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Effect of thermo-velocity barriers on fish: influence of water temperature, flow velocity and body size on the volitional swimming capacity of northern straight-mouth nase (*Pseudochondrostoma duriense*)

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Abstract

Water temperature and flow velocity directly affect the fish swimming capacity, and thus, both variables influence the fish passage through river barriers. Nonetheless, their effects are usually disregarded in fishway engineering and management. This study aims to evaluate the volitional swimming capacity of the northern straight-mouth nase (*Pseudochondrostoma duriense*), considering the possible effects of water temperature, flow velocity and body size. For this, the maximum distance, swim speed and fatigue time (FT) were studied in an outdoor open-channel flume in the Duero River (Burgos, Spain) against three nominal velocities (1.5, 2.5 and 3 m s^{-1}) and temperatures (5.5, 13.5 and 18.5°C), also including the changes between swimming modes (prolonged and sprint). Results showed that a nase of 20.8 cm mean fork length can develop a median swim speed that exceeds 20.7 BL s^{-1} (4.31 m s^{-1}) during a median time of 3.4 s in sprint mode, or 12.2 BL s^{-1} (2.55 m s^{-1}) for 23.7 s in prolonged mode under the warmest scenario. During prolonged swimming mode, fish were able to reach further distances in warmer water conditions for all situations, due to a greater swimming speed and FT, whereas during sprint mode, warmer conditions increased the swim speed maintaining the FT. In conclusion, the studied temperature range and flow velocity range influence fish swimming performance, endurance and distance travelled, although with some differences depending on the swimming mode. The provided information goes a step forward in the definition of real fish swimming capacities, and in turn, will contribute to establish clear passage criteria for thermo-velocity barriers, allowing the calculation of the proportion of fish able to pass a barrier under different working scenarios, as well designing of the optimized solutions to improve the fish passage through river barriers.

KEYWORDS
cyprinids, fish migration, open flume, survival analysis, volitional swimming, water temperature

1 | INTRODUCTION

Humans have constructed multiple barriers in rivers to cover their necessities, from dams and weirs (for power generation, water supply or flood control) to culverts (to allow water to flow under roads or trails) or gauging stations (for discharge monitoring; Belletti *et al.*, 2020). Many of these barriers have direct impacts on fish populations, as they affect the longitudinal connectivity of rivers, either physically or through the alteration of natural flow and thermal regimes, causing habitat fragmentation (Feng *et al.*, 2018; Jones & Petreman, 2015; Nilsson *et al.*, 2005). Some of these barriers are simply impassable for fish, whereas others are passable only for some individuals and/or only during specific river conditions (Cooke & Hinch, 2013; Garbin *et al.*, 2019; García-Vega *et al.*, 2022; Norman *et al.*, 2009). Despite the existence of structures to overcome these barriers (*e.g.*, fishways), these could be sometimes insufficient (Bunt *et al.*, 2016; Haro *et al.*, 2004; Valbuena-Castro *et al.*, 2020) or even behave as barriers for some individuals or species (Foulds & Lucas, 2013) or during some hydraulic scenarios (Fuentes-Pérez *et al.*, 2016).

The fish passability of a barrier or any hydraulic structure is directly linked to its hydraulic conditions (Larinier, 2002), with the flow velocity being one of the most important factors affecting it. When the flow velocity magnitude is beyond the behavioural and physiological limits of fish, that is to say, outside of their swimming capacity, it may trigger a "velocity barrier" (Haro *et al.*, 2004). The increase in flow velocity forces fish to change the swimming mode from sustained (velocity that fish can sustain indefinitely) or prolonged (velocity that fish can sustain for 20 s to 200 min) to sprint (velocity that fish can sustain for less than 20 s) (Castro-Santos, 2005; Weaver, 1964), which is directly linked to the use of muscle energy reserves (Beamish, 1978). When the velocity at the barrier exceeds the swimming capacity (or when the swimming distance with high velocities is too long), fish will fail to pass it. Even if the conditions in the velocity barrier are not entirely insurmountable, they could induce fatigue to fish due to the consumption of energy reserves (anaerobic effort), compromising their fitness and survival (Geist *et al.*, 2000; Roscoe *et al.*, 2011) upon cumulative barrier negation.

Although there are different metrics to define fish swimming capacity, the easiest one to compute and the most widely used is the critical swimming speed (U_{crit}) (Brett, 1964). Nonetheless, due to the methodological procedures and non-volitional conditions to obtain it, this metric is related to conservative values of prolonged speed, underestimating the real swimming capacity of fish and leading to question its usefulness for practical applications, such as fishway design (Castro-Santos *et al.*, 2013; Tudorache *et al.*, 2008) or barrier passability assessment. Alternatively, it is possible to use other methods that allow fish to develop their maximum swimming capacities (that is to say both prolonged and sprint), such as volitional open-channel flumes (Haro *et al.*, 2004; Hockley *et al.*, 2014; Ruiz-Legazpi *et al.*, 2018; Tudorache *et al.*, 2010). These devices are closer to the observed conditions in the field and allow the testing of a wide range of flow velocities (Castro-Santos, 2005; Weaver, 1964), making it

possible to draw the complete fish swimming capacity curve and, consequently, to compute practical metrics, such as fatigue time (FT; understood as endurance) or maximum distance travelled.

When it comes to the study of swimming capacity, besides flow velocity, it is important to consider other factors affecting it, such as the body size and the water temperature (Beamish, 1978; Hammer, 1995; Katopodis & Gervais, 2012; Videler, 1993). On the one hand, the body size is related to the aerobic metabolism, limiting the level of stored muscle energy (pre-exercise) and the metabolic disturbance (post-exercise), which affects swimming speed (Hammer, 1995; Mateus *et al.*, 2008), endurance (Ojanguren & Brana, 2003) and the recovery time (Kieffer, 2000). On the other hand, fish are poikilothermic animals and, thus, they are strongly influenced by water temperature. Temperature intervenes in multiple physiological and biochemical processes, such as growth, sexual maturation, metabolic rate and energetics (Brett, 1971; Guderley & Blier, 1988; McKenzie & Claireaux, 2010), as well as behavioural processes (Davis *et al.*, 2019), which directly affect swimming capacity (Brett, 1964; Plaut, 2001; Rome *et al.*, 1992). At sustained (aerobic) and prolonged swimming speeds [a combination of aerobic and anaerobic processes (Bilinski, 1975)], metabolic rate increases with higher temperatures until an optimum, and any increment after this optimum will negatively affect swimming capacity (Beamish, 1978; Brett, 1964). In the case of sprint swimming speed, it is considered to be largely independent of temperature (Brett, 1964), although few studies have investigated this relationship (Bayse *et al.*, 2019).

Therefore, variations in water temperature and flow regimes (*i.e.*, changes in discharge rates translated into water depth and flow velocity variations) can affect the fish's endurance to transverse an obstacle, which may limit the obstacle passage and may constitute thermal or velocity barriers for the fish migration (Haro *et al.*, 2004; Langford, 1990). Furthermore, as both water temperature and discharge act as timers or triggers for the onset and maintenance of fish migration (García-Vega *et al.*, 2022; Lucas *et al.*, 2001), changes in these factors may affect not only the ability to surpass a barrier but also the motivation to traverse it (Bayse *et al.*, 2019; Goerig *et al.*, 2017; Sanz-Ronda *et al.*, 2021). The expected effects of climate change could aggravate this situation, particularly in southern Mediterranean regions (Cramer *et al.*, 2018), where most favourable scenarios predict for this century an increase in water temperature greater than 2.6°C for the spring–summer period (Senent-Aparicio *et al.*, 2017; Solomon *et al.*, 2007), just coinciding with the spawning migration of cyprinids (Doadrio, 2002; Kottelat & Freyhof, 2007), and a reduction in winter and spring discharge, which is already taking place (Ceballos-Barbancho *et al.*, 2008; Sánchez-Hernández & Nunn, 2016). Moreover, the combined effect of climate change together with other thermal and flow regime alterations derived from river regulation, such as the surface reservoir heating, the colder water from the bottom outlet releases by irrigation or hydropower reservoirs (Feng *et al.*, 2018; García-Vega *et al.*, 2017; Prats *et al.*, 2010; Van Vliet *et al.*, 2013) and shifts in natural flows and their timing (Biemans *et al.*, 2011; Poff & Zimmerman, 2010; Williams & Wolman, 1984), may exacerbate these effects. Therefore, the

combined effect of high flow velocity and water temperature during fish movements, *i.e.*, thermo-velocity barriers, should be considered jointly, as it can put fish to the limit of their physiological and behavioural capabilities (Ruiz-Legazpi *et al.*, 2018). Nonetheless, to date, few studies have analysed the effect of temperature on fish volitional swimming capacity (Bayse *et al.*, 2019; Ruiz-Legazpi *et al.*, 2018), and its influence on most fish species remains unknown.

One of the groups of species more affected by those conditions is circum-Mediterranean and semiarid region nases (Cyprinidae, genus *Chondrostoma, Parachondrostoma* and *Pseudochondrostoma*). Their populations have considerably declined during the past decades (Ferreras Chasco, 2012), with river regulation and loss of longitudinal connectivity as the main threats to their conservation (Almaça, 1995). They are mainly categorized as "vulnerable" or "endangered" by the IUCN (2020) and mentioned in Annex II of the European Union Habitats Directive (1992). Nase is also an interesting species to study swimming performance for different temperatures, because its range occupies a wide variety of freshwater habitats, from floodplains to headwaters (Kottelat & Freyhof, 2007; Santos *et al.*, 2011), and therefore, each species may experience wide seasonal and geographical variations in temperature, from 4 to 28°C (Souchon & Tissot, 2012). In addition, nase is a rheophilic potamodromous cyprinid (Doadrio *et al.*, 2011), which displays migratory behaviour with reproductive and overwinter movements, from spring to late autumn (García-Vega *et al.*, 2022; Ovidio & Philippart, 2008; Rodriguez-Ruiz & Granado-Lorencio, 1992), and thus, with high chances of facing thermo-velocity barriers.

