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ORIGINAL ARTICLE

Artificial light at night affects fish passage rates in two small-sized Cypriniformes fish

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Abstract

An increasing presence of instream structures such as weirs, dams, culverts and reservoirs degrades habitats, fragments rivers and blocks fish movements worldwide. Longitudinal river movements are fundamental for many fish species and the most widespread solution to restore longitudinal connectivity is the implementation of different fish passage solutions. Fishway functionality, however, is highly variable. To design a functional fishway, several aspects of the fish's interaction with its environment need to be taken into consideration. Artificial light at night (ALAN) can affect a range of different behaviours in fish, from activity and movement to feeding and predator–prey relationships. In a fish passage setting, fish are exposed to artificial light at night (ALAN) in the form of light pollution, but, sometimes, also as part of the fish passage solution. Although likely highly species specific, the effect of artificial light on fish passage behaviour has been little explored. Here we study the passage behaviour of two small-sized fish species, European gudgeon (*Gobio gobio*) and Italian riffle dace (*Telestes muticellus*), over a scaled deep side notch weir in a hydraulic flume in three different light conditions: daylight, darkness and ALAN. Although both species passed the obstacle at high efficiencies under all light conditions, their passage behaviours were influenced by light, particularly at the higher levels. While ALAN reduced passage success and resulted in delayed passage for gudgeon, riffle dace passed at higher rates under the artificial light compared to night treatment. Both results indicate a risk of negative effects from ALAN on passage performance at real fishways—or movement rates in lit areas of natural streams—for both species. Independent of light conditions, individuals of both species also passed faster after repeated trials, demonstrating learning in a fish passage context.

KEYWORDS
ALAN, fish migration, fishway, *Gobio*, gudgeon, learning, light levels, *Telestes*

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1 | INTRODUCTION

Many freshwater fish populations are at risk from a range of anthropogenic stressors (Dudgeon et al., 2006; Reid et al., 2019). Among these, there is an increasing presence of instream structures such as weirs, dams, culverts and reservoirs that degrades habitat, fragments rivers, and prevents migration and longitudinal dispersal movements of aquatic organisms (Belletti et al., 2020; Nilsson et al., 2005). Longitudinal river movements are fundamental for many fish species as spawning, seeking shelter, foraging and overwintering may depend on the success of short- or long-distance fish migrations (Lucas & Baras, 2001). In addition, fish dispersal movements are often crucial for the maintenance of genetic diversity (Blanchet et al., 2010; Gouskov et al., 2016).

As barrier removal is often not an option, the most widespread solution to restore longitudinal connectivity is the implementation of different fish passage solutions (Silva et al., 2018). The function of these structures is to create an ecological corridor, allowing mobile species to pass the instream structure (Clay & Eng, 1995) safely and without delay (Castro-Santos et al., 2009; Larinier, 2002). Although the need for fish passage has been acknowledged for hundreds of years (Montgomery, 2004), many dams lack fishways, and the existing ones often work with low efficiency or mainly for strong swimming salmonids (Bunt et al., 2012; Noonan et al., 2012). Allowing passage of small-sized fish species is particularly challenging and historically neglected in both fish passage research and design (Marsden & Stuart, 2019; Silva et al., 2018).

To design a functional fishway, several aspects of the fish's interaction with its environment need to be taken into consideration (Larinier, 2002). Traditionally, special attention has been put on hydrodynamics, for example, by setting maximum velocities and turbulence thresholds according to the target fishes swimming ability (Bermúdez et al., 2010; Jones & Hale, 2020). The functionality of a fishway, however, is not just a matter of hydraulics and swimming performance but involves the full spectra of a fish's sensory system and behavioural repertoire (Jones & Hale, 2020; Williams et al., 2012). Discerning the relationship between hydrodynamic cues and other environmental stimuli is considered a key goal towards the efficient mitigation of river fragmentation (Vowles & Kemp, 2012). Relatedly, several studies have pointed out light as an important factor, which can interfere or interact with the effect of hydrodynamics (Jones & Hale, 2020; Lin et al., 2022; Russon et al., 2010).

