3 s^{-1}$)	Length (m)	Inner area (m^2)	Fishway structure	Mean reach width (m)	Mean water depth (m)	Fishway pool entrance
N1	Hoya García	X: 627272, Y: 4233623	Bypass	4.0	0.67	51.5	155	Channel with a middle section resting pool	3	0.40	Small or medium pool
N2	El Menjú	X: 639119, Y: 4231252	Bypass	3.5	0.90	52.0	154	Channel with two resting pools	8	1	Small or medium pool
T1	Post-trasvase	X: 613788, Y: 4235661	SNBO[a]	7.3	0.31	34.7	45	11 pools	5	1.20	Small or medium pool
T2	Esparragal	X: 613787, Y: 4235662	SNBO[a]	7.7	0.35	43.9	55	15 pools	3	0.20	Small or medium pool
T3	El Jarral	X: 640577, Y: 4229308	VS[a]	6.5	0.30	43.8	61	17 pools	14	1.20	Large pool >5 m^2

[a] Volumetric energy dissipation for technical fishways was 150 W/m^3 for T1 and T2, and 120 W/m^3 for T3.

fish assemblage. Furthermore, we assessed the ecological contributions (i.e., migration corridors and compensatory habitats) of the newly built fishways using the four dominant cyprinids in the fluvial sector (*L. sclateri*, *P. polylepis*, *G. lozanoi* and *A. alburnus*) as target fish. To evaluate the differences in temporal patterns, we defined the period of movement of the four target species as the window encompassed jointly by the spring and summer months based on their ecology (Froese and Pauly, 2021; Oliva-Paterna et al., 2019).

Before sampling inside the fishways, both the fish entrance and exit were blocked by nets (0.5 cm mesh size) to avoid fish escape. Afterwards, the flow discharge was notably reduced by closing the sluice gate of the fishways, thus allowing the catchability of potentially all individuals inside the pass (total captures) by electro-fishing. Two electro-fishing passes (1800 W generator, working voltage between 200 and 350 V, 2–3 A) were consecutively conducted by the same surveyor team for each sampling event, following the CEN standard protocol (CEN, 2003). Individuals were stunned by a single surveyor holding an anode, whereas two other surveyors collected stunned fish with dip nets and transferred them to plastic containers supplied with oxygen. All specimens using the fishways at that time were captured, obtaining the total captures inside the fishway as ensured from the two electrofishing passes. Furthermore, seasonal samplings were conducted in downstream reaches placed just downstream of each fishway. Downstream reaches were sampled by electrofishing passes (30–35 min) in wadable 100-m long river reaches, which were also blocked by nets to avoid fish escape. All captured fish were anaesthetized using clove oil (50 mg/l diluted in ethanol in a 1:10 proportion), subsequently identified to the species level, counted and measured (fork length FL; ± 1 mm).

As a complement to the evaluation of the use of the fishways, upstream (from downstream reach to fishway) and downstream (from fishway to downstream reach) movements were evaluated by means of a capture-mark-recapture programme (CMR) at three sampling sites: N2 (bypass - El Menjú), T2 (SNBO - Esparragal) and T3 (VS - El Jarral). Individuals larger than 8 cm of fork length (FL) belonging to the four target species were marked with Visible Implant Elastomers (VIE-tags) using different colour codes for captures inside the fishways and at downstream reaches. Recaptured individuals were re-marked in a different part of the body using a specific combination of VIE-tags that allowed us to differentiate (1) how many times each fish was caught and (2) where each marked fish comes from (if previously to its recapture it was marked inside the fishway or at a downstream reach).

Individual fish were manipulated in accordance with the European Union Directive 2010/63/UE on animal welfare in scientific activities and Spanish Act RD 53/2013, with the approval of the competent authorities (Regional Government on Natural Resources and Water Management Authority). Moreover, significant efforts were made to minimize stress and the mortality rate was less than 1%. Once the fish were recovered from the anaesthesia, all fish were released at the sampling site.

2.3. Environmental variables

On a fortnightly basis, river discharge ($m^3 s^{-1}$) and air temperature (°C) were analyzed for the studied period using online databases provided by the official monitoring service of the Segura Hydrographic Confederation at three gauging and weather stations distributed along the study area (Fig. 1) (https://www.chsegura.es/chs/cuenca/redesdecontrol/estadisticashidrologicas/; accessed 22 January 2018). Following the methodology applied by Fuentes-Pérez et al. (2017), the flow discharge ($m^3 s^{-1}$) inside each fishway was calculated at each sampling event. In addition, water temperature was measured at each sampling site, with three replicates both inside fishways and in their respective downstream reaches, using a multiparameter probe (Multi 340i WTW).

2.4. Statistical analysis

The Lilliefors test (Kolmogorov–Smirnov) was used to test the normality of the total captures as well as to the captures of each target species inside each fishway. Then, a nonparametric analysis of variance (Kruskal–Wallis test) was applied to test differences among the total captures and the captures of target species inside each fishway.

Differences between species occurrence and size distribution during the movement period (spring and summer) and the non-movement period (autumn and winter) for the target fish inside each fishway were tested by the Wilcoxon test. Finally, normality in lengths of each target species inside each fishway was tested by the Lilliefors test (Kolmogorov–Smirnov).

Spearman rank correlation analysis was used to test the correlations between environmental variables, and a *p*-value <0.05 was considered significantly correlated (rho coefficient > 0.7 was applied to establish a strong correlation between variables). We used general linear models (GLMs) to test the effects of environmental variables (flow discharges, water and air temperatures) on the captures inside fishways (Clarke et al., 2014). This analysis was performed with the *glm* function in the R package *car* (Fox and Weisberg, 2019). The sampling period (movement and non-movement period) and sampling site (each fishway) were included as factors to test the influence of different movement periods and types of fishways. GLMs were conducted using the total number of captures and the captures of each target species. All statistical analyses were performed using R software.

3. Results

3.1. Fishways use

A total of ten fish species were detected in the study area during the electrofishing surveys, although only nine species were present in each downstream reach as *E. lucius* was not detected in N1, N2 and T3, and

Table 2
Percentage of occurrence of fish species and total richness recorded at each sampling site (N1, N2, T1, T2 and T3) monitored in the main stem of the Segura River (southeastern Iberian Peninsula). Data are presented for each sampling site and divided into: inside fishways (I) and at downstream reaches (D).

Fish species	N1		N2		T1		T2		T3	
	I	D	I	D	I	D	I	D	I	D
A. alburnus	42.3	75.0	51.9	60.0	38.5	83.3	40.0	91.7	91.7	85.7
C. carpio	0	8.3	0	20.0	0	8.3	0	8.3	33.3	28.6
E. lucius	0	0	0	0	0	8.3	4.0	8.3	0	0
G. hoolbroki	3.8	25.0	0	20.0	0	0	0	0	0	7.1
G. lozanoi	92.3	100	85.2	80.0	76.9	100	72.0	100	100	92.9
L. gibbosus	15.4	58.3	29.6	20.0	15.4	75.0	24.0	83.3	45.8	42.9
L. sclateri	57.7	100	77.8	80.0	76.9	100	60.0	100	79.2	100
M. salmoides	0	8.3	0	20.0	3.8	8.3	8.0	8.3	4.2	7.1
P. polylepis	57.7	75.0	81.5	100	69.5	100	52.0	100	58.3	71.4
S. lucioperca	0	8.3	0	20.0	0	8.3	4.0	8.3	4.2	21.4
Species richness	6	9	5	9	6	9	8	9	8	9

G. holbrooki was not detected in T1 and T2 downstream reaches (Table 2). Five species were present inside all the fishways: *L. sclateri, P. polylepis*, *G. lozanoi, A. alburnus* and *L. gibbosus.* Nature-like fishways showed the lowest species richness (six species inside N1 and five inside N2) with the four largest nonnative fish (*C. carpio, M. salmoides*, *S. lucioperca* and *E. lucius*) not being detected, while T2 and T3 showed the highest richness inside fishways, with eight out of nine species present in their downstream reaches (Table 2).

A total of 12,772 fish were caught inside the five fishways from January 2016 to December 2017. The four target fish accounting for 98.8% of the total captures (*A. alburnus* 50.0%, *G. lozanoi* 37.5%, *L. sclateri* 4.3% and *P. polylepis* 7.1%). With regard to each fishway, 61.1% of the captures occurred inside T3 (VS type), followed by nature-like fishways, which accounted for 15.7% (N2) and 10.7% (N1) of the total captures. Conversely, the SNBO type had the lowest percentages, with 7.6% (T2) and 5.0% (T1) of the total captures.