Considering these points, the main goal of this work is to study the volitional swimming capacity of the northern straight-mouth nase (*Pseudochondrostoma duriense* Coelho, 1985; hereafter referred to as nase) considering the influence of water temperature, flow velocity and body size. For this, an open-channel flume has been used with three nominal velocities (1.5, 2.5 and 3 m s^{-1}) and three nominal water temperatures (5.5, 13.5 and 18.5°C), as well as telemetry (individual fish tracking) and surveillance video-camera systems. The specific objectives are (a) to establish a model for the main metrics that define the swimming capacity of nase (swim speed, FT and maximum distance travelled) and (b) to evaluate the effect of water temperature, flow velocity and body size in the previous metrics. The developed models will directly allow the assessment of when and how many fish (species, size, percentage) can pass a barrier and will quantify the influence of water temperature and flow velocity in the passage, as well as the development of fishway design criteria based on the real fish capacities and river conditions.

2 | MATERIALS AND METHODS

2.1 | Facilities and instrumentation

The volitional swimming capacity of the nase was studied in an outdoor open-channel flume located near the fishway facility of Vadocondes hydropower plant in the Duero River (Burgos, Spain; ETRS89 41° 38′ 16.05″ N; 3° 34′ 17.37″ W; Figure 1). The flume was divided into three sections: (a) head tank, (b) swimming flume and (c) staging area. The swimming flume was an 18 m long and 0.5 m wide channel of zero slope, made of polished concrete to reduce turbulence, flow friction and boundary layer effects. A system of slide gates regulated the discharge intake (supplied directly from the Duero River) and was used to set the flow velocity and water depth in the swimming flume. During trials, fish volitionally entered the flume from the staging area. A full description of the flume can be found in Sanz-Ronda *et al.* (2015) and Ruiz-Legazpi *et al.* (2018).
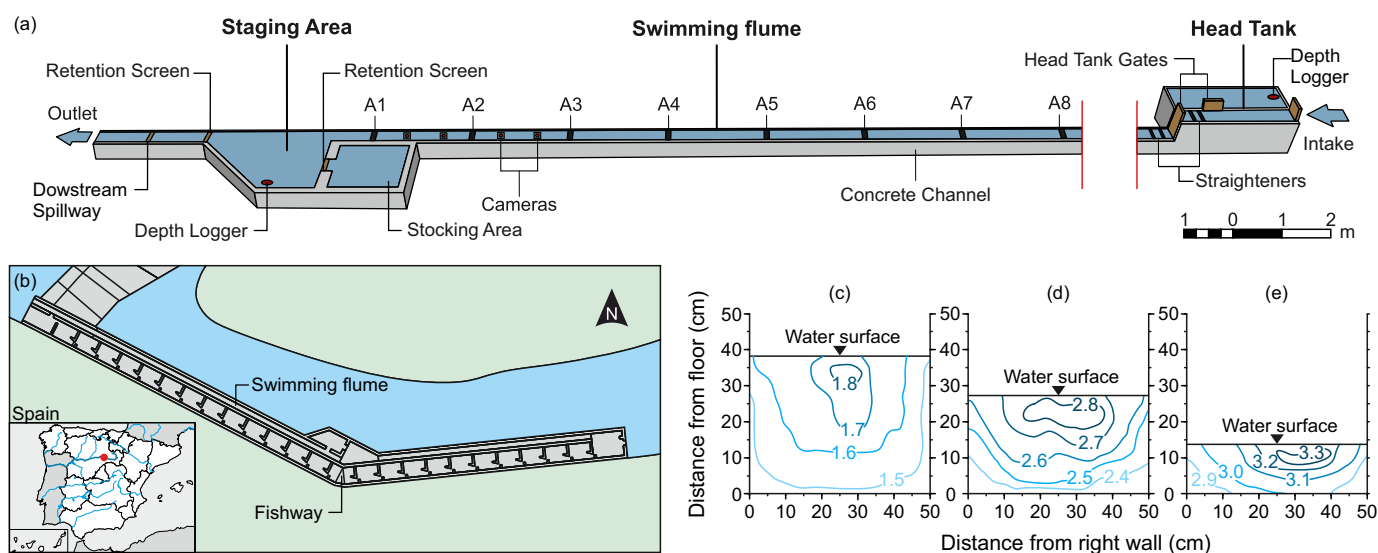
FIGURE 1 (a) Open-channel flume scheme, fish monitoring (telemetry antennas) and hydraulic control (gates, spillway, depth loggers, *etc.*) systems. (b) Location of the swimming flume near the fishway facility of Vadocondes hydropower plant in the Duero River (Spain). (c–e) Cross-sectional flow velocity profiles: flow velocity conditions referenced to the third antenna (A3) and grouped by nominal velocity: (c) 1.5, (d) 2.5 and (e) 3.0 m s^{-1}

Fish behaviour inside the flume was monitored by combining two monitoring systems. The first one was composed of a passive integrated transponder (PIT) telemetry system (ORFID® Half Duplex reader with antenna Multiplexer), with a set of eight antennas and two synchronized multiplexed readers (Figure 1a). Antennas were located every 2 m in length, with the first antenna (A1) at 0.5 m from the swimming flume entrance (this distance prevented readings of fish at the staging area swimming near the entrance) and the last antenna (A8) at 14.5 m upstream [upstream of this antenna several flow straighteners (wire net with 4 cm² mesh screen) located to achieve homogeneous conditions in the swimming flume]. The second monitoring system was a surveillance video-camera network (Sony 420TVL CCD 36 IR LEDs Day and Night CCTV; 15 fps), with four zenithal cameras installed above the flume between antennas A2 and A4, with a monitoring area of 0.8 m long and 0.5 m wide per camera (Figure 1a).

Water temperature was recorded every 30 min in the staging area (EL-USB-1-PRO, Lascar [Wiltshire, United Kingdom]; ±0.1°C). Water depth was continuously monitored every minute using two sensor probes (Orpheus Mini, OTT Hydromet GmbH [Kempten, Germany]; ±0.002 m), one in the head tank and another one in the staging area, and a video-recorded limnimeter in the swim speed flume (accuracy: 0.005 m). Flow velocity was checked using a propeller flow meter (Model 2100, Swoffer Instruments Inc. [Summer, WA, USA]; ±0.01 m s⁻¹) every 30 min at antenna A3.

2.2 | Fish collection

A total of 143 adult nase were used in the experiments. These fish were captured using electrofishing (Erreka model; 180–200 V, 2–2.3A) in two locations in the Duero basin: one in the main stem of the Duero River [mean annual discharge (MAD) of 17 m³ s⁻¹] in the vicinity of the Vadocondes HPP, and the other one in the Arlanza River, a close second-order tributary (Strahler, 1957) of the Duero River with similar dimensions and discharge (MAD of 24 m³ s⁻¹) to the other capture reach. Collections (as well as trials) were carried out in the following three periods (a) between 25 and 26 May 2012, (b) 5 and 6 May 2013 and (c) 28 and 29 November 2013 to be the representative of the natural peak movement periods of the nase (spring and autumn), as well as to cover the extent of the temperature regime in both periods. Fish were transported to the flume facilities (all travels lasted <1.5 h) in tanks (100 l capacity) with oxygen supply and water temperature monitoring.

Upon arrival, fish were anesthetized with a tricaine mesylate solution (MS-222) at a dose of 60 mg l⁻¹ [minimum dosage recommended for cyprinids (Neiffer & Stamper, 2009)] to measure the biometric parameters [fork length (L_F), ±0.1 cm and mass (M); ±1 g], and to surgically implant a PIT-tag (TIRIS model RI-TRP-WRHP; Texas Instruments, Dallas, TX, USA: 23 mm long, 3.85 mm diameter and 0.6 g weight) into the peritoneal cavity. Tag weight was always lower than 2% of the fish weight. This method has been widely applied in fish monitoring experiments, with low negative effects on behaviour

(Brown et al., 1999; Castro-Santos & Vono, 2013; Ostrand et al., 2011, among others). After handling, fish were randomly divided into two groups and held for acclimation approximately 24 h before each trial. One of them was placed in the staging area of the flume and the other one into two consecutive pools of the associated fishway facility (Figure 1b), being then poured into the staging area of the flume at the beginning of the corresponding trials (and after removing the fish from the previous one). Both resting areas had a water volume >3500 l and a water depth >1 m, and were supplied with water (50 l s⁻¹) directly from the Duero River. Fish were not artificially fed during the experiments.

All experiments and procedures were performed following European Union ethical guidelines (Directive 2010/63/UE) and Spanish Acts 32/2007 and RD 53/2013, with the approval of the competent authorities (Regional Government on Natural Resources and Water Management Authority).

2.3 | Trials

The study was divided into three experiments corresponding to three different values of water temperatures: (a) 18.5, (b) 13.5 and (c) 5.5°C (Table 1). The first two temperatures correspond to those of the central period of spawning migration (May 2012 and 2013, respectively), and the third to trophic autumn (overwinter) movements (November 2013). Due to this issue, fish number and biometric characteristics of each fish group (Table 1) were conditioned by both the presence of individuals in the river (nase is a scarce threatened species) and the season (larger fish are more common after the summer period, due to food availability, warmer temperatures and growth).

Each experiment consisted of three trials based on three nominal flow velocities: (a) 1.5, (b) 2.5 and (c) 3.0 m s⁻¹. That is to say, 3 temperatures × 3 velocities = 9 trials. Each of the velocities was achieved by the modification of the hydraulic scenario of the flume, i.e., the discharge and the water depth (Table 1). As flow velocities were not uniform across the flume, i.e., velocities were higher in the centre of the cross-section and lower close to the bed and walls, with the minimum values at the corners (Figure 1c–e), measured flow velocities ranged between 1.44 and 1.73 m s⁻¹ for the nominal velocity 1.5 m s⁻¹ (−4% and 15%, respectively): for 2.5 m s⁻¹, from 2.08 to 2.80 m s⁻¹ (−17% and +12%) and for 3.0 m s⁻¹, from 2.76 to 3.33 m s⁻¹ (−8% and +11%). Flow regimen was characterized as turbulent and subcritical for 1.5 m s⁻¹ [Froude number (Fr): 0.6–0.9; Reynolds number (Re): 142,000–222,000] and supercritical for 2.5 m s⁻¹ (Fr: 1.5–1.9; Re: 199,000–309,000) and 3.0 m s⁻¹ (Fr: 2.0–2.8; Re: 162,000–244,000) trials.