Light and dark cycles influence most freshwater life through an effect on physiology and behaviour (Davies et al., 2014). In fish, clear day-night cycles, interacting with the state of the animal and other environmental variables, are seen in, for example, movement and migration, activity, predator–prey interactions and habitat use (Helfman, 1986; Hesthagen & Garnås, 1986; Nyqvist, Calles, et al., 2022). During the last century, artificial light at night (ALAN) has been increasing worldwide (Cinzano et al., 2001; Gaston et al., 2014) and fish may be exposed to ALAN from industrial infrastructure, boat and car traffic, street lights or distant sky-glow (e.g. Foster et al., 2016; Gaston et al., 2014). ALAN levels can vary from less than one lux to several hundred lux (Blaxter & Batty, 1987; Gaston et al., 2014; Perkin et al., 2014). Light is also used directly in capture fisheries (Solomon & Ahmed, 2016) as well as, mostly experimentally, to guide or repel fish (Noatch & Suski, 2012). Consequently, the increasing presence and intensity of ALAN risks disrupting a multitude of natural processes (Hölker et al., 2010).

Related to movement behaviour in fish, ALAN can act both as an attractant and a repellant (Bassi et al., 2022). For example, Atlantic salmon (*Salmo salar*) seem to depend on daylight to traverse turbulent and high velocity hydrodynamics (Nyqvist, Nilsson, et al., 2017; Stuart, 1962), and juvenile salmonids tested in a flume with darkened borders and illuminated with an overhead fluorescent light (1313 lx) were more active, had a higher tendency to shoal and approached the weir at a higher rate in light compared to darkness (Kemp & Williams, 2009). European eels (*Anguilla anguilla*), on the other hand, seem to avoid artificial light as reflected in lower trap efficiencies at a catching weir nearby a hydropower derivation channel, when illuminated by two sodium spotlights (Cullen & Mccarthy, 2000). Flume experiments also show eels to be more likely to reject a lit part of a channel, deflected by the light from fluorescent lamp (3–6.5 lx) towards the darker side (Hadderingh et al., 1999), and to transition faster when in lit environments (Elvidge et al., 2018; Vowles & Kemp, 2021). Although likely highly species specific (Jones & Hale, 2020), for most species the effect of artificial light on their ecology in general, and passage behaviour in particular, has not been explored (Lin et al., 2021).

European gudgeon (*Gobio gobio*) and Italian riffle dace (*Telestes muticellus*) are small-sized (<20 cm) riverine and gregarious fish, that, although relatively stationary, also may partake in substantial longitudinal movements (Schiavon et al., 2022; Stott, 1967; Wocher & Rösch, 2006). European gudgeon, a Cyprinidae, is native to large parts of Europe, and has been introduced to Italy (Fortini, 2016; Kennedy & Fitzmaurice, 2006), while Italian riffle dace is a Leuciscidae native to the Italian peninsula, including areas of France and southern Switzerland (Fortini, 2016). Whereas European gudgeon has been caught in or observed passing fishways, albeit at low efficiency (e.g. Knaepkens et al., 2007; Kotusz et al., 2006), fish passage data on Italian riffle dace are missing from the scientific literature. Neither species has been studied in relation to ALAN and, for both species, little is known about their fish passage behaviour, at the same time as they are confronted with a high and increasing number of instream barriers (Belletti et al., 2020; Nilsson et al., 2005).

In this work, we aim to reduce the knowledge gap on passage behaviour, impact of artificial light and their interaction, for small-sized fish, studying passage of European gudgeon and Italian riffle dace. In a hydraulic flume, we simulated, in scaled size, the flow passing through a deep side notch weir in a pool and weir type fishway (Larinier, 2002). We quantify passage success and passage time for the two species in four different conditions: daylight, darkness and ALAN (low and high). In addition, we take advantage of the repeated passage attempts by individual fish to explore the effects of previous experience and learning on passage behaviour (Kieffer & Colgan, 1992; Odling-Smee & Braithwaite, 2003).

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2 | METHODS

In a series of experimental trials, we first tested for differences in passage behaviour of European gudgeon and Italian riffle dace between days, nights and nights with artificial light (Experiment I—main experiment) and then followed up this experiment with the same setup, but comparing behaviour between nights and nights with higher levels of artificial light (Experiment II—high level light conditions). Although no systematic mapping of light levels at night in real fishways is available, they can range from bare of artificial lights (or even darkened by cover) to directed illumination. The first experiment used light levels comparable with urban street light illuminance (Gaston et al., 2014), while the more intense light levels in Experiment II correspond to direct illumination and have been previously used in fish passage experiments (Blaxter & Batty, 1987; Vowles et al., 2014). In Experiment I, light conditions during daytime resembled ALAN conditions at night, but were included to control for non-light related effects of time of day on the fish passage behaviour. The different light intensity values are summarized in Table 1.