The total captures inside each fishsway did not show normality (Lilliefors $p < 0.05$) and differ between fishways (Kruskal–Wallis p <

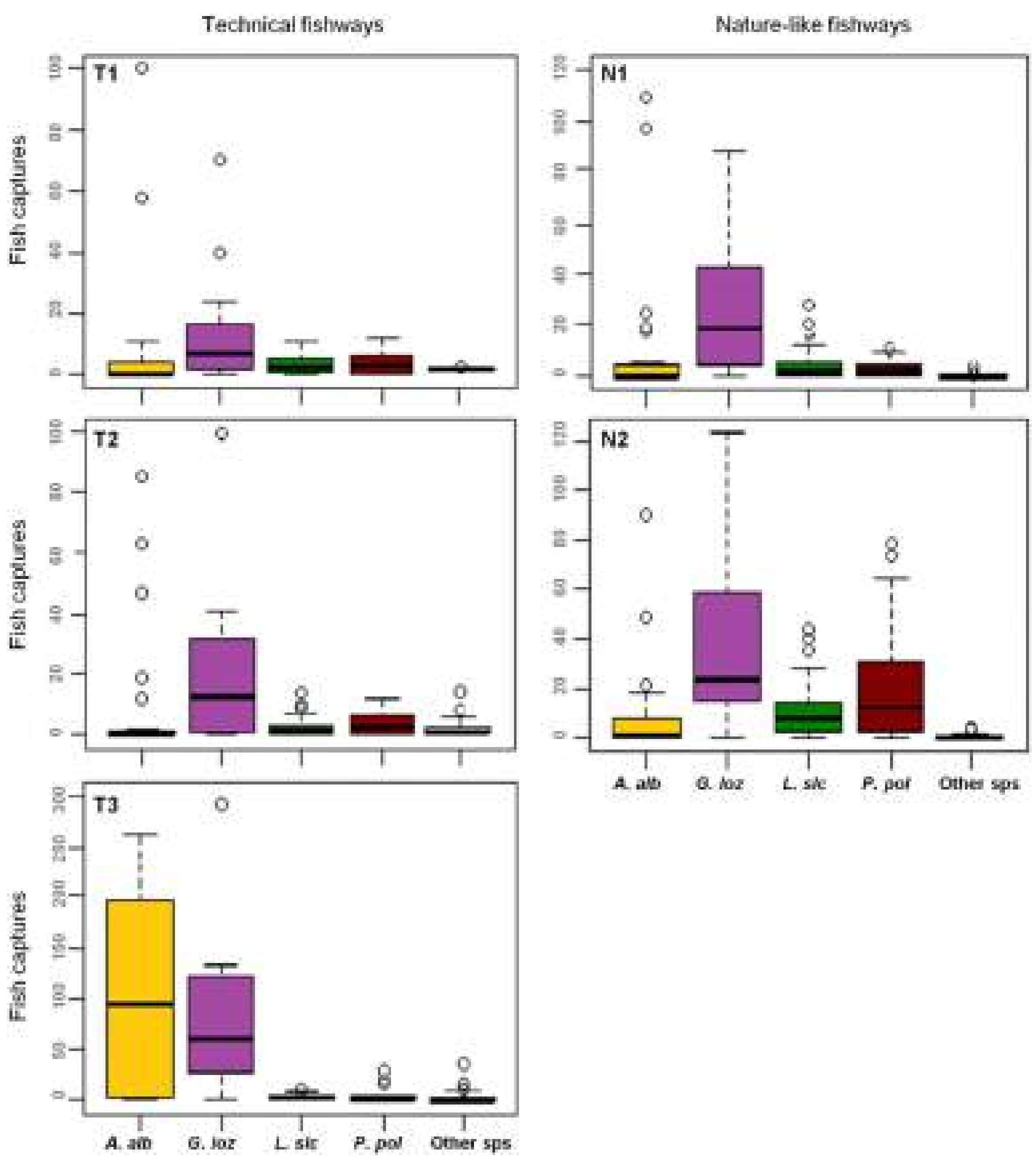

Fig. 2. Boxplots of fish captures inside the studied fishways (technical T1, T2 and T3; nature-like N1 and N2) in the Segura River (southeastern Iberian Peninsula). Median (central line), 25th and 75th percentile values, as well as maximum and minimum are represented in boxplot. Name of species were abbreviate as *A. alb* (*Alburnus alburnus*), *G. loz* (*Gobio lozanoi*), *L. scl* (*Luciobarbus sclateri*), *P. pol* (*Pseudochondrostoma polylepis*) and non-target species were summarized as "Other species".

0.05). *Alburnus alburnus* and *G. lozanoi* jointly represented 86.5% (48.2% *A. alburnus* and 38.3% *G. lozanoi*) of the total fish captured. Both were the most represented species inside each fishway, accounting for >70% of the captures with the exception of N2 (Fig. 2). *G. lozanoi* was the dominant species inside all the fishways (except inside T3), followed by *A. alburnus* (except inside N2). For both species, the Kruskal–Wallis test revealed that species captures differed among fishways: *G. lozanoi* ($chi^2_4 = 28.505$, $p < 0.001$) and *A. alburnus* ($chi^2_4 = 27.309$, $p < 0.001$). Pairwise Wilcoxon post hoc comparisons revealed that captures of *G. lozanoi* showed differences between T3 and the rest of the fishways except nature-like N2, and also between T1 and N2. The captures of *A. alburnus* were only significantly different inside T3, where a single sampling event yielded 2212 individuals that represented 17.3% of the total individuals of this species inside T3. This fishway accounted for the highest captures of both species: 85.4% for *A. alburnus* and 44.2% for *G. lozanoi* (Fig. 3). In the case of *A. alburnus*, the results of a single sampling event markedly skewed its total captures, as mentioned previously.

P. polylepis and L. *sclateri* accounted jointly for 12.2% (7.1% and 5.1%, respectively) of the total fish captured inside the fishways. The Kruskal–Wallis test also revealed that captures of both species differed among sampling sites: *P. polylepis* ($chi^2_4 = 19.618$, $p < 0.001$) and *L. sclateri* ($chi^2_4 = 17.131$, $p = 0.001$). Pairwise Wilcoxon post hoc comparisons revealed that the mean captures of both species were significantly higher inside N2, which accounted for 60.0% and 47.3% of the total captures of *P. polylepis* and *L. sclateri*, respectively (Fig. 3). The results are summarized in Supplementary Table S2.

3.2. Temporal use of fishways

Almost all fish species were detected using the fishways from the first sampling events. Only four events (3% of the total number of samplings), mostly at the beginning of the studied period, showed no captures inside fishways (two inside T1 in February 2016 and March 2017; one inside T2 in March 2016; and one inside N1 in March 2016). The four target species showed higher occurrences during the entire study period than the remaining fish species, which were generally detected inside fishways in less than 7.0% of the sampling events. The rheophilics L. *sclateri, G. lozanoi* and *P. polylepis* generally showed higher occurrences during the movement period (Wilcoxon test, $p < 0.05$), being detected in more than 70% of the total sampling events. In contrast, the occurrences were approximately 15.0% (for *G. lozanoi* and *P. polylepis*) and 26.2% for L. *sclateri* during the non-movement period. In fact, these species were significantly more often captured inside technical fishways (mainly the SNBO type) during the movement period (Wilcoxon test results; Fig. 4). In contrast, the occurrence of limnophilic *A. alburnus* inside the fishways was more regular (Wilcoxon test, $p = 0.08736$), being detected in 38.7% of the sampling events during the movement period and in 51.4% sampling events during the non-movement period, with the exception of T3, where this species showed more than 90% occurrence in both periods (Fig. 4).

The temporal patterns of captures of target species were similar to the occurrences. Winter captures were generally scarce, except inside N2, which accounted for 31.9% of the total captures for 2017 (Fig. 5). Fish were also scarce during the first spring season in which fishways were operating (2016), when the fish captures were lower than 10% inside each of the fishways (ranging from 3.1% in T3 to 9.8% in T1), however, accounted an average of 26.3% in spring 2017 (from 16.4% inside T1 to 46.4% inside T2). Sixty percent of the total captures of the four target species occurred during the non-movement period, but these percentages varied between species and fishways. The captures of L. *sclateri* were mostly concentrated during the movement period (70.6%, ranging from 61.9% inside N1 to 84.4% inside T2). Its highest captures occurred during summer but were also relatively high in autumn inside nature-like fishways (Fig. 5). In contrast, we captured *A. alburnus* mostly during the non-movement period inside all the fishways (66.6%, ranging from 50.3% inside N2 to 81.7% inside T2). This nonnative species usually showed peaks in autumn (as highlighted by an extraordinary event of 2212 individuals captured inside T3 on 26th November), although its captures were also relatively high during summer inside technical fishways. The captures of *G. lozanoi* and *P. polylepis* were higher during the non-movement period inside nature-like fishways and inside T3 but were conversely higher during the movement period inside the SNBO type (T1 and T2). The captures for the four target species were relatively constant during the study period inside N2 (Fig. 5).

No significant differences were found in the size (FL) of L. *sclateri* between the movement and non-movement periods inside any fishway (Wilcoxon test, $p > 0.05$), although larger individuals (more than 300 mm FL) were more abundant or were exclusively found during the movement period (Fig. 6). In contrast, significantly larger sizes of *G. lozanoi* were detected during the movement period inside all the fishways with the exception of T1. This pattern was also detected in *P. polylepis* and *A. alburnus* inside N1 and N2. In sum, during the movement period, large individuals of the target species were more often captured inside nature-like fishways,

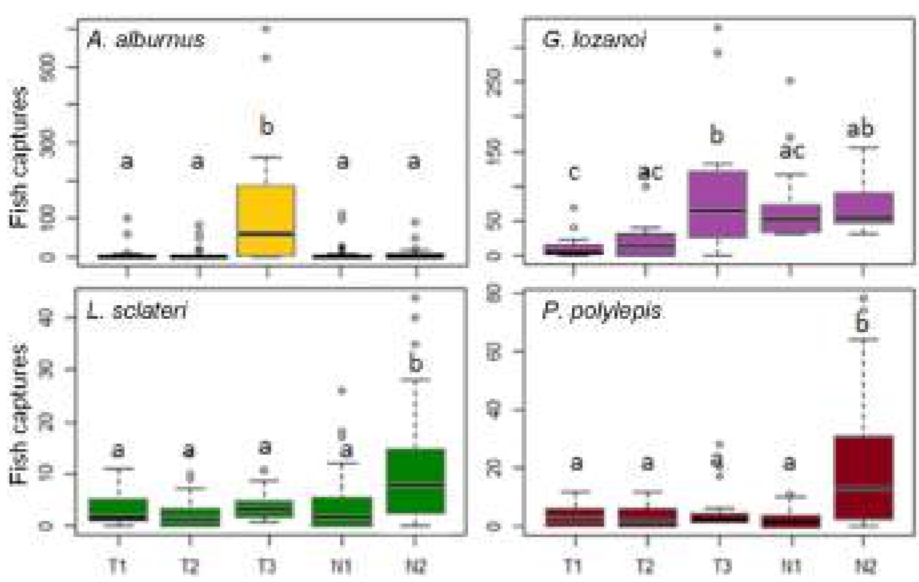

Fig. 3. Boxplots comparing total of captures during the study period for the target species inside each of the studied fishways (T1, T2, T3, N1 and N2) in the Segura River (southeastern Iberian Peninsula). Median (central line), 25th and 75th percentile values, as well as maximum and minimum are represented in boxplot. Letters above boxes indicate groupings based on significant differences ($p < 0.05$) obtained from pairwise Wilcoxon tests.

