

## Coordinated migration ensuring sexual parasitism in fish species: Extreme weather conditions induce atypically large fish dispersal movements

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### ABSTRACT

**Coordinated migration ensuring sexual parasitism in fish species: Extreme weather conditions induce atypically large fish dispersal movements**

This study reports, for the first time, a previously undocumented large and coordinated upstream migration of *Squalius pyrenaicus* (Günther, 1868) and *Squalius alburnoides* (Steindachner, 1866) in the Vascão River (Mediterranean temporary river) (Portugal), covering distances of at least 1687 metres and up to 4540 metres. These species were considered resident, but this migration happened after a dry year followed by an extremely wet winter and spring. These findings suggest that these species possess stronger dispersal capacities than previously thought, and could coordinate migrations to ensure interspecific relationships, specifically the sperm parasitism of *S. pyrenaicus* by *S. alburnoides*.

**KEY WORDS:** migration guild, spawning, Mediterranean river, parasitism, temporary river

### RESUMO

**Migração coordenada garante o parasitismo sexual em espécies de peixes: Condições climáticas extremas induzem movimentos atipicamente grandes de dispersão de peixes.**

Neste estudo reporta-se pela primeira vez uma migração conjunta e excecional de *Squalius pyrenaicus* (Günther, 1868) e *Squalius alburnoides* (Steindachner, 1866) para montante no rio Vascão (rio temporário do Mediterrâneo) (Portugal), percorrendo distâncias de pelo menos 1687 metros a 4540 metros. Estas espécies são consideradas residentes, mas esta migração excecional ocorreu após um ano seco seguido de inverno e primavera extremamente chuvosos. Esta descoberta sugere que estas espécies possuem uma maior capacidade de dispersão do que se pensava anteriormente, e que podem coordenar as migrações para garantir relações interespecíficas, nomeadamente o parasitismo de esperma de *S. pyrenaicus* por *S. alburnoides*.

**PALAVRAS CHAVE:** *guilda de migração, desova, rio Mediterrâneo, parasitismo, rio temporário.*

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## INTRODUCTION

The accelerating decline in biodiversity is a major worldwide issue (IPBES, 2019). Freshwater fish fauna is one of the most vulnerable taxa due to numerous and heterogeneous pressures such as overexploitation, water pollution, habitat degradation, flow modification, and the introduction of exotic species, all exacerbated by global warming (Doadrio, 2001; Cabral *et al.*, 2005; Maceda-Veiga, 2012; Radinger & García-Berthou, 2020). This is further intensified by the high number of endemic and rare species within a restricted distribution range (Balian *et al.*, 2008; Collen *et al.*, 2014).

The Iberian Peninsula is an extremely rich region for ichthyofauna, with 19 families and more than 70 species in freshwater ecosystems, featuring a high degree of endemism (80% of species; Doadrio *et al.*, 2011). New species continue to be described even today (Doadrio *et al.*, 2024). This area, mostly with a Mediterranean climate, has a long history of human settlement and disturbance (Gasith & Resh, 1999), which has led to a poor conservation status of its ichthyofauna. This region has the most threatened fish communities in Europe, over 50% of which are consistently classified as threatened (Doadrio *et al.*, 2011; Costa *et al.* 2021).

Spawning is a decisive phase in the life cycle of fishes, motivating their movements (Brönmark *et al.*, 2014). Fish species are considered resident if their movements are within a river stretch, and migratory if they migrate between river zones or involve substantial movements, usually more than 5 km (Melcher & Holzer, 2008). Typically, migratory species are classified as potamodromous or diadromous, the former completing their life cycle in freshwaters and the latter between marine and freshwater ecosystems (McDowall, 1997; 2008). In the Iberian Peninsula, human-made river obstacles have substantially affected river connectivity, leading to the disappearance of diadromous fish in most parts of this territory (Mota *et al.*, 2016). In ad-

dition, decreasing flow and flow intermittency, aggravated by climate change, also affected the migration of potamodromous and resident fish species between permanent pools and spawning areas (Branco *et al.*, 2017; Henriques *et al.*, 2010; Pires *et al.* 2014). As stated by Ordeix and Casals (2024) in a recent review paper, information about migratory behaviours and patterns is scarce for most Iberian freshwater native fish. Here, we present a large migration record for two Iberian chub species, *Squalius pyrenaicus* (Günther, 1868) and *Squalius alburnoides* (Steindachner, 1866), in the context of extreme weather patterns in the Vascão River in Portugal.