In each experiment, fish were randomly divided into two groups per trial with similar fork length and mass between the two groups, i.e., 9 trials × 2 groups = 18 tests (Table 1). The trials were initiated by the configuration of the corresponding hydraulic scenario in the swimming flume and the opening of the retention screen of the staging area, allowing the tagged fish to volitionally enter the swimming

TABLE 1 Characterization of swim speed trials through hydraulic, biometric and environmental parameters

Informative parameters / Nominal parameters / Hydraulic and environmental parameters

Experiment	Trial	Group	Participation % (n/N)	Flow velocity (m s⁻¹)	Water temperature (°C)	Measured flow velocity (m s⁻¹)	Measured water temperature (°C)	Discharge (m³ s⁻¹)	Water depth (m)
1	1	1	57% (8/14)	3.0	18.5	2.79 ± 0.03	18.3 ± 0.4	0.182	0.12
	1	2	21% (3/14)	3.0	18.5	2.84 ± 0.05	18.1 ± 0.4	0.181	0.13
	2	1	50% (7/14)	1.5	18.5	1.47 ± 0.07	18.2 ± 0.4	0.271	0.38
	2	2	43% (6/14)	1.5	18.5	1.53 ± 0.08	18.7 ± 0.5	0.271	0.38
	3	1	50% (7/14)	2.5	18.5	2.41 ± 0.02	17.8 ± 0.8	0.324	0.26
	3	2	0% (0/14)	2.5	18.5	2.39 ± 0.01	18.3 ± 0.6	0.325	0.27
2	4	3	30% (11/37)	3.0	13.5	2.88 ± 0.03	12.9 ± 0.3	0.181	0.14
	4	4	54% (20/37)	3.0	13.5	2.85 ± 0.04	13.5 ± 0.4	0.181	0.15
	5	3	51% (19/37)	1.5	13.5	1.47 ± 0.05	13.3 ± 0.5	0.274	0.41
	5	4	14% (5/37)	1.5	13.5	1.49 ± 0.06	13.7 ± 0.2	0.275	0.43
	6	3	24% (9/37)	2.5	13.5	2.43 ± 0.06	12.8 ± 0.4	0.324	0.24
	6	4	43% (16/37)	2.5	13.5	2.41 ± 0.02	13.2 ± 0.3	0.324	0.25
3	7	5	0% (0/19)	3.0	5.5	2.91 ± 0.03	5.2 ± 0.4	0.183	0.14
	7	6	41% (9/22)	3.0	5.5	2.89 ± 0.05	5.6 ± 0.4	0.182	0.13
	8	5	89% (17/19)	1.5	5.5	1.52 ± 0.06	5.2 ± 0.4	0.273	0.34
	8	6	9% (2/22)	1.5	5.5	1.56 ± 0.06	5.6 ± 0.4	0.273	0.33
	9	5	26% (5/19)	2.5	5.5	2.40 ± 0.01	5.0 ± 0.3	0.323	0.23
	9	6	55% (12/22)	2.5	5.5	2.47 ± 0.05	5.4 ± 0.4	0.323	0.24

Biometric parameters

Experiment	Group	N	Fork length (cm)	Mass (g)	Condition factor (g cm⁻³)
1	1	14	17.6 ± 1.8	62 ± 20	1.10 ± 0.07
	2	14	16.9 ± 2.6	62 ± 33	1.20 ± 0.13
	Total	28	17.3 ± 2.2 [14.0, 21.8] ($P = 0.3575$)	62 ± 27 [32, 146] ($P = 0.4761$)	1.15 ± 0.12 [1.13, 2.06]
2	3	37	19.8 ± 2.3	93 ± 33	1.16 ± 0.10
	4	37	20.3 ± 2.1	98 ± 28	1.15 ± 0.12
	Total	74	20.0 ± 2.2 [16.2, 25.0] ($P = 0.2580$)	96 ± 31 [48, 171] ($P = 0.2796$)	1.16 ± 0.11 [0.97, 1.56]
3	5	19	24.2 ± 2.5	210 ± 95	1.40 ± 0.28
	6	22	25.1 ± 2.4	237 ± 76	1.45 ± 0.27
	Total	41	24.7 ± 2.5 [20.2, 30.0] ($P = 0.3073$)	225 ± 85 [106, 414] ($P = 0.2446$)	1.43 ± 0.27 [1.13, 2.06]
Total		143	20.8 ± 3.5 [14.0, 30.0]	126 ± 82 [32, 414]	1.23 ± 0.21 [0.97, 2.06]

Note: N refers to the total number of fish by group and treatment condition and n the number of fish that actively participated in the experiments (*i.e.*, with at least one attempt). For environmental and biometric parameters, the mean ± standard deviation, the range (in square brackets) and the P-value (P) of Mann–Whitney Wilcoxon test (in brackets) are provided. Fork length–mass relation resulted in an allometric growth model following the equation $M = 0.004 \cdot L_F^{3.3771}$ ($R^2 = 0.9459$).

flume. All fish groups were exposed to the three flow velocities (*i.e.*, each of the fish groups participated in three tests), with a duration of 4 h per test starting at 11 A.M. local time, with more than 12 h of recovery time among consecutive tests. The use of the same fish more than once could lower their swimming performance in subsequent experiments, due to the decrease in muscle glycogen for the lactate production caused by burst activity during sprinting performance (Silva *et al.*, 2009). Most studies report that full metabolic recovery (indicated by replenishment of muscle glycogen stores and clearance of muscle lactate load) requires from 8 to 24 h after an exhausting exercise (Milligan *et al.*, 2000). More specifically, Wardle (1978) found that after an 8 h rest, the 50%–80% of the muscle glycogen is restored. In particular, swimming experiments in fishways with confined and reused fish showed no variations in the swimming performance after 12 h resting (Bravo-Córdoba *et al.*, 2018; Sanz-Ronda *et al.*, 2019). Therefore, the 12 h recovery period among consecutive tests should be sufficient for the fish to restore the muscle glycogen and metabolize most part of lactate. No fish died as a direct result of handling or during the experiments.

2.4 | Data processing and analysis

The swimming capacity was explained through three metrics: (a) maximum distance, (b) FT and (c) swimming speed (absolute –swim speed– and relative –ground speed–) (Sanz-Ronda *et al.*, 2015).

Maximum distance (D_{max}) in metres (m) was defined as:

$$D_{max} = 0.5 + D_j + D_{j_+} \tag{1}$$

where 0.5 is the distance (m) between the flume start and A1, D_j is the distance between the last antenna (antenna *j*) where the fish was detected and the first antenna (A1) and D_{j_+} is the distance that the fish swam upstream of antenna *j*.

FT in seconds (s) was defined as:

$$FT = T_{0.5} + T_j + T_{j_+} \tag{2}$$

where $T_{0.5}$ refers to the time spent to pass the first 0.5 m in the flume (a quarter of the elapsed time between A1 and A2), T_j is the time elapsed to travel the distance between the last antenna (antenna *j*) where fish was detected and A1 and T_{j_+} is the time swimming upstream of the last antenna (antenna *j*).

Ground speed (U_g) was defined as:

$$U_g = D_{max} \times FT^{-1} \tag{3}$$

where D_{max} is the maximum distance and FT.

Swim speed (U_s) was defined as:

$$U_s = U_g + U_f \tag{4}$$

where U_g is the ground speed and U_f is the flow velocity. U_f is defined as the mean flow velocity against each fish swam, *i.e.*, the measured flow velocity (Table 1). All those velocities (U_i) can be defined as absolute velocities in m s^{-1} or as relative velocities in body lengths per second (BL s^{-1}), dividing U_i in m s^{-1} by L_F.

All statistical analyses were performed using *R* version 4.1.0 (R Core Team, 2021). Mann–Whitney Wilcoxon test was performed to find differences in the fork length and mass for the two fish groups used in each experiment. This test was used to find the differences in the maximum distance of ascent, swim speed and FT by group considering only the active fish in each trial. In addition, Kruskall–Wallis (KW) test was used to find the differences in the maximum distance of ascent, swim speed and FT by nominal velocity and water temperature. When KW test was significant, *post hoc* Dunn's multiple comparison test with Bonferroni correction was performed. These nonparametric tests applied as variables were not normally distributed.

Survival analysis was used to evaluate the studied metrics (Castro-Santos, 2005; Haro *et al.*, 2004), by applying the concept of survival time (*i.e.*, time until an event occurs) to swimming capacity (*i.e.*, the maximum distance that a fish can swim, the maximum speed that a fish can develop or time until a fish stops to swim). Any fish that reached the upper antenna (A8; 14.5 m from the flume entrance) was included as censored. This means that a censored fish may have travelled more distance, developed a greater speed or spent a longer FT than that established for it if the flume was larger or the experiments had continued (Hosmer & Lemeshow, 1999; Kleinbaum & Klein, 2005). In addition, only one attempt by fish in each test was considered, *i.e.*, the one on which the maximum distance was reached, to represent the maximum swimming capacity of fish.

To define the swimming mode shift, *i.e.*, the swim speed threshold where fish change between prolonged and sprint swimming modes, the moving-point regression approach was used (Castro-Santos, 2005). This method fits successive models of *FT* against U_s with an incrementing hypothetical speed threshold, and the best model is selected based on the minimum AIC (most favourable trade-off between precision and accuracy of the estimate), as well as considering the minimum shift in the distance between swimming mode curves (ideally a continuous transition is expected between modes). As the difference in AIC values (ΔAIC) between two models up to 2 represents strong reliable support for one model over another (Burnham *et al.*, 2011), a range of potential breaking points was calculated considering ΔAIC = 2.

Parametric regression models were fitted using the *survival* R package (Therneau & Grambsch, 2000). Different distributions (exponential, Weibull and log-logistic) were first considered, with stepwise variable selection (significance level $\alpha = 0.05$). The best model was selected according to AIC.

$$\text{Exponential}: S(Y) = \exp[-\exp(\omega - \mu)] \tag{5}$$

$$\text{Weibull}: S(Y) = \exp\left[-\exp\left(\frac{\omega - \mu}{\sigma}\right)\right] \tag{6}$$

$$\text{Log} - \text{logistic} : S(Y) = \frac{1}{1 + \exp\left(\frac{\omega - \mu}{\sigma}\right)} \tag{7}$$

where $S(Y)$ is the survivorship (probability) function for the response variable (Y), $\omega = \ln(Y)$, σ is the shape parameter and $\mu = \beta \cdot X$ (the vector product of predictors (X) and their coefficients (β)).