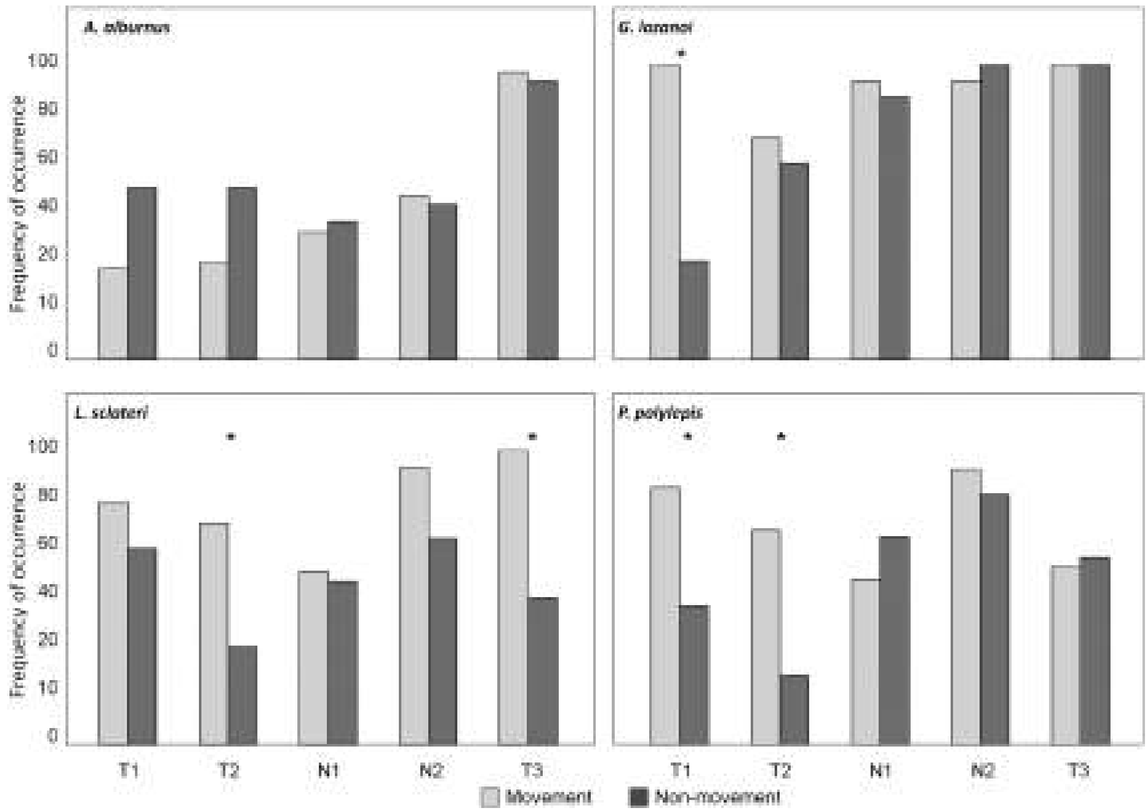

Fig. 4. Frequency of occurrence of the target species during the movement (light gray bars) and the nonmovement (dark gray bars) periods inside the fishways (T1, T2, T3, N1 and N2) monitored in the Segura River (southeastern Iberian Peninsula). Significant differences between-periods obtained from Wilcoxon test ($p < 0.05$) are indicated with asterisks above bars.

meanwhile smaller sizes were detected inside technical fishways in some cases, such as *A. alburnus* inside T2 or T3 and *P. polylepis* in T3 (Fig. 6).

In addition, we marked a total of 2002 individuals of the four target species to determine movements between fishways and downstream reaches. Three fishways from different typologies were selected at sampling sites T2 (SNBO), T3 (VS) and N2 (bypass), where 1075 individuals were marked inside the fishways and 927 in downstream reaches (Table 3). A total of 18.3% of the fish marked inside the fishways was later recaptured inside of them; in addition, 5.5% was recaptured twice, and 0.3% was recaptured three times. The N2 fishway had the highest fish marked (68.5%) and also the highest percentages of recaptures: 20.2% for first recaptures; 7.1% for seconds and 0.4% for third recaptures, and was the only fishway with one individual captured four times (Table 3). In downstream reaches, 5.7% of marked fish was recaptured, and only 0.1% was recaptured twice. The T2 downstream reach had the highest fish marked (73.2%) and also the highest percentage of recaptures: 7.2% for first recaptures, and was the only downstream reach with second recaptures (Table 3).

Fish upstream (from downstream reach to fishway) and downstream (from fishway to downstream reach) movements were confirmed by recaptures at two sampling sites (T2 and N2) consistently with the detection of specimens with different colour codes in VIE-tags. *Luciobarbus sclateri* and *G. lozanoi* were the species with ascending and descending movements, whereas *P. polylepis* was only detected in upstream movements. No tagged fish of *A. alburnus* were captured, probably due to the small number of tagged fish (Table 3).

3.3. Environmental variables

Significant correlations (Spearman $p < 0.05$) were found between air temperatures from the three weather stations, and also between the river flow discharges from the three gauging stations; therefore, we considered that the air temperature and the river flow discharge were similar throughout the study area. At each sampling site, a strong correlation (Spearman rho >0.7) was found between the air and water temperatures (Table S3, Fig. S1). In contrast, the results did not display strong correlations between river flow discharge and flow discharge inside the fishways (Table S3), which was expected in view of the hydrological design of fishways to maintain stable flow discharges (Fig. S2).

The potential effects of environmental variables (river flow discharge, flow inside the fishway and water temperature) on the captures inside fishways were studied using GLMs. Due to the correlation found between water and air temperature, the latter was excluded from the GLM analysis. Water temperature and sampling site (fishway as a factor) were significantly related to the total captures inside the fishways (Table 4).Specially, the captures increased with water temperature (Fig. 7), with T3 being the most differentiated fishway with a significant interaction (water temperature*sampling site) (estimate = 15.14, $p = 0.002$). The same interaction were also related to the captures of each target species (Table 4), and in addition, the movement period was related to the captures of *P. polylepis* and the river flow discharge to the captures of L. *sclateri*.

4. Discussion

The present two-year study assessed the use of different multispecies fish passage facilities built in a heavily modified Mediterranean-type river, providing useful data on the response of the whole fish assemblage. After assessing different typologies of fishways, our results showed early and extensive use of both nature-like and technical types mainly by the dominant river-resident cyprinids, although they displayed differences in their use of fishway types and among temporal periods.

A temporal monitoring programme for two complete annual cycles enabled us to verify that the most representative fish species occurring in the study area (the four target cyprinids) were regularly detected inside the assessed fishways, but size diversity and fish captures varied between

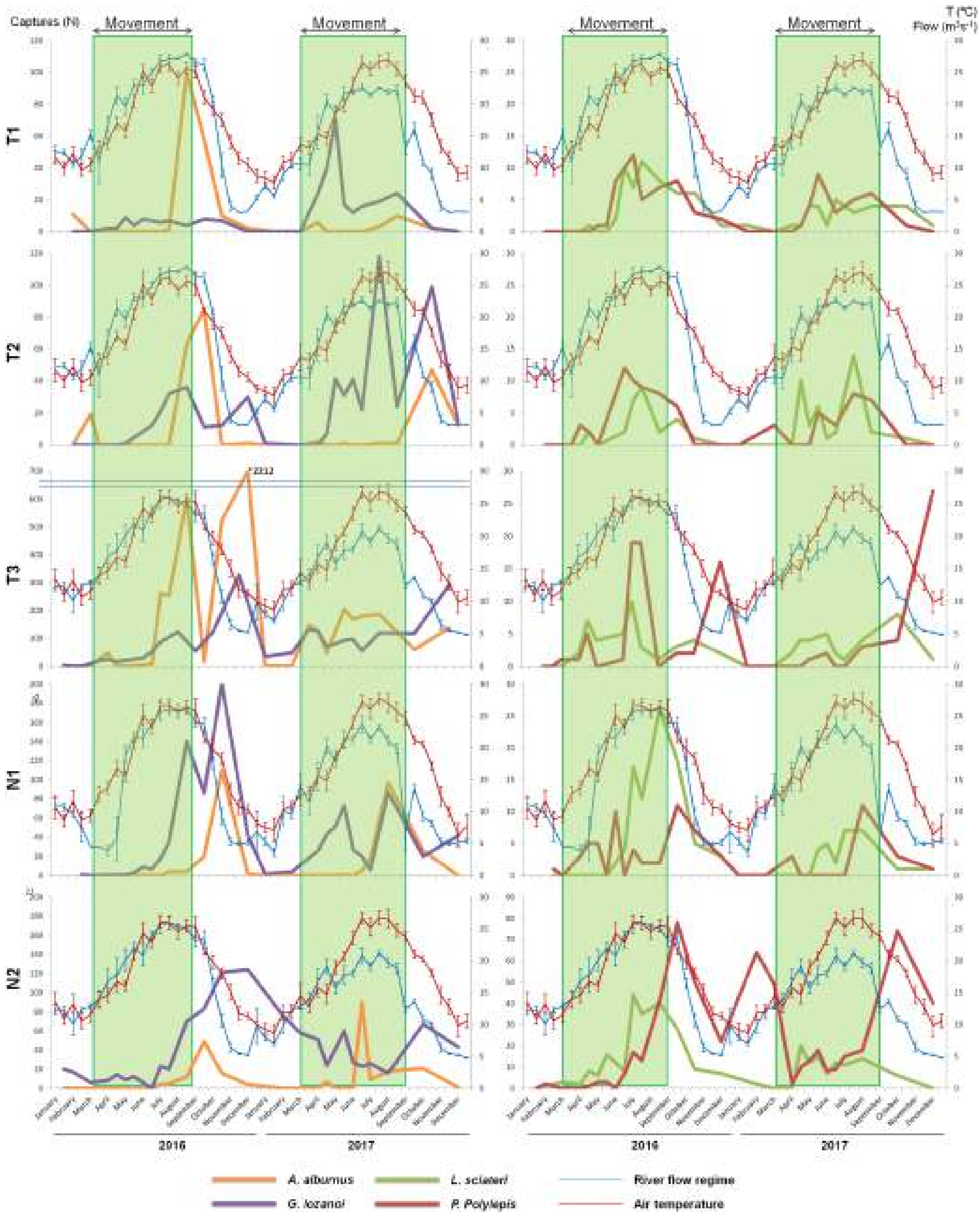

Fig. 5. Temporal variation in captures for the four target fish species during the study period inside the fishways (T1, T2, T3, N1 and N2) monitored in the main stem of the Segura River (southeastern Iberian Peninsula). Mean fortnightly values (I.C. (95%)) of river flow discharge and air temperature were also represented for the study period and movement periods were highlighted.