2.1 | Fish

Both species were collected in tributaries to Orba River in the Province of Alessandria, Italy, using electrofishing, and brought to the hatchery in Predosa, Italy. European gudgeon were captured in Rocca Grimalda Channel (44°39′47″ N, 8°49′51.5″ E) on 19 September 2022, whereas Italian riffle dace were caught in Lemme River (44°37′07″ N, 8°50′36.5″ E) on 21 November.

The study was performed in accordance with the Ufficio Tecnico Faunistico e Ittiofauna of the Provincia di Alessandria (n.50338 of 20 September 2022), under the provisions of art.2 of the national Decree n.26/2014 (implementation of Dir. 2010/63/EU).

European gudgeon (mean fork length [FL] ± standard deviation [SD] = 10 ± 0.6 cm; mean weight [W] ± SD = 11.3 ± 2.2 g) were PIT-tagged on 20 September (n = 14) and 4 November (n = 46), whereas Italian riffle dace (FL ± SD = 7.8 ± 1.2 cm; W ± SD = 5.7 ± 3.1 g) were tagged on 25 November (n = 60). Fish were anaesthetized (clove oil; Aromlabs, USA; approximately 0.05 mL clove oil/L water) before tagging. A 2–4 mm incision was made anterior of the pelvic fin, on the ventral side of the fish, slightly offset from the centre and a Passive Integrated Transponder (PIT-tag; Oregon, USA; 12 × 2.1 mm; 0.10 g) was inserted through the incision. The tag was pushed forward in the abdominal cavity to align with the fish body (e.g. Nyqvist, Schiavon, et al., 2022; Schiavon et al., 2023). Fish were measured for length and weight before being left to recover in an aerated water tank. Tag-to-fish weight ratios were 1% (±0.2%) for European gudgeon and 2.2% (±0.8%) for Italian riffle dace, well within recommendations for natural fish performance (Brown et al., 1999). In line with expectations (Schiavon et al., 2023), no tagging-related mortality was observed. After tagging, fish were kept in spring fed flow through tanks (59 × 150 × 20 cm) and left to recover for at least 3 days before starting the experiments. Fish were fed with commercial fish pellets (Tetra, TabiMin, Germany) regularly, and held under light conditions of the hatchery (windows and artificial lights during daytime, darkness at night). Three Italian riffle dace died during the progression of the experiments (two in Experiment I, one in Experiment II) and were excluded from the analysis (two of them jumped out from holding tanks during night and one got crushed while handling the shelter).

TABLE 1 The different light conditions used in the experiments: daylight (Day), complete darkness (Night) and night with artificial light (ALAN). Light intensity is expressed in lux, with average value and standard deviation.

	Light intensity (lx)	
Light treatment	**Experiment I**	**Experiment II**
Day	6 ± 0.7	/
Night	0	0
ALAN	4 ± 0.7	118 ± 10

2.2 | Equipment and experimental setup

The experiments were conducted in a recirculating open channel flume (30 × 30 × 140 cm) made of plexiglass (Figure 1). A pump (HF-4, Pedrollo, Italy) connected a downstream water tank through a series of fixed and flexible pipes, and regulated water levels together with a sliding metallic gate in the downstream end of the flume. Water temperature was kept constant (mean temperature ± SD = 13.15 ± 0.02°C), periodically switching on and off a chiller (TK-2000, TECO, USA) to counter heating from the action of the pump. The flow rate was monitored using a AquaTransTM AT600 flowmeter sensor and controlled by means of an inverter (MT 12, DGFIT, New Zealand) and a flow opening valve located at the pump outlet.

To create the required hydrodynamic conditions inside the flume, simulating the flow inside a fishway, a deep side notch weir (Larinier, 2002) was fitted to the flume dimensions (Figure 1). The weir consisted of a 30 × 30 × 1.3 cm grey-painted plexiglass panel, incised on one side to create the passage notch (5 cm wide). A bottom sill of 5 × 5 cm was left, according to Larinier (2002). The weir was fixed at the flume borders in the top part, not interfering with hydrodynamics. A gum gasket prevented leaks from the side of the weir.