A nested model was developed for the relation of the FT and the swim speed (considering also the water temperature as covariable) to account for the differences by swimming mode, a classical model in the fish swimming capability literature (Castro-Santos, 2005; Castro-Santos et al., 2013; Sanz-Ronda et al., 2015). This model will follow the form:

$$\ln(\text{FT}) = \beta_0 + \beta_1 \times T_w + \beta_2 \times U_s + \beta_3 \times T_w \times U_s + \beta_4 \times S_{\text{mode}} + \beta_5 \times T_w \times S_{\text{mode}} + \beta_6 \times U_s \times S_{\text{mode}} + \beta_7 \times T_w \times U_s \times S_{\text{mode}} + \varepsilon \tag{8}$$

where β's are the regression coefficients, U_s is the swim speed in BL s^{-1}, T_w = nominal water temperature (i.e., categorical with three levels: (a) 5.5, (b) 13.5 and (c) 18.5°C) and S_{mode} is the swimming mode, with two categories, 0 if prolonged and 1 if sprint. As U_s accounts partially for the effect of the body length, the relation between the FT and the L_F was evaluated via linear regression.

The model for the maximum distance was constructed considering all data together to collect the overall strategies fish developed facing the velocity barrier. It means data were not separated using swimming mode, although a nested model using sprint and prolonged modes is provided as Supporting Information Appendix S1:

$$\ln(D_{\text{max}}) = \beta_0 + \beta_1 \times L_F + \beta_2 \times M + \beta_3 \times U_f + \beta_4 \times T_w + \varepsilon \tag{9}$$

where β's are the regression coefficients, L_F = fork length in cm, M = mass in g, U_f = flow velocity defined as mean flow velocity against which each fish swam in m s^{-1} (i.e., measured flow velocity) and T_w = nominal water temperature [i.e., categorical with three levels: (a) 5.5, (b) 13.5 and (c) 18.5°C].

Finally, a nested model for the swim speed (in m s^{-1}) was developed to account for differences by swimming mode, following the form:

$$\ln(U_s(\text{m} \cdot \text{s}^{-1})) = \beta_0 + \beta_1 \times L_F + \beta_2 \times M + \beta_3 \times U_f + \beta_4 \times T_w + \beta_5 \times S_{\text{mode}} + \beta_6 \times L_F \times S_{\text{mode}} + \beta_7 \times M \times S_{\text{mode}} + \beta_8 \times U_f + \beta_9 \times T_w \times S_{\text{mode}} + \varepsilon \tag{10}$$

where β's are the regression coefficients, L_F = fork length in cm, M = mass in g, U_f = flow velocity defined as mean flow velocity against which each fish swam in m s^{-1} (i.e., measured flow velocity), T_w = nominal water temperature [i.e., categorical with three levels: (a) 5.5, (b) 13.5 and (c) 18.5°C] and S_{mode} is the swimming mode, with two categories, 0 if prolonged and 1 if sprint. The units of U_s in m s^{-1} were selected instead BL s^{-1} to not dilute the effect of the fork length in the model. A global model (without differentiating by swimming

mode), as well as a model by swimming mode but in BL m^{-1}, is provided as Supporting Information Appendix S1.

3 | RESULTS

3.1 | General results

Table 2 shows a summary of the observed results from the nine trials. In general, significant differences were found in the observed variables (maximum distance, swimming speed and FT) depending on the nominal flow velocity and water temperature (Table 2). On the one hand, for all studied metrics and for any temperature, almost no differences were found between 2.5 and 3 m s^{-1}, whereas significant differences were observed between the subcritical (1.5 m s^{-1}) and the supercritical flow velocities (2.5 and 3 m s^{-1}). On the other hand, for any flow velocity, a greater swimming capacity was generally observed with the increase in water temperature, with the exception of the FT (Table 2).

It is important to note that despite two homogenous groups in fish number and body size made for each trial (Table 1), not all fish actively participated in the experiments (Table 3). For example, no fish from Group 2 made an attempt in Trial 3 (2.5 m s^{-1} and 18.5°C) and from Group 5 in Trial 7 (3 m s^{-1} and 5.5°C). In general, no differences in the studied metrics were observed between the active fish in both groups per trial (Table 3), with the exception of Groups 3 and 4 in Trial 6 for the maximum distance travelled, where the active fish in one group had significantly larger body size than the other (median L_F 18.5 vs. 20.6 cm), and Groups 5 and 6 in Trial 9 for the FT, where one of the active groups was significantly larger (in number) than the other (5 vs. 12 fish).

3.2 | Swimming modes: FT – swim speed model

The point where the swimming mode shift occurs was strongly influenced by water temperature, occurring the change from prolonged to sprint later with warmer water temperature (Figure 2). Moving-point regression showed a significant breakpoint close to 18.1 BL s^{-1} for the warmest water temperature (18.5°C) [range with ΔAIC = 2: (17.7, 20.1 BL s^{-1})]; 14.5 BL s^{-1} for 13.5°C [range: (13.4, 15.2 BL s^{-1})] and near 10.5 BL s^{-1} for the coldest water temperature (5.5°C) (only two possible values: 7.9 and 10.5 BL s^{-1}; Figure 2).

Based on these breakpoints, with the lowest water velocity (1.5 m s^{-1}), most fish (96.4%) swam in prolonged mode, whereas with higher velocities, most developed sprinting performance (71.4% with 2.5 m s$^{-1\%}$ and 92.2% with 3.0 m s^{-1} of nominal flow velocity; Table 4).

Table 5 shows the regression model for the prediction of the FT for both swimming modes in relation to the swim speed and the water temperature. In prolonged mode, the swim speed is negatively correlated with the FT; that is, at greater developed speeds nase endurance is lower (i.e., the FT is shorter), reduced by [exp(−0.3163) − 1] = −27.1% per m s^{-1} of flow velocity. On the contrary, the water

TABLE 2 Median and quartiles (25% and 75%) of the observed maximum distance, swim speed, ground speed and fatigue time (FT) of nase, swimming against the three studied nominal flow velocities (1.5, 2.5 and 3.0 m s^{-1}) and water temperatures (5.5, 13.5 and 18.5°C)

| | | Nominal flow velocity | | | | | | | | |
| | | 1.5 m s^{-1} | | | 2.5 m s^{-1} | | | 3.0 m s^{-1} | | |
Variable	Water temperature (°C)	Median (IQrange)	Sig. T_w	Sig. U_f	Median (IQrange)	Sig. T_w	Sig. U_f	Median (IQrange)	Sig. T_w	Sig. U_f
Maximum distance (m)	5.5	6.5 (4.7–10.0)	a		2.9 (2.5–3.1)		x	2.7 (2.5–2.9)	d	X
	13.5	12.5 (10.4–14.5)	b		4.0 (3.1–5.5)	c	y	3.2 (2.7–4.0)	d,e	Y
	18.5	10.8 (6.5–14.5)	a,b		4.0 (3.5–4.0)	c	z	4.0 (3.3–4.1)	e	Z
Swimming speed (BL s^{-1}) Swim Speed	5.5	9.2 (8.1–9.6)			11.0 (10.5–11.7)			13.0 (12.5–13.3)		
	13.5	9.9 (9.1–10.9)	a		16.3 (15.6–17.4)	b	x	18.2 (16.6–20.4)		x
	18.5	10.8 (9.5–12.4)	a		19.3 (17.0–19.7)	b	y	20.8 (20.5–24.5)		y
Ground Speed	5.5	2.4 (2.0–3.0)	a,b	w	1.8 (1.6–2.0)		x	1.9 (1.7–2.2)		w,x
	13.5	2.4 (1.9–3.1)	a,c		4.2 (3.9–5.1)	d	y	4.3 (3.5–5.6)		y
	18.5	2.8 (1.4–3.7)	b,c		5.8 (3.5–6.4)	d	z	5.7 (5.4–6.6)		z
FT (s)	5.5	14.3 (8.1–17.8)			6.4 (5.5–7.4)	b	x	6.0 (5.2–6.3)		x
	13.5	26.4 (17.2–34.4)	a		4.2 (3.6–5.6)	c	y	3.7 (3.0–4.5)	d	y
	18.5	24.7 (8.7–55.0)	a		5.2 (3.5–6.6)	b,c	z	3.4 (3.2–3.7)	d	z

Note: Letters represent the significant differences ($\alpha = 0.05$) according to the pair-wise Dunn test (Kruskall–Wallis comparison with Bonferroni correction) for differences by water temperature in a certain flow velocity (Sig. T_w) and by flow velocity for a certain water temperature (Sig. U_f). The medians that do not share a letter are significantly different.

TABLE 3 Mann–Whitney Wilcoxon test for the comparison by group of the studied metrics considering only the active fish in each trial

| | | | | | | Mann–Whitney Wilcoxon test P-value | | | |
Experiment	Trial	Group	Participation	Flow velocity (m s^{-1})	Water temperature (°C)	Fork length	Maximum distance	Swim speed	FT
1	1	1	57% (8/14)	3	18.5	0.6090	0.7450	0.6303	0.4970
		2	21% (3/14)	3	18.5				
	2	1	50% (7/14)	1.5	18.5	0.6146	0.3395	0.8357	0.6282
		2	43% (6/14)	1.5	18.5				
	3	1	50% (7/14)	2.5	18.5	-	-	-	-
		2	0% (0/14)	2.5	18.5				
2	4	3	30% (11/37)	3	13.5	0.2823	0.1134	0.5553	0.3423
		4	54% (20/37)	3	13.5				
	5	3	51% (19/37)	1.5	13.5	0.3737	0.6052	0.6293	0.4892
		4	14% (5/37)	1.5	13.5				
	6	3	24% (9/37)	2.5	13.5	0.0201[a]	0.0241[b]	0.1515	0.1066
		4	43% (16/37)	2.5	13.5				
3	7	5	0% (0/19)	3	5.5	-	-	-	-
		6	41% (9/22)	3	5.5				
	8	5	89% (17/19)	1.5	5.5	0.6412	0.0952	1.0000	0.2924
		6	9% (2/22)	1.5	5.5				
	9	5	26% (5/19)	2.5	5.5	0.7914	0.8306	0.1037	0.0136[c]
		6	55% (12/22)	2.5	5.5				