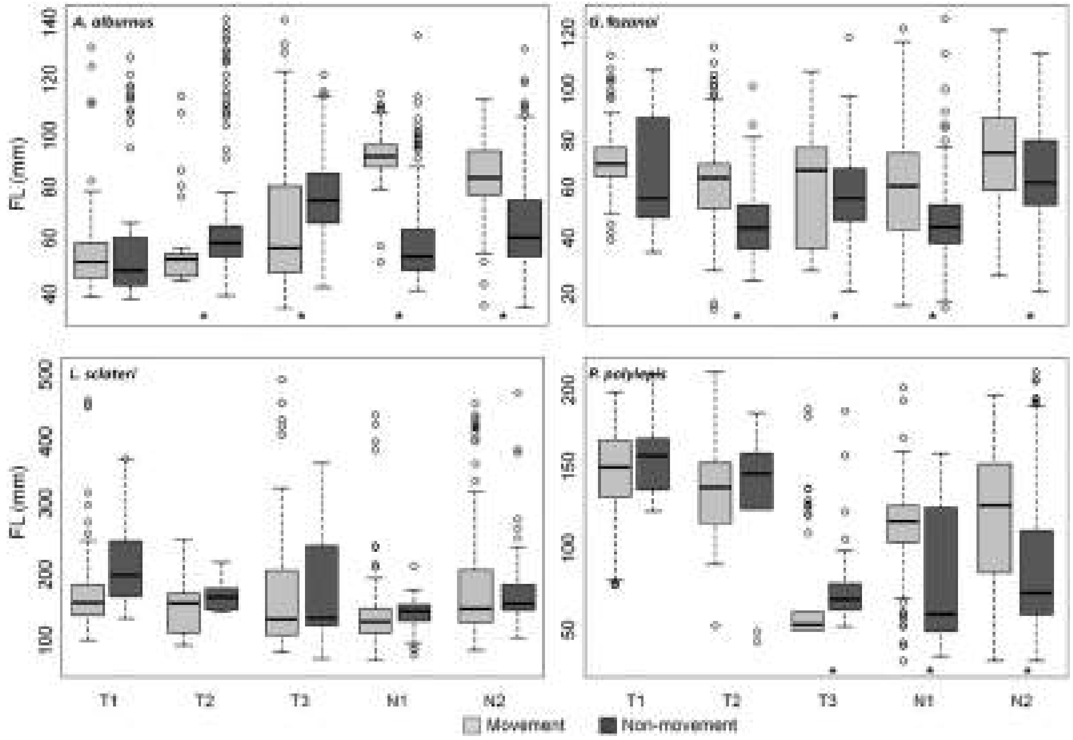

Fig. 6. Boxplots comparing fish size (FL: fork length in mm) for the target species during the movement and the nonmovement period inside the fishways (T1, T2, T3, N1 and N2) monitored in the Segura River (southeastern Iberian Peninsula). Boxplots display mean (central line), 25th and 75th percentile, as well as maximum and minimum with outliers. Significant differences in fish size between periods are indicated with asterisks (Wilcoxon test, $p < 0.05$).

Table 3
Results of capture-mark-recapture survey (CMR) conducted in the Segura River (southeastern Iberian Peninsula). Number of fish marked (N) and recaptures (%) of the four target species inside each fishway (T2, T3 and N2) and in their respective downstream reaches are shown. Detections of fish movements were indicated as upstream (recapture from downstream reach to fishway) and downstream (recapture from fishway to downstream reach).

	T2	T3	N2
N (inside fishways)	**154**	**185**	**736**
L. sclateri	51	56	299
P. polylepis	70	8	257
A. alburnus	0	23	14
G. lozanoi	33	98	166
Recaptures inside			
1st recapture (total)	14.94%	13.51%	20.24%
L. sclateri	56.5%	48.8%	47.7%
P. polylepis	43.5%	–	24.8%
A. alburnus	–	4.0%	–
G. lozanoi	0	48.0%	27.5%
2nd recapture (total)	2.60%	1.62%	7.06%
L. sclateri	100%	33.3%	51.99%
P. polylepis	–	–	30.8%
G. lozanoi	–	66,70%	30,8
3rd recapture (total)	**–**	**–**	**0.41%**
G. lozanoi	–	–	33.3%
P. polylepis	–	–	66.7%
N (downstream reach)	**679**	**139**	**109**
L. sclateri	351	118	16
P. polylepis	256	12	87
A. alburnus	7	0	1
G. lozanoi	65	9	5
Downstream recaptures			
1st recapture (total)	**7.22%**	**1.44%**	**1.83%**
L. sclateri	77.6%	50%	100%
P. polylepis	16.3%	50%	–
G. lozanoi	6.1%	–	–
2nd recapture (total)	**0.15%**	**–**	**–**
L. sclateri	100%	–	–
Up-movement	Yes	–	Yes
Down-movement	–	–	Yes

fishway types and periods. The fish captures inside fishways were associated with the fishway typology sensu *lato* (i.e. hydraulics, dimension, flow discharge, attraction, entrance location) (Bravo-Córdoba et al., 2021; Bunt et al., 2012) and probably with the pool entrance characteristics. Water temperature played the most important role among the

Table 4
General linear models (GLM) conducted for assessing effects of environmental variables on total fish captures and on captures of each target fish species inside fishways (dependent variables) of the Segura River (southeastern Iberian Peninsula). Only significant effects of environmental variables or factors were shown (*p < 0.05; ** $p < 0.01$; *** p < 0.001). Six outliers identified as data above the 95th percentile were not included in the models.

	χ^2	Df	Pr (>χ^2)
Total of captures			
Sampling site	36.94	1	1.21×10^{-08}
Water temperature	46.93	4	1.58×10^{-07}
Sampling site*Water temperature	14.25	4	0.0065
L. sclateri			
River flow discharge	9.14	1	0.0025
Water temperature	21.49	1	3.56×10^{-05}
Sampling site	69.88	4	2.41×10^{-13}
River flow discharge*Water temp*Sampling site	25.63	4	3.77×10^{-04}
P. polylepis			
Water temperature	23.46	1	1.28×10^{-05}
Sampling site	75.09	4	1.91×10^{-14}
Movement period	19.04	1	1.28×10^{-04}
Sampling site*Movement period	57.29	4	1.08×10^{-11}
G. lozanoi			
Water temperature	16.38	1	5.18×10^{-04}
Sampling site	31.25	4	2.72×10^{-05}
Sampling site*Water temperature	14.60	4	0.0056
A. albunus			
Water temperature	25.47	1	4.50×10^{-06}
Sampling site	63.45	4	5.47×10^{-13}
Sampling site*Water temperature	21.41	4	2.63×10^{-04}

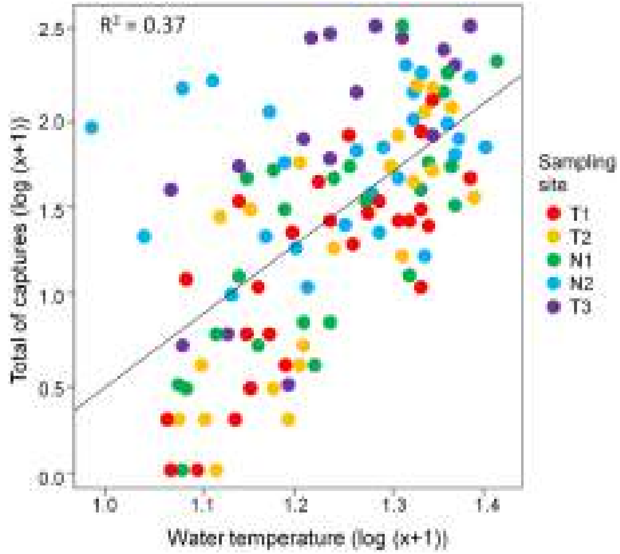

Fig. 7. Relationship between water temperature and total captures inside the fishways (T1, T2, T3, N1 and N2) monitored in the main stem of the Segura River (southeastern Iberian Peninsula). Black line represents a significant linear regression ($p < 0.05$). Log transformation was used to represent the data.

environmental variables to explain variability in fishway use by fish assemblages. We also detected use-related differences between the expected non-movement and movement periods, maybe based on the use of fishways as migration corridors, such as by potamodromous fish. Moreover, although most of the species occurring in the study area do not undertake extensive migratory movements (e.g., *G. lozanoi*, *A. alburnus*, *L. gibossus*), all of them make short-distance movements between different habitats for population maintenance (Mclaughlin et al., 2013; Northcote, 1998; Tummers et al., 2016). Furthermore, fishways may provide new compensatory habitats for small and juvenile individuals throughout the annual cycle, mostly for rheophilics such as *G. lozanoi* and *P. polylepis* in nature-like fishways and for limnophilics such as *A. alburnus* in some technical types of fishways.