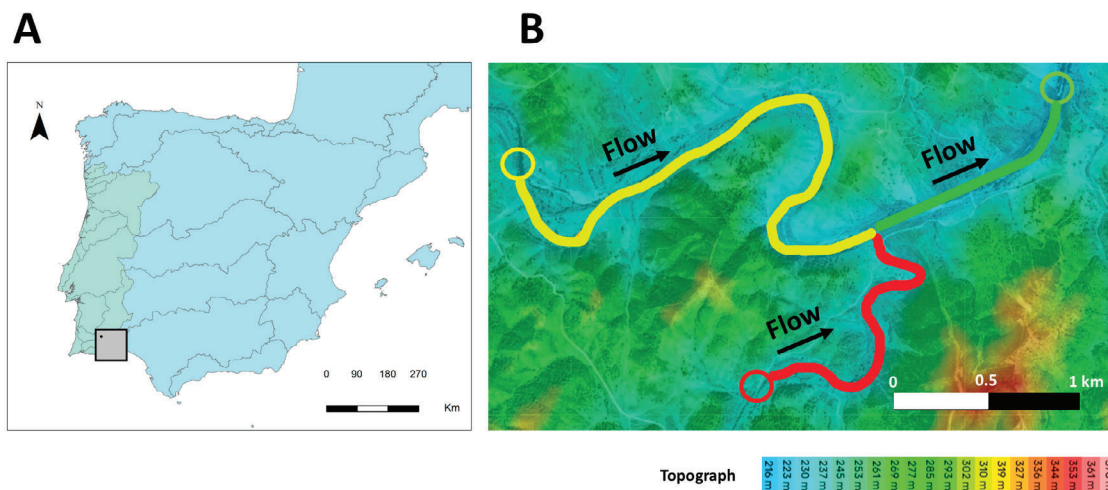
*S. pyrenaicus* and *S. alburnoides* are two small leuciscidae fishes, the former measuring less than 30 cm in length and the latter less than 13 cm. Both species are endemic to the Iberian Peninsula and co-occur in southwestern Atlantic drainages, such as the Tagus and Guadiana river basins (Doadrio *et al.*, 2001). *S. pyrenaicus* is considered Near Threatened (NT) and *S. alburnoides* is considered Vulnerable (A3ce) by the IUCN (Crivelli, 2006). *S. alburnoides* exhibits a complex life cycle (Collares-Pereira *et al.*, 2021) and behaviour, including intraspecific cleaning (Soares *et al.*, 2024) and interspecific sperm parasitism of *S. pyrenaicus*, which is part of their asexual reproduction mechanisms (gynogenesis, hybridogenesis, and meiotic hybridogenesis) (Alves *et al.*, 2001; Sousa-Santos *et al.*, 2006). Both species are found in the Vascão River (Portugal) (Guadiana River basin), one of the last “wild rivers” in Europe, known for its biodiversity importance and pristine habitats. This Mediterranean temporary river is reduced to a series of isolated pools in summer (Reis & Araujo, 2016).

Here, we report for the first time a previously undocumented large and coordinated upstream migration of *S. pyrenaicus* and *S. alburnoides*, after an extreme and sequentially dry and wet year. We further discuss the implications of such observation, including the implication for their interspecific relationships.

## MATERIALS AND METHODS

The whole Vascão River basin was scanned from its spring to the confluence of the Guadiana River, in the scope of the MusselFlow project, focused on endangered freshwater mussels (see for example, Reis et al. 2024), addressing all summer pools, including the permanent and the more intermittent ones. This was done by using satellite imagery and inspecting all riverbeds during the years of 2017–2019. Since 2020, the first section of the Vascão River, with approximately 14 km, and its permanent pools have been analysed for monitoring fish behaviour (bimonthly). This section contains the most preserved ictiofauna communities, mostly composed of native species, yet also including two invasive species, the pumpkinseed, *Lepomis gibbosus* (Linnaeus, 1758) and the Eastern mosquitofish, *Gambusia holbrokii* (Girard, 1859) (see Soares et al. 2024). The study area of the present work is located in the river section described, and contains two permanent pools only (see Figure 1), with the composition described in Table 1. The Vascão River tributary, Vscanito stream, is