[a]Group 3 Trial 6 median L_F = 18.5 cm (IQrange = 18–19.8 cm) *vs.* Group 4 Trial 6 median D_{max} = 20.6 cm (IQrange = 19.95–22.1 cm).
[b]Group 3 Trial 6 median D_{max} = 3.1 m (IQrange = 2.5–4 m) *vs.* Group 4 Trial 6 median D_{max} = 4.75 m (IQrange = 3.95–5.83 m).
[c]Group 5 Trial 9 median fatigue time (FT) = 5.13 s (IQrange = 5.12–5.47 s) *vs.* Group 6 Trial 9 median FT = 7.08 s (IQrange = 6.31–8.21 s).
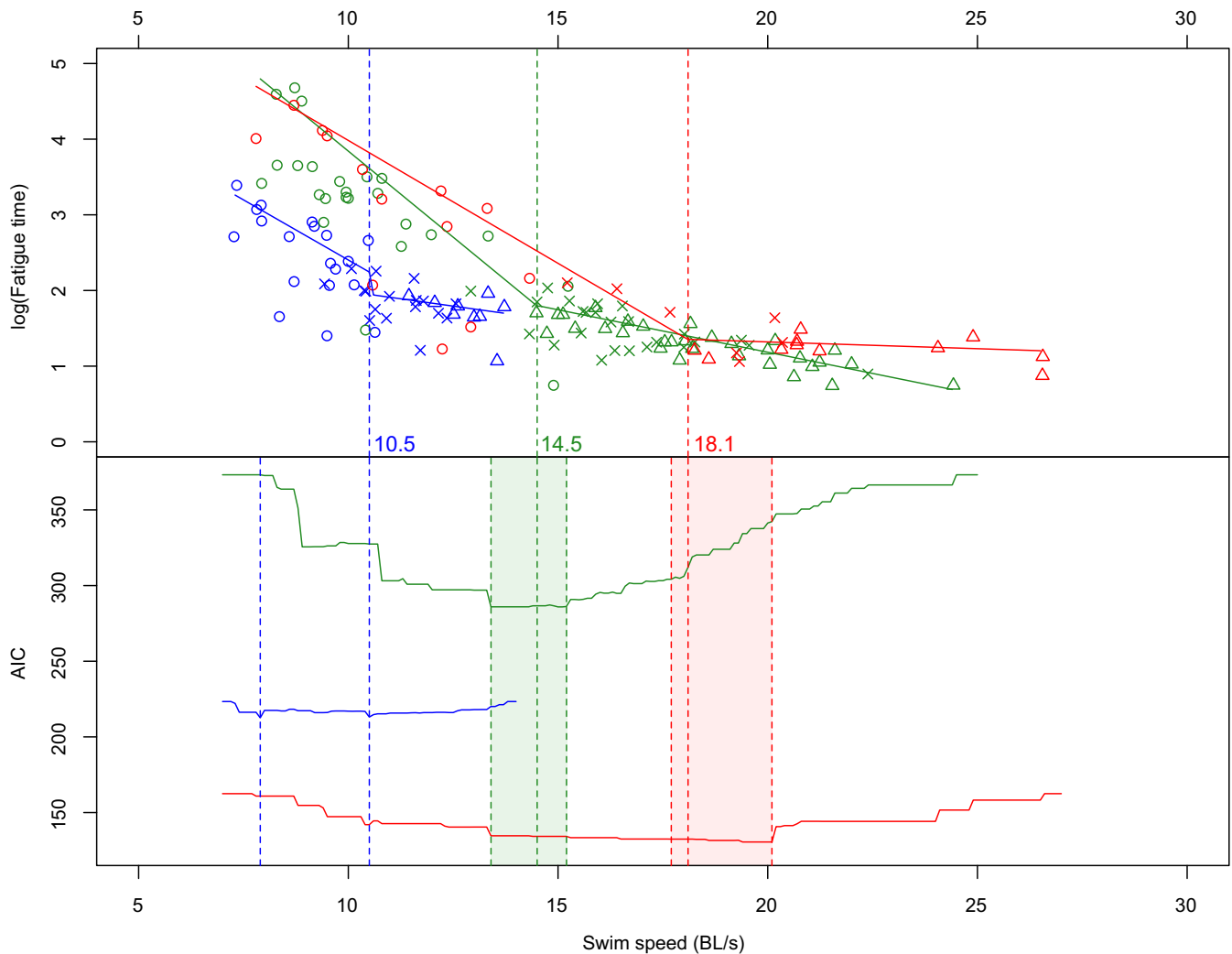
FIGURE 2 Swim speed-fatigue time (FT) relationship over the three studied nominal water temperatures (5.5, 13.5 and 18.5°C) (regression lines and observations). The vertical dashed line indicates the optimized breakpoint between the prolonged (left) and sprint (right) swimming modes based on minimum AIC values and minimum distance between mode curves at the breakpoints. Shadow areas delimited by dotted lines represent the breaking points range of ΔAIC = 2: 5.5°C: points 7.9 and 10.5 BL s^{-1}; 13.5°C: (13.4, 15.2) BL·s^{-1}; 18.5°C: (17.7, 20.1) BL s^{-1}. ○ 1.5 m s^{-1}; ✕ 2.5 m s^{-1}; △ 3.0 m s^{-1}; ■ 5.5°C, ■ 13.5°C and ■ 18.5°C.

TABLE 4 Number of fish in each experiment swimming with prolonged (P) or sprinting (S) speed based on the calculated breaking points

| | Nominal flow velocity | | | | | | | |
| | 1.5 m s^{-1} | | 2.5 m s^{-1} | | 3.0 m s^{-1} | | Global | |
Nominal water temperature	P	S	P	S	P	S	P	S
5.5 °C	18	1	4	13	0	9	22 (48.9%)	23 (51.1%)
13.5 °C	22	2	2	23	1	30	25 (31.3%)	55 (68.7%)
18.5 °C	13	0	3	4	0	11	16 (51.6%)	15 (48.4%)
Global	53 (94.6%)	3 (5.4%)	9 (18.4%)	40 (81.6%)	1 (2.0%)	50 (98.0%)	63 (40.4%)	93 (59.6%)

temperature has a positive effect on FT, where the FT is increased by 405.5% from 5.5°C (baseline level in the model) to 18.5°C (Table 5 and Figure 2). Nonetheless, only significant effect for the interaction between swim speed and the water temperature was found with the increase from 5.5 to 13.5°C. When considering other variables constant, a nase swimming in prolonged mode with a swim speed of 10.1 BL s^{-1} (mean observed value of swim speed against a flow velocity of 1.5 m s^{-1}) presents an FT more than four (4.13) times greater in water temperature of 13.5°C than in 5.5°C or even almost five (4.8) times when compared to 18.5°C.

TABLE 5 Summary of the regression nested model for the fatigue time (FT; Weibull was the best distribution; *P*-valour <0.0001; shape parameter = 0.263)

Variables	Prolonged ($n = 63$)			Sprint ($n = 93$)		
	β	S.E.	P	β	S.E.	P
Intercept	5.5696	0.5321	< 0.0001	2.7699	0.6806	< 0.0001
Swim speed (BL s^{-1})	−0.3163	0.057	< 0.0001	−0.078	0.0567	0.17
Water temperature (13.5°C)	2.8642	0.6408	< 0.0001	0.6522	0.7278	0.37
Water temperature (18.5°C)	1.6204	0.6299	0.0101	−1.0727	0.9423	0.25
Swim speed × water temperature (13.5°C)	−0.1435	0.0651	0.0274	−0.034	0.0585	0.56
Swim speed × water temperature (18.5°C)	−0.0051	0.062	0.9344	0.0595	0.0643	0.35