4.1. Fishway use by fish assemblage: Technical vs. nature-like fishways

The monitoring programme of the present study started during the first three months when fishways were operational, so we were able to record the early fish use events for all the assessed fishways. Most of the species had been present since the first fish survey, so the early use of these new infrastructures by different species could initially indicate the successful ecological functionality of these multispecies fishways (Tummers et al., 2016). In addition, the very high rate of captures of the target cyprinids, especially two representative potamodromous fish of the Iberian rivers (i.e., *L. sclateri* and *P. polylepis*), may also suggest their suitability as a functional restoration tool for fish passage (Benitez et al., 2015). In previous studies conducted in similar fishways built for Iberian cyprinids, located on the furthest upstream side of the dam, with the entrance located close to the riverbank and with a total discharge (fishway plus attraction flow) higher than 10% of the river reach, attraction efficiency was observed to be higher than 50% (Bravo-Córdoba et al., 2021; Sanz-Ronda et al., 2015 and Sanz-Ronda et al., 2021). Passage higher than 85% was detected as a result of the study of passage performance of technical pool-type fishways previously developed in T2 and T3, where L. *sclateri* and *P. polylepis* successfully used these two passage facilities (Sanz-Ronda et al., 2019). Even so, more detailed studies focused on fish passage are needed to confirm their use as migration corridors.

We detected almost the totality of the fish species from the assemblage inside T2 and T3, being the two most successful technical fishways in terms of species richness, with T3 also showing the highest capture rate, which could be conditioned by some sampling events with significantly high abundance of two small resident cyprinids: *G. lozanoi* and *A. alburnus*. In addition, all large nonnative limnophilics with different swimming abilities were captured inside them (i.e., *C. carpio*, *S. lucioperca, M. salmoides* and *E. lucius*), although the dominant captured fish were the small limnophilic *A. alburnus* and the rheophilic *G. lozanoi*, which are also nonnative to the study area. This occurrence of a wide variety of species supports the notion that, despite technical fishways not offering the most suitable environmental and hydraulic characteristics for species with different swimming abilities (tight entrance, steeper slope, etc.), pool-type designs focused on multiple species (i.e. including large resting areas and lower velocities) could be as effective as nature-like fishways (Bravo-Córdoba et al., 2021; Mitsopoulus et al., 2021; Romão et al., 2017).

However, in the present study, SNBO types (submerged notch with a bottom orifice) were significantly less used by fish species in terms of captures. The low detection could be due to a fast passage of the fish (Romão et al., 2019; Sanz-Ronda et al., 2019), which might suggest that the fish use the type of fishway mainly as corridors. But this result could also be due to downstream reach characteristics at these two sampling sites. The width of the reach and the size of the entrance pool (Table 3) induce greater flow fluctuations in the first pools of fishways T1 and T2 than in T3, where the characteristics of the downstream reach create more stable conditions that facilitate its use as compensatory habitat. These results are in concordance with the idea that although barbels are known to prefer submerged notches (Silva et al., 2020), the implementation of vertical slot is preferable because this choice of fishway type provides more stable hydraulic conditions that could be better suited to the upward passage of species with lower swimming ability (Bravo-Córdoba et al., 2021, Bravo-Córdoba et al., 2018; Romão et al., 2017; Travade and Larinier, 2002). In addition, some structures, such as technical fishways, could offer the opportunity to control certain nonnative fish if selective traps are included (Pratt et al., 2009; Rahel and Mclaughlin, 2018; Starrs et al., 2015; Stuart et al., 2006). In fact, our study shows the efficacy of technical fishways for mass captures of some nonnative small cyprinids, which could indicate the potential use of these structures in fish population control. However, more information on nonnative fish passage, especially upstream movements, is needed to assess the feasibility and possible success of implementing traps as a control measure.

Inside nature-like fishways, we detected five (N2) or six (N1) species, with this typology being preferred by potamodromous fish but also extensively used by *G. lozanoi* (see Fig. 2). However, large nonnative species such as *C. carpio, M. salmoides* and *S. lucioperca* were not detected. Nature-like designs attempt to mimic riffle/run habitats of natural river reaches, thus offering more fish-friendly environmental conditions (e.g., substrate and vegetation) and hydraulic characteristics (e.g., lower depth and higher mean velocity, with resting areas behind boulders and rocks) than technical types for rheophilic fish (Katopodis et al., 2001; Larinier, 2002; Pander et al., 2013). In addition, although nature-like fishways provide different environments and diverse hydraulic features that facilitate fish passage for a wider range of fish sizes and swimming abilities (Bunt et al., 2012; Katopodis and Williams, 2012), mimicked Mediterranean hydraulic features (mainly related to flow and environmental conditions) could be harder for limnophilic fish to pass (Colin et al., 2018). These results were reflected in the absence of captures of large limnophilics inside N1 and N2 in our study. According to this pattern, nature-like fishways have been proven to be used by rheophilic fish, though their use as compensatory habitats is precluded for medium- and large-sized nonnatives. Moreover, other studies have even shown passage problems for large nonnatives (e.g., *Exos lucius*) in this type of fishway (Calles and Grendberg, 2007). This result could be especially relevant in semi-arid climatic regions where altered environments promote the establishment and spread of nonnative fish species. In these highly invaded rivers, the implementation of multispecies fishways must take into account the risk of invasion when reconnecting human-isolated river reaches (Brevé et al., 2014; Radinger and García-Berthou, 2020; Starrs et al., 2015). At this point, management decisions could involve conflicts between recovering native species movements and limiting nonnative fish spread (Ordeix, 2017; Rahel and McLaughlin, 2018; Starrs et al., 2015). Studies considering the response of nonnative fish to multispecies fishways in highly invaded aquatic ecosystems such as heavily regulated Iberian rivers (Clavero et al., 2013; Fornaroli et al., 2020; Ilhéu et al., 2014; Sánchez-Pérez et al., 2020), could provide insightful information for fish management and help to implement appropriate cost-effective restoration measures (Radinger and García-Berthou, 2020; Santos et al., 2012).

4.2. Ecological contributions of multi-species fishways

In general, rheophilic fish were more frequently detected during the defined movement period (spring and summer) inside fishways, even more significantly inside SNBO types, where occurrence data could suggest their preferred use as migration corridors for L. *sclateri, P. polylepis* and *G. lozanoi*. More than 70% of L. *sclateri* were captured in this period, which could be an indicator of their effectiveness in facilitating migration movements for this potamodomous endemic Iberian fish. Moreover, although movements of large individuals of L. *sclateri* could also be detected during autumn (Ordeix, 2017; Romão et al., 2019; Sanz-Ronda et al., 2021), we mostly observed larger reproductive individuals during the movement period. The also potamodromous *P. polylepis*, a water column fish, showed significantly higher occurrences during the movement period only inside the SNBO type, which may be due to its migratory behaviour (Sanz-Ronda et al., 2016 and 2019). However, large individuals remained inside nature-like fishways, which could also confirm successful migratory movements across these bypasses. In the case of *G. lozanoi*, this species showed high occurrences and larger individuals during the movement period inside all fishway types, which confirmed short-distance movements observed during its reproductive period (Amat-Trigo et al., 2013; Benitez et al., 2015). However, most of it captures occurred during the considered non-movement period (autumn and winter), especially inside nature-like fishways and vertical slots. An intensive use of nature-like fishways by L. *sclateri* and *P. polylepis* during the non-movement period was also observed, which could confirm the majority use of this type as new compensatory habitats for rheophilics. The habitat conditions inside this typology seem to be similar to those in small upstream tributaries of the Segura River basin, where the rheophilic species show high population density (Martínez-Morales et al., 2010). Although these results could indicate the usefulness of natural-like bypasses as compensatory habitat, their effects are limited due to their small size (they only comprise a few square meters of new habitat), so it would be advisable to build or adapt more river reaches with this type of infrastructures in order to achieve a decisive influence on populations.

The limnophilic *A. alburnus* was the only target fish that jointly showed higher capture rates during the non-movement period inside the five fishways and displayed significant differences in the size of captured individuals between periods. The temporal pattern found in this study might be conditioned by its characteristic movements forming high-density shoals related to dispersal migrations, which confirm its high capacity to colonize new fluvial sectors (Amat-Trigo et al., 2019). In fact, some peaks of captures inside fishways as well as GLM analyses revealed that technical vertical slot type T3 was the most differentiated as a consequence of its correlation with the captures of this limnophilic fish, although *G. lozanoi* also added a relatively high number of captures during the non-movement period. Therefore, these findings confirmed that fish with different movements not only related to spawning were using these multispecies infrastructures (Benitez et al., 2015).

The results from the capture-mark-recapture (CMR) surveys provided evidence on the up- and downstream movements of the three rheophilic target fish. Although the results of fish passage data were scarce, they could be indicative of the successful fishway negotiation of these cyprinids, including endemic L. *sclateri*, which would help to mitigate the isolation of fish populations by recovering their longitudinal connectivity (Aparicio et al., 2012; Branco et al., 2013; Santos et al., 2005; Sanz-Ronda et al., 2021). Despite the results displaying high recapture rates inside all fishways, nature-like type N2 showed higher values, which reinforces the idea that this typology provides greater availability of key habitat that offers compensatory resources such as food or fish refuge (Katopodis and Williams, 2012; Pander et al., 2013).

Each studied fishway differed from its adjacent downstream and upstream river reaches, providing lower water depth, smaller channel width and greater habitat variability inside them. New habitats inside fishways can be considered as important compensatory habitats where many life stage-specific processes take place, offering additional resources as well as refuge for small sizes and juvenile rheophilic fish to face flow variations throughout the year (Pander and Geist, 2018; Pander et al., 2013). According to the forming processes such as gravel relocation, nature-like fishways are expected to be colonized more rapidly by aquatic invertebrates, vegetation and riparian plants, increasing the availability of resources such as food and refuge, especially relevant for early life stages and juvenile development (Dürregger et al., 2018). However, more detailed information on naturalisation of the fishways types is required to confirm potential microhabitat effects (Boavida et al., 2010; Ramler and Keckeis, 2019), and studies to assess the fish attraction are needed to ensure succesful design and implementation.