an ephemeral river that was only sampled in the scope of the present study, due to the absence of permanent pools. This stream flows only during the winter when abundant precipitation occurs. In the 2023/2024 winter, it flowed for a particularly long period, yet by June 2024 it had completely dried up, which was confirmed by inspecting the entire stream on foot. This stream basin also has no artificial ponds or lakes. In 2023, the Vascão River basin area registered an anomaly of more than 2.5°C for average temperatures, making it the second warmest year in Portugal on record. Additionally, precipitation reached only 50% of the normal levels for 1981–2010 (IPMA, 2023). Our monitoring revealed that several historically permanent pools dried up, while others reached historically low levels (F. Banha, personal observation). Conversely, in the early months of 2024, despite higher-than-normal temperatures, precipitation was normal in January and 300% above normal in March (IMPA, 2024 a,b,c), resulting in a permanent and abundant flow in the Vascão River and its tributaries (F. Banha, personal observation).



**Figure 1.** (A) Location of the Vascão river in the Iberian Peninsula. The black dot on the upper part of the square corresponds to the study area location. (B) Yellow circle - upstream summer pool; yellow line - Vascão river upstream stretch until the Vscanito stream confluence; Green circle - downstream summer pool; green line - Vascão river downstream stretch until the Vscanito stream confluence; Red circle location ( $37^{\circ}23'50.53''\text{N}$ ;  $7^{\circ}56'37.57''\text{W}$ ) where fishes were captured in the Vscanito stream; red line - Vscanito stream stretch until the Vascão river confluence. Terrain altimetry was displayed in colour shades from blue (minimum 216 m) to rose (maximum 370 m) with increasing altitude. (A) *Localização do rio Vascão na Península Ibérica. O ponto preto na parte superior do quadrado corresponde a localização da área de estudo.* (B) *Círculo amarelo – pego permanente a montante; linha amarela – troço a montante do rio Vascão até à confluência com a ribeira do Vscanito; círculo verde – pego permanente a jusante; linha verde – troço a jusante do rio Vascão até à confluência com a ribeira do Vscanito; círculo vermelho – localização ( $37^{\circ}23'50.53''\text{N}$ ;  $7^{\circ}56'37.57''\text{W}$ ) onde os peixes foram capturados na ribeira do Vscanito; linha vermelha – troço da ribeira do Vscanito até à confluência com o rio Vascão. A altimetria do terreno é representada por um gradiente de cor, com o aumento da altitude a variar do azul (mínimo 216 m) até ao rosa (máximo 370 m).*

**Table 1.** Fish community sampled at the two nearby permanent summer pools of the Vascão River, near our detection point in the Vascanito stream. The features of the summer pools are described, and CPUE (number of fish per minute) is provided for each fish species. *Comunidade piscícola amostrada nos dois pêsos permanentes no rio Vascão mais próximos do nosso ponto de deteção na ribeira do Vascanito. As características dos pêsos de verão são descritas, sendo também fornecido o CPUE (número de peixes por minuto) para cada espécie de peixe.*