Note: Results are presented by swimming mode for an easy interpretation. The β terms are the regression coefficients, S.E. is the standard error and *P* stands for *P*-value. Water temperature of 5.5°C is considered the reference level for this categorical variable.
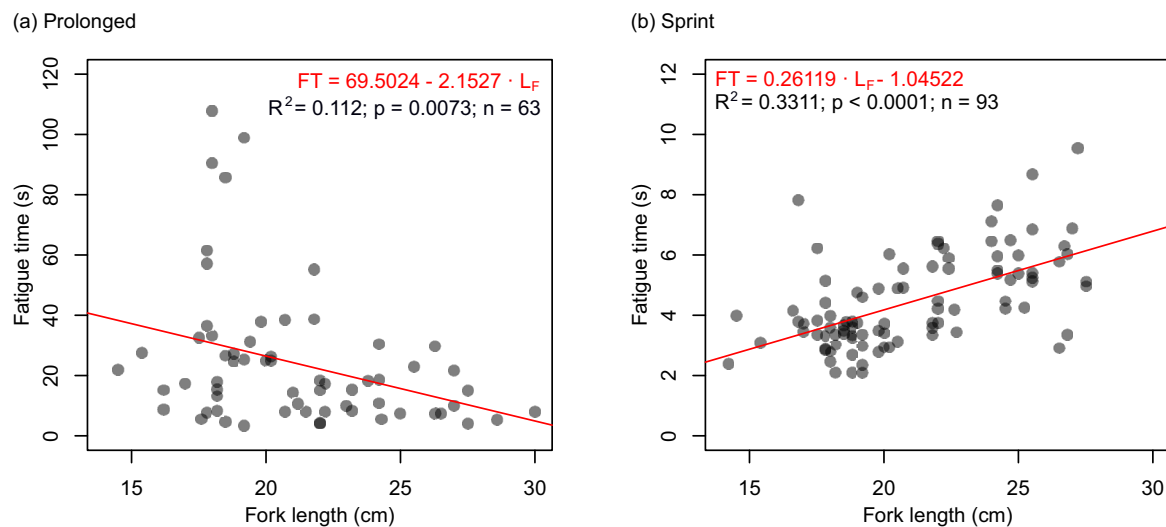
FIGURE 3 Relation of fatigue time (FT) and fork length *via* linear regression (solid line and equation). L_F, fork length; *n*, number of fish; *P*, *P*-value of the linear regression; R^2, coefficient of determination
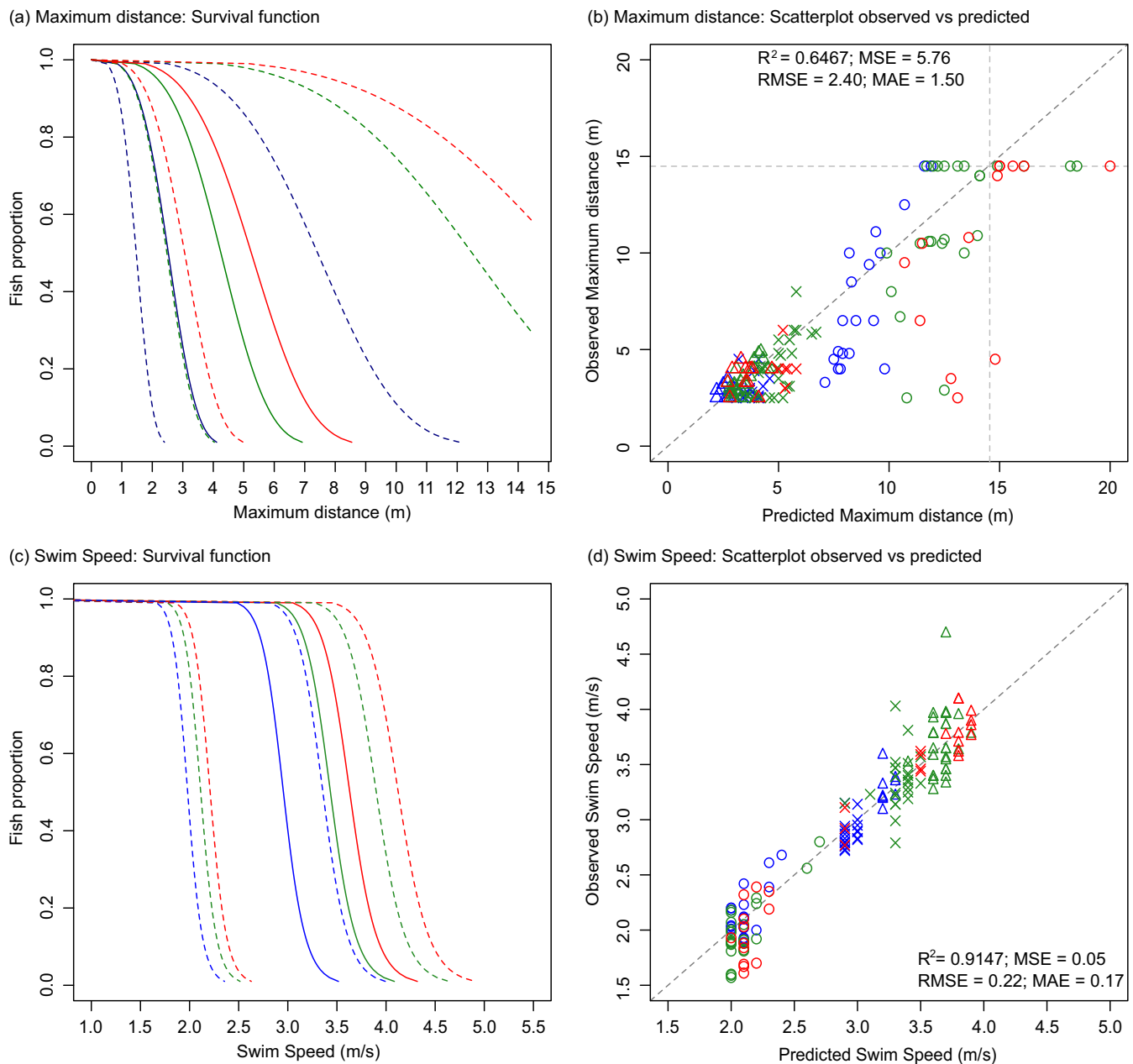
In sprint mode, the swim speed is negatively correlated with the FT; that is, at greater developed speeds, nase endurance is lower (*i.e.*, the FT is shorter), although without a strong significant effect ($P = 0.17$), reduced by −7.5% per m s^{-1}. On the contrary, the water temperature does not show a significant influence on the FT model, neither directly nor by the interaction with the swim speed. Thereby, when considering other variables constant, a nase swimming in sprint mode with a swim speed of 18.2 BL s^{-1} (mean observed value of swim speed against a flow velocity of 3.0 m s^{-1}) presents a similar FT (only 1.01 times greater) in water temperature of 13.5°C (or 1.03 if 18.5°C) than in 5.5°C.

In contrast, the relationship between FT with fork length depended on the swimming mode, with a positive relation in sprint mode (*i.e.*, the larger the fish, the greater the endurance) and a weak negative relation in prolonged mode (*i.e.*, the larger the fish, the lesser the endurance; although in this case, results are influenced by larger fish which swam in the colder 5.5°C trial; Tables 1 and 5 and Figure 3).

TABLE 6 Summary of the regression model for the maximum distance (Weibull parametric distribution; total considered attempts $n = 156$; censored $n = 17$) after stepwise variable selection

Variables	β	S.E.	P
Intercept	1.9235	0.2962	<0.0001
Fork length (cm)	0.0966	0.0156	<0.0001
Mass (g)	−0.0020	0.0007	0.0035
Flow velocity (m s^{-1})	−1.0778	0.0406	<0.0001
Water temperature (13.5°C)	0.5203	0.0854	<0.0001
Water temperature (18.5°C)	0.7313	0.1160	<0.0001
Log (scale)	−1.3573	0.0688	<0.0001
Shape (Weibull)	0.257		

Note: The β terms are the regression coefficients, S.E. is the standard error and *P* stands for *P*-value. Water temperature of 5.5°C is considered the reference level for this categorical variable. The scale parameter is the reciprocal of the shape parameter.

(a) Maximum distance: Survival function

(b) Maximum distance: Scatterplot observed vs predicted

(c) Swim Speed: Survival function

(d) Swim Speed: Scatterplot observed vs predicted

FIGURE 4 Estimated survival function of nase proportion (a) ascending a given distance and (c) swimming in a given swim speed over the three studied nominal flow velocities (1.5, 2.5 and 3.0 m s^{-1}) and water temperatures (5.5, 13.5 and 18.5°C), considering a median size nase (L_F = 20.8 cm and M = 111 g). ■ 5.5°C, (P), ✕ 2.5 m s^{-1} (S), ■ 13.5°C, and ■ 18.5°C. At velocity of 1.5 m s^{-1}, nase is considered to swim in prolonged (P) mode, whereas at 2.5 and 3.5 m s^{-1} in sprint (S) mode (Table 4). Observed data *vs.* predicted based on the generated models for (b) maximum distance and (d) swim speed (MSE, mean squared error; MAE, mean absolute error; R^2, coefficient of determination; RMSE, root mean squared error). Vertical and horizontal dotted line represents the maximum distance of the flume. (b) - - - 1.5 m s^{-1}, —— 2.5 m s^{-1}, - - - 3.0 m s^{-1}, ■ 5.5°C, ■ 13.5°C, and ■ 18.5°C, ○ 1.5 m s^{-1}, ✕ 2.5 m s^{-1}, △ 3.0 m s^{-1}, ■ 5.5°C, ■ 13.5°C and ■ 18.5°C
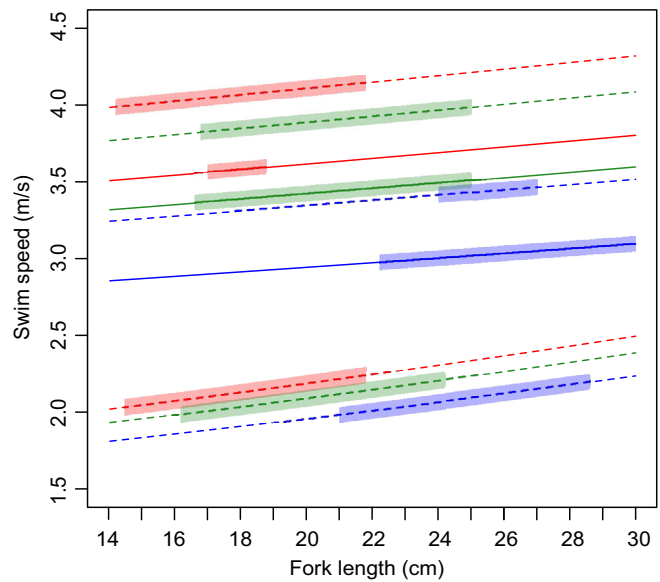
3.3 | Maximum distance

Table 6 shows the regression model for the prediction of the maximum distance travelled. On the one hand, the flow velocity is negatively correlated with the maximum distance; that is, at greater velocities, nase can ascend shorter distances, reduced by −66% per m s^{-1}. When considering other variables constant, nase can ascend a distance approximately three

(2.94) times greater against a subcritical flow (1.5 m s^{-1}) than against a supercritical one (2.5 m s^{-1}), or up to five (5.04) times greater when compared to 3.0 m s^{-1} (Figure 4a). On the other hand, the water temperature has a positive effect on the maximum distance travelled. Thereby, when water temperature rises from 5.5°C (baseline level in the model) to 13.5°C, the total distance of ascent is increased by 68%, and by 107.8%, if it rises up to 18.5°C (Table 6 and Figure 4a). This difference in the

(a) Maximum distance of ascent
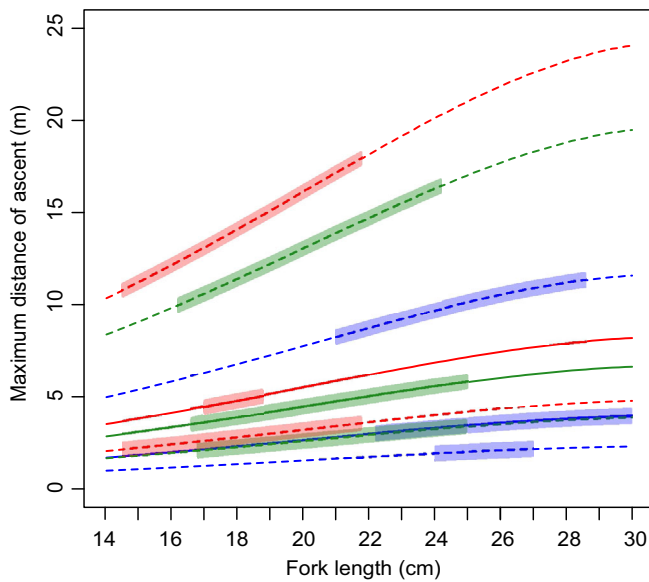
(b) Swim speed

FIGURE 5 Model predictions of the (a) maximum distance travelled and (b) swim speed relative to fork length, over the three studied nominal flow velocities (1.5, 2.5 and 3.0 m s^{-1}) and water temperatures (5.5, 13.5 and 18.5°C). At velocity of 1.5 m s^{-1}, nase is considered to swim in prolonged (P) mode, whereas at 2.5 and 3.5 m s^{-1} in sprint (S) mode (Table 4). Shadow areas represent the fork length range of the individuals that actively participated in the study (*i.e.*, those individuals with at least one attempt). - - - 1.5 m s^{-1}, —— 2.5 m s^{-1}, - - - 3.0 m s^{-1}, ■ 5.5°C, ■ 13.5°C and ■ 18.5°C.