River flow discharge and water temperature are considered the main drivers of fish behaviour (Cooke et al., 2012; Mims and Olden, 2012). In this study, capture variability was significantly related to water temperature and river flow discharge in the case of L. *sclateri*. Water temperature is widely recognized as the main factor conditioning cyprinid movements in the Iberian Peninsula and could be driving fish movements for most of the studied species (García-Vega et al., 2021; Rodriguez-Ruiz and Granado-Lorencio, 1992; Santos et al., 2012; Starrs et al., 2015). As indicated by our GLM analysis, we can confirm the strong influence of the water temperature on fishway use by fish. This factor generally co-varies with flow regime (Murchie et al., 2008) and is generally strongly influenced by flow patterns in regulated rivers (Fornaroli et al., 2020; García-Vega et al., 2021), as reflected in our results by the significant correlations (Table S3).

The flow discharge inside the fishways was designed to be independent of the river flow discharge and to maintain a relatively constant flow over time, which is especially important in Mediterranean rivers strongly affected by flow fluctuations throughout the year (Bravo-Córdoba et al., 2021; Romão et al., 2017). The results did not show any significant effect on fish captures of the flow inside the fishways (Table 4), which together with a high occurrence of small sizes and juveniles could indicate minimal influence on fish passage (Romão et al., 2019). The highest flow stability inside the fishways could favour their use as refuges (micro- or mesohabitats), mainly for small individuals, which are especially important in rivers with wide flow fluctuations (Miró et al., 2018; Silva et al., 2020). In addition to the strong flow alteration, in the middle part of the Segura River there is a reduction in the availability of refuges or sheltered habitats a as consequence of fluvial and riparian degradation. In fact, the usefulness of fishways as key compensatory habitats for juvenile cyprinids is enhanced in this area where larvae and juveniles are more likely to be washed away during high flow discharges (Elosegi et al., 2010).

5. Conclusions and recommendations

Multispecies fishways could be a useful tool in connectivity restoration in strongly regulated Mediterranean rivers if they are well designed and implemented, and would not only be suitable for migration and other kinds of movements necessary for river fish populations but also play an important role as compensatory habitats for fish with different biological requirements and behaviours. For the successful implementation of multispecies fishways, it is essential not only to know their effectiveness for native species but also to understand how the whole assemblage will use these facilities, especially in areas highly invaded by nonnative fish where the risk of spreading invasive species must be properly taken into account in ecological restoration planning (Pratt et al., 2009; Radinger and García-Berthou, 2020; Terêncio et al., 2021).

Technical fishways could be as efficient as nature-like fishways in highly regulated rivers, as they are logistically easier to implement (Branco et al., 2013; Katopodis and Williams, 2012; Larinier, 2008; Noonan et al., 2012) and, consequently, they are the typology most frequently built (Silva et al., 2020). However, in the present study, nature-like fishways seem to be an appropriate design to be implemented based on the local hydrology, characteristic of Mediterranean rivers, as well as on the fish ecology, because this design was the most used by the most abundant resident river fish (rheophilic cyprinids) and because they were not apparently used by nonnative fish (especially large limnophilics). As nature-like bypasses offer a better alternative for a more holistic approach for river restoration to try to re-establish a more natural dynamic in river systems (Pander et al., 2013), our results suggest that nature-like fishways may be considered more favourably in river restoration projects. Nevertheless, more studies in different river basins will be necessary to establish the behaviour of both native and nonnative fish in this type of infrastructure.

Special attention to flow design inside fishways is essential given the strong flow variability in Mediterranean rivers for successful operation but also as a tool that facilitates or precludes their use by certain fish, where flow effects could be used as a management measure of the fish assemblage structure (Starrs et al., 2015). In fact, captures inside technical type fishways in the present study could indicate the potential use of these passes in nonnative fish control. However, previously to the development of this strategy, studies assessing the upstream passage of nonnatives are necessary in order to consider the feasibility of deploying fish traps. Increased knowledge regarding the benefits and costs of multispecies fishways will help to achieve more successful results when restoration measures for river connectivity are implemented, and it could inform water and wildlife managers as a basis for encouraging appropriate policy-making processes.

CRediT authorship contribution statement

Ana Sánchez-Pérez: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing. **Mar Torralva:** Investigation, Writing - review, Project administration, Funding acquisition. **José Manuel Zamora-Marín:** Methodology, Investigation, Writing – review. **Francisco Javier Bravo-Córdoba:** Investigation, Writing – review. **Francisco Javier Sanz-Ronda:** Investigation, Writing - review, Funding acquisition. **Francisco José Oliva-Paterna:** Conceptualization, Methodology, Investigation,Writing - review & editing, Project administration, Funding acquisition. All authors reviewed and contributed to the manuscript, as well as approved the final version.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.154613.

References

Ackerman, N.K., Pyper, B.J., David, M.M., Wyatt, G.J., Cramer, D.P., Shibahara, T.M., 2019. Passage effectiveness at a pool-and-weir fishway designed to accommodate Pacific Lampreys. N.Am. J. Fish. Manag. 39 (3), 426–440.

Aldaya, M.M., Custodio, E., Llamas, R., Fernández, M.F., García, J., Ródenas, M.Á., 2019. An academic analysis with recommendations for water management and planning at the basin scale: a review of water planning in the Segura River basin. Sci. Total Environ. 662, 755–768. https://doi.org/10.1016/j.scitotenv.2019.01.266.

Amat-Trigo, F., Oliva-Paterna, F.J., Verdiell-Cubedo, D., Ruiz-Navarro, A., Torralva, M., 2013. Edad y crecimiento de Gobio lozanoi Doadrio & Madeira, 2004 (Cypriniformes: Cyprinidae) en sectores fluviales de la cuenca del río Segura (SE península ibérica). An. Biol. 35, 109–121.

Amat-Trigo, F., Torralva, M., Ruiz-Navarro, A., Oliva-Paterna, F.J., 2019. Colonization and plasticity in population traits of the invasive Alburnus alburnus along a longitudinal river gradient in a Mediterranean river basin. Aquat. Invasions 14, 310–331. https://doi.org/10.3391/ai.2019.14.2.10.

Amat-Trigo, F., Torralva, M., González-Silvera, D., Martínez-López, F.J., Oliva-Paterna, F.J., 2021. Plasticity in reproductive traits, condition and energy allocation of the non-native pyrenean gudgeon Gobio lozanoi in a highly regulated Mediterranean river basin. Water 13, 387. https://doi.org/10.3390/w13030387.

Aparicio, E., Pintor, C., Durán, C., Carmona-Catot, G., 2012. Fish passage assessment at the most downstream barrier of the Ebro River (NE Iberian Peninsula). Limnetica 31, 37–46. https://doi.org/10.23818/limn.31.04.

Belmar, O., Bruno, D., Martínez-Capel, F., Barquín, J., Velasco, J., 2013. Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean basin. Ecol. Indic. 30, 52–64. https://doi.org/10.1016/j.ecolind.2013.01.042.

Benitez, J.-P., Nzau Matondo, B., Dierckx, A., Ovidio, M., 2015. An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. Aquat. Ecol. 49, 481–497. https://doi.org/10.1007/s10452-015-9541-4.

Boavida, I., Santos, J.M., Cortes, R., Pinheiro, A.N., Ferreira, M.T., 2010. Assessment of instream structures for habitat improvement for two critically endangered fish species. Aquat. Ecol. 45, 113–124. https://doi.org/10.1007/s10452-010-9340-x.

Branco, P., Santos, J.M., Katopodis, C., Pinheiro, A., Ferreira, M.T., 2013. Effect of flow regime hydraulics on passage performance of Iberian chub (Squalius pyrenaicus) (Günther, 1868) in an experimental pool-and-weir fishway. Hydrobiologia https://doi.org/10.1007/s10750-013-1532-7.

Branco, P., Amaral, S.D., Ferreira, M.T., Santos, J.M., 2017. Do small barriers affect the movement of freshwater fish by increasing residency? Sci. Total Environ. 581–582, 486–494. https://doi.org/10.1016/j.scitotenv.2016.12.156.

Bravo-Córdoba, F.J., Sanz-Ronda, F.J., Ruiz-Legazpi, J., Valbuena-Castro, J., Makrakis, S., 2018. Vertical slot versus submerged notch with bottom orifice: looking for the best technical fishway type for Mediterranean barbels. Ecol. Eng. 122, 120–125. https://doi.org/10.1016/j.ecoleng.2018.07.019.

Bravo-Córdoba, F.J., Valbuena-Castro, J., García-Vega, A., Fuentes-Pérez, J.F., Ruiz-Legazpi, J., Sanz-Ronda, F.J., 2021. Fish passage assessment in stepped fishways: passage success and transit time as standardized metrics. Ecol. Eng. 162. https://doi.org/10.1016/j.ecoleng.2021.106172.

Brevé, N.W.P., Buijse, A.D., Kroes, M.J., Wanningen, H., Vriese, F.T., 2014. Supporting decision-making for improving longitudinal connectivity for diadromous and potamodromous fishes in complex catchments. Sci. Total Environ. 496, 206–218. https://doi.org/10.1016/j.scitotenv.2014.07.043.

Brink, K., Gough, P., Royte, J., Schollema, P.P., Wanningen, H., 2018. From Sea to Source 2.0. Protection and Restoration of Fish Migration in Rivers Worldwide. World Fish Migration Foundation, Groningen, The Netherlands.

Bruno, D., Belmar, O., Sánchez-Fernández, D., Guareschi, S., Millán, A., Velasco, J., 2014. Responses of Mediterranean aquatic and riparian communities to human pressures at different spatial scales. Ecol. Indic. 45, 456–464. https://doi.org/10.1016/j.ecolind.2014.04.051.