| Upstream pool                        |      |        |         |            |            |        |
|--------------------------------------|------|--------|---------|------------|------------|--------|
| Sampling month                       | June | August | October | January    | April      |        |
| Area (m <sup>2</sup> )               | 3760 | 2404   | 1504    | -          | -          |        |
| Maximum depth (m)                    | 1.5  | 1.1    | 0.9     | >2         | >2         |        |
| River flow                           | pool | pool   | pool    | river flow | river flow |        |
| CPUE (number of fish per minute)     |      |        |         |            |            |        |
| Fish species                         | June | August | October | January    | April      | MEDIAN |
| <i>Anaocypris hispanica</i>          | 0.00 | 0.14   | 0.00    | 0.00       | 0.03       | 0.00   |
| <i>Anguilla anguilla</i>             | 0.00 | 0.00   | 0.00    | 0.00       | 0.00       | 0.00   |
| <i>Cobitis paludica</i>              | 0.00 | 0.14   | 0.00    | 0.00       | 0.00       | 0.00   |
| <i>Gambusia holbrooki</i>            | 0.10 | 0.00   | 1.00    | 0.00       | 0.00       | 0.00   |
| <i>Iberochondrostoma lemmingii</i>   | 0.00 | 0.00   | 0.10    | 0.00       | 0.00       | 0.00   |
| <i>Lepomis gibbosus</i>              | 0.40 | 0.57   | 0.57    | 0.00       | 0.00       | 0.40   |
| <i>Luciobarbus comizo</i>            | 0.00 | 0.00   | 0.00    | 0.00       | 0.00       | 0.00   |
| <i>Luciobarbus sclateri</i>          | 0.10 | 0.14   | 0.00    | 0.00       | 0.00       | 0.00   |
| <i>Luciobarbus sp.</i>               | 0.00 | 0.00   | 0.13    | 0.03       | 0.07       | 0.03   |
| <i>Pseudochondrostoma willkommii</i> | 0.00 | 0.14   | 0.10    | 0.00       | 0.03       | 0.03   |
| <i>Squalius alburnoides</i>          | 3.20 | 2.14   | 0.23    | 0.20       | 0.37       | 0.37   |
| <i>Squalius pyrenaicus</i>           | 0.10 | 0.86   | 0.03    | 0.00       | 0.03       | 0.03   |
| Downstream pool                      |      |        |         |            |            |        |
| Sampling month                       | June | August | October | January    | April      |        |
| Area (m <sup>2</sup> )               | 694  | 408    | 231     | -          | -          |        |
| Maximum depth (m)                    | 0.9  | 0.7    | 0.5     | >2         | >2         |        |
| River flow                           | pool | pool   | pool    | river flow | river flow |        |
| CPUE (number of fish per minute)     |      |        |         |            |            |        |
| Fish species                         | June | August | October | January    | April      | MEDIAN |
| <i>Anaocypris hispanica</i>          | 0.17 | 0.00   | 0.00    | 0.08       | 0.00       | 0.00   |
| <i>Anguilla anguilla</i>             | 0.00 | 0.20   | 0.10    | 0.00       | 0.00       | 0.00   |
| <i>Cobitis paludica</i>              | 0.00 | 0.00   | 0.00    | 0.02       | 0.03       | 0.00   |
| <i>Gambusia holbrooki</i>            | 0.50 | 0.00   | 0.00    | 0.00       | 0.13       | 0.00   |
| <i>Iberochondrostoma lemmingii</i>   | 0.08 | 1.20   | 0.20    | 0.00       | 0.00       | 0.08   |
| <i>Lepomis gibbosus</i>              | 0.33 | 6.80   | 3.00    | 0.02       | 0.70       | 0.70   |
| <i>Luciobarbus comizo</i>            | 0.08 | 0.00   | 0.00    | 0.00       | 0.00       | 0.00   |
| <i>Luciobarbus sclateri</i>          | 0.33 | 0.20   | 0.30    | 0.00       | 0.00       | 0.20   |
| <i>Luciobarbus sp.</i>               | 1.58 | 4.40   | 2.50    | 0.12       | 0.00       | 1.58   |
| <i>Pseudochondrostoma willkommii</i> | 0.50 | 2.80   | 0.90    | 0.00       | 0.00       | 0.50   |
| <i>Squalius alburnoides</i>          | 3.42 | 4.00   | 3.30    | 0.23       | 0.60       | 3.30   |
| <i>Squalius pyrenaicus</i>           | 0.42 | 0.20   | 0.10    | 0.03       | 0.10       | 0.10   |

On April 8, during one of our bi-monthly monitoring sessions, we spotted several fishes, apparently Iberian chubs, in the Vascão stream, Vascão river tributary (coordinates: 37°23'50.53"N; 7°56'37.57"W) (Revezes, Tavira, Portugal) (Fig. 1). After the encounter, we checked our database related to permanent pools that did not dry during the summer-autumn of 2023 and measured the distance from the detection point in this ephemeral stream to the main river. Additionally, we confirmed in the literature (e.g., Collares-Pereira et al. 2021; Henriques et al. 2010) that our species were presenting a previously undocumented large and coordinated upstream migration. On April 12, the location was sampled with an electric fishing device.

## RESULTS

One *S. pyrenaicus* (total length 12.5 cm) and 13 *S. alburnoides* (mean total length 7.92 cm  $\pm$  0.5 SD) were captured, measured, and returned to the water. Additionally, further individuals of both species were spotted (F. Banha, personal observation), namely two more *S. pyrenaicus* and more than a dozen *S. alburnoides*, but these individuals were lost in the abundant vegetation (*Ranunculus aquaticus*) that occurred in the water.

The presence of these individuals at this location represents an upstream migration of 1687 m from the confluence with the Vascão River, with a slope of 0.7% and an altitude difference of 12 m. Before the restoration of the Vascão River flow by the end of 2023, the nearest permanent pools were located 1166 m downstream from the confluence point and 3152 m upstream from the same point. Although we do not know where the fishes migrated from, the total distance involved could be between 2853 and 4540 m, respectively. These distances were covered in almost 3-4 months of permanent flow in the Vascão River and its tributary.