TABLE 7 Summary of the regression nested model for the swim speed (log-logistic was the best distribution; *P*-valour <0.0001; shape parameter = 0.0378) after stepwise variable selection (mass was excluded due to their non-significance in the model)

Variables	Prolonged (*n* = 63)			Sprint (*n* = 93)		
	β	S.E.	*P*	β	S.E.	*P*
Intercept	−0.1008	0.1044	0.3342	0.3408	0.1020	0.0008
Fork length (cm)	0.0132	0.0050	0.0086	0.0051	0.0035	0.1453
Flow velocity (m s^{-1})	0.3391	0.0306	<0.0001	0.2549	0.0268	<0.0001
Water temperature (13.5°C)	0.0649	0.0304	0.0330	0.1501	0.0239	<0.0001
Water temperature (18.5°C)	0.1094	0.0429	0.0107	0.2058	0.0340	<0.0001

Note: The β terms are the regression coefficients, S.E. is the standard error and *P* stands for *P*-value. Water temperature of 5.5°C is considered the reference level for this categorical variable.

maximum distance is related to the development of a greater swim speed in warmer water (Table 2).

Figure 4a shows the nase proportion that would be able to overcome a given distance based on the nominal flow velocities and water temperatures, and Figure 4b shows the model fit ($R^2 = 0.65$; Table 6). For instance, the 50% of a nase population [with an average body size similar to the mean values of the studied population, *i.e.*, mean $L_F = 20.8$ cm and $M = 111$ g (mass calculated *via* the F_L–M relationship; Table 1)] would reach, against a flow velocity of 1.5 m s^{-1}, a distance up to 15.4 m with a water temperature of 18.5°C; 12.5 m if water temperature = 13.5°C and 7.4 m if temperature = 5.5°C. If the flow velocity is 2.5 m s^{-1}, it would reach a distance up to 5.2, 4.2 and 2.5 m with water temperatures of 18.5, 13.5 and 5.5°C, respectively. Finally, in the case of a flow velocity of 3.0 m s^{-1}, it would ascend distances up to 3.1, 2.5 and 1.5 m with water temperatures of 18.5, 13.5 and 5.5°C, respectively.

In addition, fork length and mass were found to significantly affect the maximum distance travelled, although with the opposite effect (Table 6). It is expected that, the longer the fish, the further it will swim, but the heavier the fish, the lesser distance it will swim, although the mass influence is very low. Thus, for two fish with the same length, the one with the lowest weight is expected to swim further. Distance of ascent increased by 10% per cm and reduced by −0.2% per g (Table 6). Thus, a nase of 25.9 cm and 231 g (90th percentile of F_L) could swim about 1.7 times further than a nase of 16.8 cm and 54 g (10th percentile of F_L) when considering other possible affecting co-variables as constant (Table 6 and Figure 5a).

3.4 | Swim speed

Table 7 shows the regression model for the prediction of the swim speed (in m s^{-1}) for sprint and prolonged swimming modes. In both modes, the flow velocity is positively correlated with the swim speed; that is, at greater velocities, nase develop greater swim speed,

increased by 40.4% per m s^{-1} in prolonged and by 29% per m s^{-1} in sprint. When considering other variables constant, nase can develop a swim speed approximately up to two (1.69) times greater against a supercritical flow (3.0 m s^{-1}) than against a subcritical one (1.5 m s^{-1}; 1.49 times if 2.5 s^{-1} *vs.* 1.5 m s^{-1}; Table 7 and Figure 4c). It is important to note that, at 1.5 m s^{-1}, most nase would swim in prolonged mode, whereas at 2.5 and 3 m s^{-1}, the swimming would be in sprint (Table 4). On the contrary, the water temperature has a positive effect on the swim speed also in both modes. Thereby, in prolonged mode, when the water temperature rises from 5.5°C (baseline level in the model) to 13.5°C, the total swim speed is increased by 6.7%, and by 11.6%, if it rises up to 18.5°C. In sprint mode, the total swim speed is increased by 16.2% from 5.5 to 13.5°C, and by 22.9%, if it rises up to 18.5°C (Table 7 and Figure 4c).

Figure 4c shows the nase proportion that would be able to develop a given swim speed based on the nominal flow velocities and water temperatures, as well as the model fit (R^2 = 0.92; Table 7 and Figure 4d). For instance, the 50% of a nase population (with an average body size similar to the mean values of the studied population, *i.e.*, mean L_F = 20.8 cm and M = 111 g) would develop, against a flow velocity of 1.5 m s^{-1}, a prolonged swim speed up to 2.2 m·s^{-1} m with a water temperature of 18.5°C; 2.1 m s^{-1} if water temperature = 13.5°C and 2.0 m s^{-1} if temperature = 5.5°C. If the flow velocity is 2.5 m s^{-1}, it would develop a sprint swim speed up to 3.6, 3.4, and 3.0 m s^{-1} with water temperatures of 18.5, 13.5, and 5.5 °C, respectively. Finally, in the case of a flow velocity of 3.0 m s^{-1}, it would develop sprint swim speeds up to 4.1, 3.9 and 3.4 m s^{-1} with water temperatures of 18.5, 13.5 and 5.5 °C, respectively.

In addition, fork length was found to affect the swim speed, but only with significant influence in the prolonged mode, with an increase in swim speed by 1.3% per cm (Table 7). Thus, a nase of 25.9 cm and 231 g (90th percentile of F_L) could develop a swim speed (in prolonged mode and against a flow velocity of 1.5 m s^{-1}) about 1.1 times greater than a nase of 16.8 cm and 54 g (10th percentile of F_L) when considering other possible affecting co-variables as constant (Table 7 and Figure 5b).

4 | DISCUSSION

Few studies have highlighted the importance of water temperature to assess fish passage through river barriers and, none of those studies have addressed how both, water temperature and flow velocity, influence the swimming capacity of the northern straight-mouth nase. This work confirms the need of switching the classical "velocity barrier" term to "thermo-velocity barrier" during barrier assessment, as well as the importance of swimming capacity studies.

Information regarding the swimming capacity of nase in general, and northern straight-mouth nase in particular, is scarce. In this regard, Branca (2015) defined a U_{crit} value of 0.55 m s^{-1} (3.39 BL s^{-1}) for this species, with a water temperature of 15°C and fish length from 15 to 20 cm. Considering other species from the same monophyletic group and similar length range, Alexandre *et al.* (2016)

defined a U_{crit} of 0.54 m s^{-1} (16 °C) for *Pseudochondrostoma willkommii* (Steindachner, 1866), whereas Romão *et al.* (2012) estimated 0.69–0.76 m s^{-1} (17.7°C) for *Pseudochondrostoma polylepis* (Steindachner, 1864). All these values from the literature (<4 BL s^{-1}) are near three times below the prolonged speed values observed in this study. The results of this study show that a nase of 20.8 cm fork length can develop a median swim speed that exceeds 12.2 BL s^{-1} (2.55 m s^{-1}) during a median time of 23.7 s in prolonged mode, or 20.7 BL s^{-1} (4.31 m s^{-1}) for 3.4 s in sprint mode under similar water temperature conditions to the migration period (18.5°C). These results are close to those observed for the Iberian barbel (*Luciobarbus bocagei* Steindachner, 1865), an endemic rheophilic cyprinid with similar habitat and spawning migration season. The Iberian barbel can maintain swim speeds of 20 BL s^{-1} (3.7 m s^{-1}) for 7 s in sprint mode, and 10 BL s^{-1} (1.8 m s^{-1}) during 60 s in prolonged mode (mean L_F of 18 cm and water temperature of 18.5°C) (Ruiz-Legazpi *et al.*, 2018). Moreover, the results are below than those reported for a 15.5 cm-sized sympatric brown trout (*Salmo trutta* Linnaeus, 1758), that at 12°C showed swim speeds of 25 BL s^{-1} (4.0 m s^{-1}) for 6 s in sprint mode and 15 BL s^{-1} (2.4 m s^{-1}) during 30 s in prolonged mode (Castro-Santos *et al.*, 2013).

The results here described correspond to a volitional performance, which is more approximate to natural conditions, allowing fish to express normal migratory behaviour (Haro *et al.*, 2004), and thus, more practical for management applications. Studies in respirometers or enclosed swimming chambers provide accurate predictions of maximum speeds derived from muscle physiology, although restrict the ability of fish to recruit different muscle groups and behavioural strategies, such as burst-and-coast swimming (Castro-Santos *et al.*, 2013). Nonetheless, forced swimming may be more accurate to determine physiologic fish fatigue limits, as fish are forced to reach exhaustion and impingement levels (*i.e.*, swimming failure), although fatigue speed and time to fatigue determined for fishes confined in a respirometer do necessarily translate directly to free-swimming individuals in the field (Peake & Farrell, 2006).

The two non-sustained speeds described in this manuscript were named as prolonged and sprint. Nonetheless, these metrics may differ from the terms defined by Brett (1964) in his theoretical approach. Although a biological explanation for the existence of these two swimming modes has never been provided, the specialized literature tends to relate this swimming change with a transition from aerobic to anaerobic metabolism (Brett, 1962; Goolish, 1991; Rome *et al.*, 1992; Webb, 1975). The results of this work show that the mode-shift for nase occurred with median FTs lower than 10 s (for the three studied temperatures), whereas Brett's (1964) observations were around 20 s. The obtained values are consistent with those for other species in volitional swimming flumes (Castro-Santos, 2005; Ruiz-Legazpi *et al.*, 2018). Most of the fish swam in prolonged mode with the lowest flow velocity (1.5 m s^{-1}), whereas in sprint mode they swam with the highest values (2.5 and 3.0 m s^{-1}), although few individuals were found with the opposite behaviour. In this regard, Castro-Santos *et al.* (2013) avoided both terms and named the two observed swimming modes as "Sprint 1" and "Sprint 2," because with volitional swimming

flumes, it is not possible to establish the exact moment when fish stopped the oxygen consumption nor when the fish changed its swimming mode, if there was more than one transition or even if there was a swimming mode change during a race.