Bunt, C.M., Castro-Santos, T., Haro, A., 2012. Performance of fish passage structures at upstream barriers to migration. River Res. Appl. 28, 457–478. https://doi.org/10.1002/rra.1565.

Calles, E.O., Greenberg, L.A., 2007. The use of two nature-like fishways by some fish species in the Swedish River Emån. Ecol. Freshw. Fish 16, 183–190. https://doi.org/10.1111/j.1600-0633.2007.00210.x.

CEN, 2003. Water Quality: Sampling of Fish With Electricity. European Standard EN – 14011: 2003. European Committee for Standarization, Brussels.

CHS, 2015. Plan hidrológico de la demarcación del Segura 2015/21, Confederación Hidrográfica del Segura. Ministerio de Medio Ambiente. Available at https://www.chsegura.es. (Accessed 22 April 2021).

Clarke, K.R., Gorley, R., Sommerfield, P.J., Warwick, R.M., 2014. Change in Marine Communities: An Approach to Statistical Analysis And Interpretation. 3rd edition. PRIMER-E, Plymouth.

Clavero, M., Hermoso, V., Aparicio, E., Godinho, F.N., 2013. Biodiversity in heavily modified waterbodies: native and introduced fish in Iberian reservoirs. Freshw. Biol. 58, 1190–1201. https://doi.org/10.1111/fwb.12120.

Colin, N., Villéger, S., Wilkes, M., de Sostoa, A., Maceda-Veiga, A., 2018. Functional diversity measures revealed impacts of non-native species and habitat degradation on species-poor freshwater fish assemblages. Sci. Total Environ. 625, 861–871. https://doi.org/10.1016/j.scitotenv.2017.12.316.

Cooke, S.J., Hinch, S.G., 2013. Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and practice. Ecol. Eng. 58, 123–132. https://doi.org/10.1016/j.ecoleng.2013.06.005.

Cooke, S.J., Paukert, C., Hogan, Z., 2012. Endangered river fish: factors hindering conservation and restoration. Endanger. Species Res. 17, 179–191. https://doi.org/10.3354/esr00426.

Dürregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., Geist, J., 2018. The importance of stream interstitial conditions for the early-life-stage development of the European nase (Chondrostoma nasus L.). Ecol. Freshw. Fish:1–13. https://doi.org/10.1111/eff.12403.

DVWK, 2002. Fish Passes: Design, Dimensions And Monitoring. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy ISBN 1566701112.
Elosegi, A., Díez, J., Mutz, M., 2010. Effects of hydromorphological integrity on biodiversity and functioning of river ecosystems. Hydrobiologia 657, 199–215. https://doi.org/10.1007/s10750-009-0083-4.
European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 Establishing a Framework for the Community Action in the Field of Water Policy. Diario Oficial De Las Comunidades Europeas. Available at https://www.boe.es/doue/2000/327/L00001-00073.pdf. (Accessed 13 October 2021).
Fornaroli, R., Muñoz-Mas, R., Martínez-Capel, F., 2020. Fish community responses to antecedent hydrological conditions based on long-term data in Mediterranean river basins (Iberian Peninsula). Sci. Total Environ. 728, 138052. https://doi.org/10.1016/j.scitotenv.2020.138052.
Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression. Third edition. Sage, Thousand Oaks CA Available online: https://socialsciences.mcmaster.ca/jfox/Books/Companion/ (Accessed 19 December 2021).
Froese, R., Pauly, D. (Eds.), 2021. FishBase. World Wide Web Electronic Publication Available at www.fishbase.org. Version 04/2021 (Accessed May 2021).
Fuentes-Pérez, J.F., García-Vega, A., Sanz-Ronda, F.J., De Azagra, Martínez, Paredes, A., 2017. Villemonte's approach: a general method for modeling uniform and non-uniform performance in stepped fishways. Knowl. Manag. Aquat. Ecosyst. 418, 23. https://doi.org/10.1051/kmae/2017013.
García-Vega, A., Fuentes-Pérez, J.F., Bravo-Córdoba, F.J., Ruiz-Legazpi, J., Valbuena-Castro, J., Sanz-Ronda, F.J., 2021. Pre-reproductive movements of potamodromous cyprinids in the Iberian Peninsula: when environmental variability meets semipermeable barriers. Hydrobiologia. https://doi.org/10.1007/s10750-021-04537-6.
Grindlay, A.L., Zamorano, M., Rodríguez Muñoz, I., Molero, E., Urrea, M.A., 2011. Implementation of the European Water Framework Directive: integration of hydrological and regional planning at the Segura River Basin, southeast Spain. Land Use Policy 28, 242–256. https://doi.org/10.1016/j.landusepol.2010.06.005.
Hermoso, V., Clavero, M., 2011. Threatening processes and conservation management of endemic freshwater fish in the Mediterranean basin: a review. Mar. Freshw. Res. 62, 244–254. https://doi.org/10.1071/MF09300.
Hershey, H., 2021. Updating the consensus on fishway efficiency: a meta-analysis. Fish Fish. 00, 1–14. https://doi.org/10.1111/faf.12547.
Hooke, J.M., 2006. Human impacts on fluvial systems in the Mediterranean region. Geomorphology 79, 311–335. https://doi.org/10.1016/j.geomorph.2006.06.036.
Ilhéu, M., Matono, P., Bernardo, J.M., 2014. Invasibility of mediterranean-climate rivers by non-native fish: the importance of environmental drivers and human pressures. PLoS One 9, e109694. https://doi.org/10.1371/journal.pone.0109694.
Jones, P.E., Consuegra, S., Börger, L., Jones, J., Garcia de Leaniz, C., 2020. Impacts of artificial barriers on the connectivity and dispersal of vascular macrophytes in rivers: a critical review. Freshw. Biol. 65, 1–16. https://doi.org/10.1111/fwb.13493.
Katopodis, C., Williams, J.G., 2012. The development of fish passage research in a historical context. Ecol. Eng. 48, 8–18. https://doi.org/10.1016/j.ecoleng.2011.07.004.
Katopodis, C., Kells, J.A., Acharya, M., 2001. Nature-like and conventional fishways: alternative concepts? Can. Water Resour. J. 26, 211–232. https://doi.org/10.4296/cwrj2602211.
Kemp, P.S., 2012. Bridging the gap between fish behaviour, performance and hydrodynamics: an ecohydraulics approach to fish passage research. River Res. Appl. 28, 403–406. https://doi.org/10.1002/rra.1599.
Kemp, P.S., O'Hanley, J.R., 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. Fish. Manag. Ecol. 17, 297–322. https://doi.org/10.1111/j.1365-2400.2010.00751.x.
Larinier, M., 2002. Chapter 5. Pool fishways, pre-barrages and natural bypass channels. Bull. Fr. Pêche Piscic, pp. 54–82 https://doi.org/10.1051/kmae/2002108 364 suppl.
Mallen-Cooper, M., Brand, D.A., 2007. Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? Fish. Manag. Ecol. 14, 319–332. https://doi.org/10.1111/j.1365-2400.2007.00557.x.
Martínez-Morales, I., José Oliva-Paterna, F.J., Verdiell-Cubedo, D., Torralva, M., 2010. Inventario y estado de conservación de la fauna piscícola en la cuenca alta del río Segura (SE Península Ibérica). An. Biol. 32, 47–58.
Mclaughlin, R.L., Smyth, E.R.B., Castro-Santos, T., Jones, M.L., Koops, M.A., Pratt, T.C., Vélez-Espino, L.A., 2013. Unintended consequences and trade-offs of fish passage. Fish Fish. 14, 580–604. https://doi.org/10.1111/faf.12003.
Mims, M.C., Olden, J.D., 2012. Life history theory predicts fish assemblage response to hydrologic regimes. Ecology 93, 35–45. https://doi.org/10.2307/23144019.
Miró, J.J., Estrela, M.J., Caselles, V., Gómez, I., 2018. Spatial and temporal rainfall changes in the Júcar and Segura basins (1955–2016): fine-scale trends. Int. J. Climatol. 38, 4699–4722. https://doi.org/10.1002/joc.5689.
Murchie, K.J., Hair, K.P.E., Pullen, C.E., Redpath, T.D., Stephens, H.R., Cooke, S.J., 2008. Fish response to modified flow regimes in regulated rivers: research methods, effects and opportunities. RiverRes. Appl. 24, 197–217. https://doi.org/10.1002/rra.1058.
Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science 308, 405–408. https://doi.org/10.1126/science.1107887.
Noonan, M.J., Grant, J.W.A., Jackson, C.D., 2012. A quantitative assessment of fish passage efficiency. Fish Fish. 13, 450–464. https://doi.org/10.1111/j.1467-2979.2011.00445.x.
Northcote, T.G., 1998. Migratory behaviour of fish and its significance to movement through riverine passage facilities. In: Jungwirth, M., Schmutz, S., Weiss, S. (Eds.), Migration And Fish Bypasses. Fishing News Books, Blackwell Science, Oxford, pp. 3–18.
O'Hanley, J.R., Wright, J., Diebel, M., Fedora, M.A., Soucy, C.L., 2013. Restoring stream habitat connectivity: a proposed method for prioritizing the removal of resident fish passage barriers. J. Environ. Manag. 125, 19–27. https://doi.org/10.1016/j.jenvman.2013.02.055.
Odeh, M. (Ed.), 1999. Innovations in Fish Passage Technology. American Fisheries Society. Bethesda, MA, United States.
Olden, J.D., Kennard, M.J., Leprieur, F., Tedesco, P.A., Winemiller, K.O., García-Berthou, E., 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. Divers. Distrib. 1–18. https://doi.org/10.1111/j.1472-4642.2010.00655.x.
Oliva-Paterna, F.J., Verdiell-Cubedo, D., Ruiz-Navarro, A., Torralva, M., 2014. La ictiofauna continental de la Cuenca del río Segura (S.E. Península Ibérica): décadas después de Mas (1986). An. Biol. 36, 37–45. https://doi.org/10.6018/analesbio.36.7.
Oliva-Paterna, F.J., Lafuente, E., Olivo del Amo, R., Sanz-Ronda, F.J., Sánchez-Balibrea, J., Díaz-García, R., Torralva, M., 2016. LIFE+ Segura Riverlink: a green infraestruture approach to restore the longitudinal connectivity. FiSHMED Fishes Mediterr. Environ. 2016 (007) 3 pp.
Oliva-Paterna, F.J., Zamora-Marín, J.M., Franco Galera, J.M., Zamora-López, A., Sánchez-Pérez, A., Amat-Trigo, F., Guillén Beltrán, A., Guerrero Gómez, A., Torralva, M., 2019. Peces dulceacuícolas de la cuenca del río Segura. ANSE. Asociación de Naturalistas del Sureste, Murcia, Spain.
Ordeix, M., 2017. Fish migration and fish ramp assessment at a gauging station on a Mediterranean river (Catalonia, NE Iberian Peninsula). Limnetica 36 (2), 427–443. https://doi.org/10.23818/limn.36.13.
Pander, J., Geist, J., 2018. The contribution of different restored habitats to fish diversity and population development in a highly modified river: a case study from the River Günz. Water 10, 1202. https://doi.org/10.3390/w10091202.
Pander, J., Mueller, M., Geist, J., 2013. Ecological functions of fish bypass channels in streams: migration corridor and habitat for rheophilic species. River Res. Appl. 29, 441–450. https://doi.org/10.1002/rra.1612.
Pratt, T.C., O'Connor, L.M., Hallett, A.G., McLaughlin, R.L., Katopodis, C., Hayes, D.B., Bergstedt, R.A., 2009. Balancing aquatic habitat fragmentation and control of invasive species: enhancing selective fish passage at sea lamprey control barriers. Trans. Am. Fish. Soc. 138 (3), 652–665. https://doi.org/10.1577/T08-118.1.
Pringle, C.M., 2003. What is hydrologic connectivity and why is it ecologically important? Hydrol. Process. 17, 2685–2689. https://doi.org/10.1002/hyp.5145.
Radinger, J., García-Berthou, E., 2020. The role of connectivity in the interplay between climate change and the spread of alien fish in a large Mediterranean river. Glob. Chang. Biol. 00, 1–16. https://doi.org/10.1111/gcb.15320.
Rahel, F.J., McLaughlin, R.L., 2018. Selective fragmentation and the management of fish movement across anthropogenic barriers. Ecol. Appl. 28, 2066–2081. https://doi.org/10.1002/eap.1795.
Ramler, D., Keckeis, H., 2019. Effects of large-river restoration measures on ecological fish guilds and focal species of conservation in a large European river (Danube, Austria). Sci. Total Environ. 686, 1076–1089. https://doi.org/10.1016/j.scitotenv.2019.05.373.
Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2018. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. https://doi.org/10.1111/brv.12480.
Rodriguez-Ruiz, A., Granado-Lorencio, C., 1992. Spawning period and migration of three species of cyprinids in a stream with Mediterranean regimen (SW Spain). J. Fish Biol. 41, 545–556. https://doi.org/10.1111/j.1095-8649.1992.tb02682.x.
Romão, F., Quaresma, A.L., Branco, P., Santos, J.M., Amaral, S., Ferreira, M.T., Katopodis, C., Pinheiro, A.N., 2017. Passage performance of two cyprinids with different ecological traits in a fishway with distinct vertical slot configurations. Ecol. Eng. 105, 180–188. https://doi.org/10.1016/j.ecoleng.2017.04.031.
Romão, F., Quaresma, A.L., Santos, J.M., Branco, P., Pinheiro, A.N., 2019. Cyprinid passage performance in an experimental multislot fishway across distinct seasons. Mar. Freshw. Res. https://doi.org/10.1071/MF18232.
Roscoe, D.W., Hinch, S.G., 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. Fish Fish. 11, 12–33. https://doi.org/10.1111/j.1467-2979.2009.00333.x.
Sánchez-Pérez, A., Oliva-Paterna, F.J., Colin, N., Torralva, M., Górski, K., 2020. Functional response of fish assemblage to multiple stressors in a highly regulated Mediterranean river system. Sci. Total Environ. 730, 138989. https://doi.org/10.1016/j.scitotenv.2020.138989.
Santos, J.M., Ferreira, M.T., Godinho, F.N., Bochechas, J., 2005. Efficacy of a nature-like bypass channel in a Portuguese lowland river. J. Appl. Ichthyol. 21, 381–388. https://doi.org/10.1111/j.1439-0426.2005.00616.x.
Santos, J.M., Silva, A., Katopodis, C., Pinheiro, P., Pinheiro, A., Bochechas, J., Ferreira, M.T., 2012. Ecohydraulics of pool-type fishways: getting past the barriers. Ecol. Eng. 48, 38–50. https://doi.org/10.1016/j.ecoleng.2011.03.006.
Sanz-Ronda, F.J., Ruiz-Legazpi, J., Bravo-Córdoba, F.J., Makrakis, S., Castro-Santos, T., 2015. Sprinting performance of two Iberian fish: Luciobarbus bocagei and Pseudochondrostoma duriense in an open channel flume. Ecol. Eng. 83, 61–70. https://doi.org/10.1016/j.ecoleng.2015.05.033.
Sanz-Ronda, F.J., Bravo-Córdoba, F.J., Fuentes-Pérez, J.F., Castro-Santos, T., 2016. Ascent ability of brown trout, Salmo trutta, and two Iberian cyprinids − Iberian barbel, Luciobarbus bocagei, and northern straight-mouth nase, Pseudochondrostoma duriense − in a vertical slot fishway. Knowl. Manag. Aquat. Ecosyst. 417, 10. https://doi.org/10.1051/kmae/2015043.
Sanz-Ronda, F.J., Bravo-Córdoba, F.J., Sánchez-Pérez, A., García-Vega, A., Valbuena-Castro, J., Fernandes-Celestino, L., Torralva, M., Oliva-Paterna, F.J., 2019. Passage performance of technical pool-type fishways for potamodromous cyprinids: novel experiences in semiarid environments. Water 11, 2362. https://doi.org/10.3390/w11112362.
Sanz-Ronda, F.J., Fuentes-Pérez, J.F., García-Vega, A., Bravo-Córdoba, F.J., 2021. Fishways as downstream routes in small hydropower plants: experiences with a potamodromous cyprinid. Water 13, 1041. https://doi.org/10.3390/w13081041.
Silva, A.T., Hatry, C., Thiem, J.D., Gutowsky, L.F.G., Hatin, D., Zhu, D.Z., Dawson, J.W., Katopodis, C., Cooke, S.J., 2015. Behaviour and locomotor activity of a migratory catostomid during fishway passage. PLoS One 10 (4), e0123051. https://doi.org/10.1371/journal.pone.0123051.