## DISCUSSION

Both species, *S. pyrenaicus* and *S. alburnoides*, were considered resident, meaning they only move within a particular river segment or less than 5

km, according to Melcher & Holzer (2008). However, their movements have not been thoroughly studied. Only one study has been performed on a similar Iberian species, *Squalius torgalensis*, which found that movements during flow continuum are around 200 metres, with an outlier of 1400 metres (Henriques et al., 2010). Recently, Ordeix and Casals (2024) described both species as potamodromous, while showing or citing no information about their movements. There is some vagueness and ambiguity in water feature terms, regarding their extent or the distinction between different units, such as different river stretches or lakes, as an example (Santos et al., 2005). Thus, apart from distances that are more innocuous, this inconsistency leads to different classifications regarding potamodromy. For example, *Rutilus rutilus* (Linnaeus, 1758), also a Leuciscidae species, is considered potamodromous, yet normally only migrates 400 m upstream to spawn (Vøllestad & L'Abée-Lund, 1987), reaching a maximum of 2.5 km (Geeraerts et al., 2007). Such distances are below those reported in our study. A migration between the main channel and tributary (i.e., two river segments), is one of the criteria allowing both studied species to be classified as potamodromous (Melcher & Holzer, 2008). However, for another possible criterion, the maximum distance covered (4540 metres) is lower than established for potamodromous species by Melcher & Holzer (2008). However, considering the criteria stated by Northcote (1997), and our movement reported from the main river to a tributary, the studied species could be considered potamodromous. Moreover, another factor to maintain the same category is stated by Flecker et al. (2010), who considered resident fishes those that only move short distances, about 100 m.

Another notable aspect of the reported occurrence is the joint migration of both species. *S. alburnoides* parasitizes *S. pyrenaicus* for reproduction purposes (Sousa-Santos et al., 2006). Thus, coordinated migration abilities aiming at spawning would ensure the maintenance of this interspecific relationship. Additionally, the number of fishes captured, and their proportions compared to those in summer pools in the main river, are in accordance with the partial migration phenomena, where a population contains both

migratory and resident individuals (Chapman *et al.*, 2012). For instance, Peñáz *et al.* (2002) reported for the large European potamodromous species *Barbus barbus* that more than 70% of the population are resident individuals, and those that migrate, more than 90%, move less than 1000 m in the context of a permanent river. Similarly, in a permanent river in Portugal, the population of *Luciobarbus bocagei* is composed of more than 60% that do not move more than 1000 m (Branco *et al.* 2017).

It is expected that in Southern Europe, including the Iberian Peninsula, there will be an increase in average annual temperatures of up to 4°C and a substantial decrease in river flow (IPCC, 2024), with Iberian rivers being the most affected by water scarcity in Europe, namely the Tagus River (Lobanova *et al.*, 2008). Some projections show that these fishes will lose habitat suitability in the south of the Iberian Peninsula in the next 20 years (Reis *et al.*, 2024). In addition, the Iberian Peninsula is one of the most impacted areas in Europe due to the loss of connectivity (Rodeles *et al.*, 2020). This issue can exacerbate the effects of drought, as fish assemblages have been found to struggle more to recover from drought conditions in areas affected by reservoirs, particularly downstream (Boix *et al.*, 2010). Even small weirs, which could otherwise be crossable, may become problematic; it has been hypothesised that under such conditions, these barriers may select for resident individuals (Branco *et al.*, 2017). Therefore, connectivity issues may persist even after dam removal and in so-called “free-flowing river” scenarios (Stoffers *et al.*, 2024). Alongside connectivity loss, water abstraction significantly alters Iberian streams and impacts fish communities. These effects are reflected in fish metrics such as catch per unit effort, number of benthic species, number of intolerant species, and the proportional abundance of intolerant individuals (Benejam *et al.*, 2010).

Still, the present work shows that these small fish, in the presence of a river without major obstacles, can cope with severe drought periods and colonise/recolonise river stretches when conditions allow, demonstrating higher dispersal capacities than previously expected.

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## AUTHOR CONTRIBUTIONS

F.B.: Conceptualization, Data collection, Writing-Original draft preparation; P.B.: Data collection; All Authors: Writing- Reviewing and Editing.

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