Body size is usually recognized as one of the most important factors influencing fish swimming capacity (Beamish, 1978; Hammer, 1995; Plaut, 2001). In this study, significant positive relationships were found between the fork length with both the maximum distance travelled and the swim speed. The greater swimming ability associated with larger sizes has, on the one hand, a biomechanical base, as larger fish have larger propellant systems, and thus, greater muscular strength (Webb & Weihs, 1986), and on the other hand, a biochemical base, as larger fish have a greater anaerobic scope, which allows developing a greater swimming capacity (Ferguson et al., 1993; Goolish, 1989). In our case, the FT was also positively related to fork length in sprint swimming, whereas in prolonged mode, the relation was weaker and negative. This result can be probably because in the prolonged mode, larger fish swam in the colder trial, and lower water temperature reduced the aerobic capacity of fish, as will be discussed later. Other works with Iberian barbel and a larger range of fish size showed clear positive relations between fork length and swimming capacity (Ruiz-Legazpi et al., 2018; Sanz-Ronda et al., 2015).

Regarding body mass, this variable showed a negative relationship with the maximum distance, whereas it did not result significant in the swim speed. Swimming capacity reflects a sacrifice between length and weight (Alexandre et al., 2014), where the key component seems the energy reserve. Higher reserves imply not only an increase in mass that means worse hydrodynamics and greater resistance to movement (Boily & Magnan, 2002), but also better anaerobic metabolism and greater power (Moyle & Cech, 1996).

Although a maximum distance travelled was observed for higher values of fork length in all experimented temperatures, the biometric characteristics of fish differed between groups, with fish with significantly larger body size in autumn colder experiments. Consequently, this could have introduced a small bias in the model, as the largest individuals were used for the experiments with colder temperatures (overestimation), and the smallest for the warmest (underestimation). The difference in biometrics seems to be related to the seasonal growth of the nase, which usually starts in May and continues for 2–6 months depending on fish age (Herrera & Fernández-Delgado, 1994), and probably also to a size selection during autumn trophic activity. Therefore, capturing nase with a similar length range in different seasons is complicated. During the study, fish collections and experiments were carried out at different times to be representative of the natural peak movement periods of the nase, i.e., the spring spawning migration and the trophic autumn movements, as well as to include the effect of the different temperatures.

As poikilothermic animals, water temperature influences largely fish's swimming capacity (Beamish, 1978; Webb, 1975). This global effect is due to physical (e.g., the viscosity of water) and physiological reasons (e.g., oxygen consumption and muscle contraction). Water kinematic viscosity is inversely proportional to temperature;

consequently, if temperature decreases, the viscosity will increase. More specifically, a 10°C decrease in temperature, from 15 to 5°C, produces a 33% increase in dynamic viscosity (Fuiman & Batty, 1997). This means an increment in the value of the drag coefficient and therefore higher drag forces that fish must overcome (Chow, 1959). Thus, to maintain the same swim speed, fish need to develop greater physical power when the water temperature falls down (Temple & Johnston, 1997). On the contrary, the temperature is directly related to oxygen consumption during the aerobic swimming of fish (Brett, 1964), increasing the metabolic rate with the temperature until an optimum, and any increase after this point affects negatively (Beamish, 1978; Hammer, 1995). Water temperature also affects anaerobic swimming, as it is dominated by white muscle fibres (Claireaux et al., 2006; Kieffer, 2000), and their contraction capacity is slower at low temperatures (Rome et al., 1984).

In both swimming modes, anaerobic processes intervene (Beamish, 1978), that is to say, both induce fatigue. Nonetheless, in prolonged mode, aerobic processes are still present, which is translated into a major influence of temperature. In this mode, the endurance increased with temperature. This is supported by the observed results, probably indicating the approximation to the optimum metabolic rate (near 18.5°C). A similar relation was observed in Ruiz-Legazpi et al. (2018) for Iberian barbel in the range from 13.5 to 18.5°C, and Bayse et al. (2019) for American shad [Alosa pseudoharengus (Wilson 1811)] in the range from 11.1 to 21.4°C, although less visible as they only considered two temperature values. In the same way and consequently, other studies considering U_{crit} (and thus, lower values prolonged speeds) also showed a positive relationship with temperature (Hammer, 1995; Leonard et al., 1998; O'Steen & Bennett, 2003; Tudorache et al., 2008). A favourable metabolic rate and a lower drag can also explain the swimming speed increment when the temperature rises to 18.5°C.

In the case of sprint swimming mode, the temperature effects on swimming performance were less clear, and this mode is thought to be independent of temperature (Brett, 1971), although few studies have investigated this relationship directly (Bayse et al., 2019; Haro et al., 2004; Ruiz-Legazpi et al., 2018). Sprint swimming mode relies almost exclusively on anaerobic metabolism, sustained by glycogen, adenosine triphosphate and phosphocreatine stored in white muscle (Milligan, 1996). Results show that FT holds independent of water temperature in sprint mode, with a non-significant influence of the interaction of swim speed and water temperature. Nonetheless, an increase in swim speed during sprint mode is expected when the temperature rises (16.2% and 22.9% from 5.5 to 13.5 and 18.5 °C, respectively), which can be related to the higher efficiency of white muscle contraction for higher temperatures and lower drag forces (Rome et al., 1984; Temple & Johnston, 1997). Ruiz-Legazpi et al., 2018 also observed the same effect for Iberian barbel.

Swimming performance is the combination of swim speed and FT, which leads to a distance traversed by fish. Thus, the increase in swim speed with temperature can be directly translated to longer distances of ascent. These greater values were more obvious for lower flow velocities (1.5 m s^{-1}), where aerobic processes are involved, and

warmer temperatures (13.5 and 18.5°C) where metabolic rates are closer to the optimal. The observations showed an increase in median distance of ascent between 5.5 and 13.5°C from 1.2 times for 3.0 m s^{-1} to 1.9 times for 1.5 m s^{-1}, whereas between 13.5 and 18.5°C, the increase ranged from 0.9 to 1.3 times for 1.5 and 3 m s^{-1}, respectively. Similar observations were made for Iberian barbel (Ruiz-Legazpi *et al*., 2018) and other Nearctic species, such as blueback herring [*Alosa aestivalis* (Mitchill, 1814)], walleye [*Sander vitreus* (Mitchill, 1818)] and males of American shad, and had a negative correlation for females, whereas other species did not show these relationships (Castro-Santos, 2002; Haro *et al*., 2004).

Flow velocity was also an important variable that conditioned swimming performance. The increase in flow velocity forces fish to increase their swim speed. During high flow velocities, fish need to overcome the increase in drag forces exerted by the water flow, which is proportional to the dynamic pressure (Chow, 1959), *i.e.*, the square of the flow velocity (Mott, 2006). This means that, if the flow velocity is doubled, the drag force will be four times greater, and thus, fish must quadruple the developed physical power to move forward. The direct consequence is that they have to modify their swimming mode, changing from prolonged to sprint, something to be expected when confronted with barriers, in which the increase in water velocity is usually noticeable. This swift in swimming mode happens at higher water and swimming speeds when temperature increases. The water velocity breakpoint where most nase change their swimming mode is around 2 m s^{-1} for colder water and near 2.5 m s^{-1} in warmer water, where fish develop sprint swimming speed higher than 10.5 and 18.1 BL s^{-1}, respectively. Sprint swimming mode involves greater fatigue and stronger fitness, and it will be more costly in energetic terms (Castro-Santos, 2002). This implies the change from an exclusive operation of red muscles to a mix of red and white muscles, with more limited contraction properties for the latter (Randall & Brauner, 1991; Wardle, 1975) and, despite the fact that they allow to achieve greater swim speed, the endurance is lower, which leads to shorter travelling distances. This agrees with the observed results by Haro *et al*. (2004) for alosines, Castro-Santos *et al*. (2013) for salmonids and Sanz-Ronda *et al*. (2015) for cyprinids.

Considering these observations, the studied temperature range and flow velocity range influence fish swimming performance, endurance and distance travelled, although with some differences depending on the swimming mode. Nonetheless, any other patterns of influence of water temperature and flow velocity outside of the studied ranges and seasons cannot be discarded (Castro-Santos, 2002; Hammer, 1995). Swimming performance is affected by behavioural processes, and fish are expected to be much more motivated to pass velocity barriers during the reproductive season, when, in the case of cyprinids, the temperature increases (García-Vega *et al*., 2022), or falls in the case of salmonids (Goerig *et al*., 2017). Moreover, differences in the swimming ability of fish are expected in other reaches and habitats, directly related to their morphology or their genetic origin (Alexandre *et al*., 2014; Sánchez *et al*., 2022), which must be considered. Therefore, despite the fact that thermal response of swim speed could be somehow predictable, the ecological, physiological and phylogenetic factors that underlie the relationship remain unclear.

5 | CONCLUSIONS

This study highlights the influence of water temperature and flow velocity on fish swimming capacity, and therefore, it must be considered when assessing the fish passage through a barrier or designing a fish passage solution. Thus, special attention must be paid to alterations in thermal and flow river regimes, derived from man-made structures or future climate change scenarios, as they may potentially affect passage through barriers. In this sense, the present work provides the necessary tools to assess these scenarios for a migratory freshwater fish species representative of nases from both circum-Mediterranean and semiarid regions: the northern straight-mouth nase. This information allows establishing clear passability criteria for thermo-velocity barriers along time (*e.g*., maximum velocities and water drops in fishways, maximum swimming distances over weir faces, gauging stations, culverts, as well as the different permeability of the obstacles depending on the season), which in turn allows calculating the proportion of fish able to pass a barrier under different working scenarios as well as designing specific solutions to improve the passage (*e.g*., fishways) based on the real fish capacities (conservative values in classical fishway design guidelines when compared with the obtained results). Thus, this work has direct implications for fish management and conservation.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.