Silva, A.T., Lucas, M.C., Castro-Santos, T., Katopodis, C., Baumgartner, L.J., Thiem, J.D., Aarestrup, K., Pompeu, P.S., O'Brien, G.C., Braun, D.C., Burnett, N.J., Zhu, D.Z., Fjeldstad, H.P., Forseth, T., Rajaratnam, N., Williams, J.G., Cooke, S.J., 2017. The future of fish passage science, engineering, and practice. Fish Fish. 1–23. https://doi.org/10.1111/faf.12258.

Silva, A.T., Bermúdez, M., Santos, J.M., Rabuñal, J.R., Puertas, J., 2020. Pool-type fishway design for a potamodromous cyprinid in the Iberian Peninsula: the Iberian barbel — synthesis and future directions. Sustainability 12, 3387. https://doi.org/10.3390/su12083387.

Starrs, T., Starrs, D., Lintermans, M., Fulton, C.J., 2015. Assessing upstream invasion risk in alien freshwater fishes based on intrinsic variations in swimming speed performance. Ecol. Freshw. Fish 1–7. https://doi.org/10.1111/eff.12256.

Stuart, I.G., Williams, A., McKenzie, J., Holt, T., 2006. Managing a migratory pest apecies: a selective trap for common carp. N.Am. J. Fish. Manag. 26 (4), 888–893. https://doi.org/10.1577/m05-205.1.

Stuart, I.G., Baumgartner, L.J., Zampatti, B.P., 2008. Lock gates improve passage of small-bodied fish and crustaceans in a low gradient vertical-slot fishway. Fish. Manag. and Ecol. 15, 241–248.

Terêncio, D.P.S., Pacheco, F.A.L., Sanches Fernandes, L.F., Cortes, R.M.V., 2021. Is it safe to remove a dam at the risk of a sprawl by exotic fish species? Sci. Total Environ. 771, 144768. https://doi.org/10.1016/j.scitotenv.2020.144768.

Thiem, J.D., Binder, T.R., Dumont, P., Hatin, D., Hatry, C., Katopodis, C., Stamplecoskie, K.M., Cooke, S.J., 2012. Multispecies fish passage nehaviour in a vertical slot fishway on the Richelieu River, Quebec, Canada. River Res. Appl. https://doi.org/10.1002/rra.2553.

Travade, F., Larinier, M., 2002. Chapter 12. Monitoring techniques for fishways. Bull. Fr. Pêche Piscic, pp. 166–180 https://doi.org/10.1051/kmae/2002101 364 suppl.

Travade, F., Porcher, J.P., 2002. Chapter 1. Fishways: biological basis, limits and legal considerations. Bull. Français la Pêche la Piscic, pp. 9–20 https://doi.org/10.1051/kmae/2002110 364 suppl.

Tummers, J.S., Hudson, S., Lucas, M.C., 2016. Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach. Sci. Total Environ. 569–570, 850–860. https://doi.org/10.1016/j.scitotenv.2016.06.207.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of earth's ecosystems. Science 277. https://doi.org/10.1007/978-0-387-73412-5.