The upstream end of the flume was delimited by a flow straightener, and the downstream end by a fine-meshed rack. The weir was positioned at a distance of 46 cm from the upstream border, dividing the experimental arena into two parts (Figure 1): downstream arena (94 cm) and upstream arena (46 cm). Total discharge was set to 4.44 L/s and water depths to 20 cm upstream the weir and 12 cm downstream the weir. This resulted in an 8 cm drop and a streaming flow type, creating an extended turbulent zone in the part immediately downstream of the notch. Velocity coming out from the weir bottleneck was around 1.25 m/s (Larinier, 2002). The flow pattern was similar to what fish would encounter in a real fishway (even if the hydrodynamics can be more complex; Romão et al., 2018) and the drop in line with recommendation for small-sized fish in fish passage

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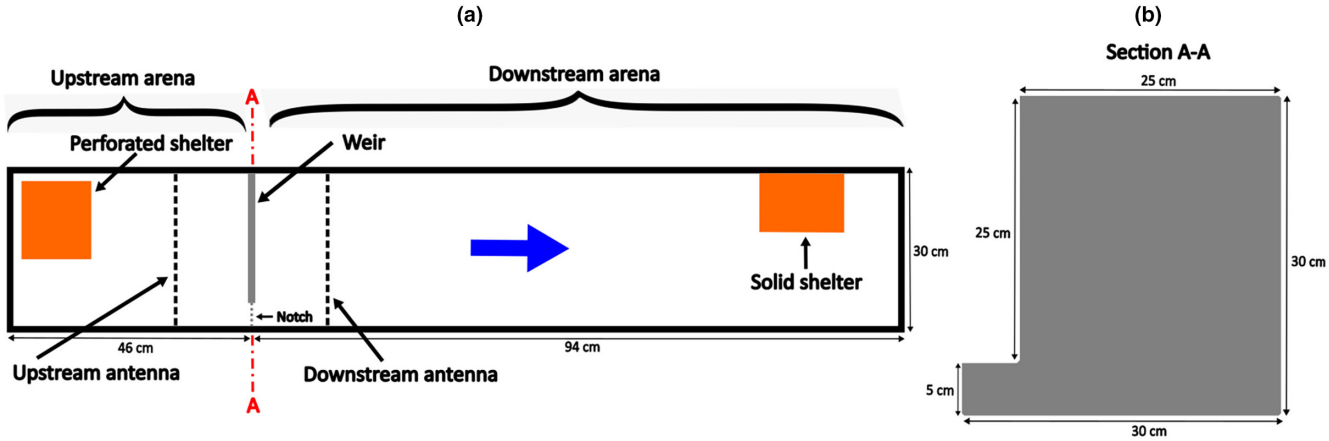


FIGURE 1 A scaled drawing of the experimental arena: (a) top view of the experimental arena inside the flume (the blue arrow indicates the flow direction), (b) front view (section A-A) of the deep side notch weir. The upstream end of the flume is delimited by a flow straightener, and the downstream end by a fine-meshed rack.

guidelines (DWA-German Association for Water, Wastewater and Waste, 2014; Marsden & Stuart, 2019; Schmutz & Mielach, 2013).

In the downstream end of the swimming arena a solid brick, covering about a third of the width of the flume, offered the fish shelter from the flow (Figure 1). Upstream, a perforated brick gave shelter to discourage passed fish from moving back in a downstream direction (Figure 1). The hatchery's ceiling lamp (neon LED 150×15 cm, 20 W, Philips, The Netherlands) was used under lit conditions. During daytime, small windows facing the outdoors contributed with light according to prevailing environmental conditions. To lower light intensities, for the main experiment (Experiment I), the trials were run with overhead cover (thin plywood) across the whole flume. For the follow-up, high light intensity condition experiment (Experiment II), the overhead cover was removed downstream of the weir to provide higher light levels in the testing arena. A sensor-logger (MX2202, HOBO, 10% accuracy) was fastened on the top of the downstream shelter to continuously log temperature (°C) and light intensity (lux).

Two synced PIT-antennas (ORSR; Oregon, USA) were used to track the movement of the fish in the flume (Figure 1). The antennas were attached to the external wall of the flume, detecting approach to the weir and presence in the upstream arena (passage). The experiments were recorded from the side of the flume using a video camera (Sony 4K, FDR-AX43, 100fps) in lit conditions. In darkness, an IR-camera (Survey3, Mapir, USA) supported by an IR-lamp (DOME 5 MPX, Proxe, Italy) was used.

2.3 | Experiment

2.3.1 | Experiment I

Sixty fish were tested for all three treatments in Experiment I. Three days before the start of the experimental trials, fish were divided into six groups (of 10 fish each) and left to recuperate for a couple of days in perforated boxes (37×54×13 cm) within larger flow-through tanks. Individuals were assigned to groups randomly. For Italian riffle dace, to achieve size balanced groups, fish were first size sorted and six small (6–7.5 cm), two medium (7.5–9 cm) and two big (>9 cm) fish were randomly assigned to each group. European gudgeon was relatively uniform in size so no size sorting was applied.

Daylight (mean light intensity [LI] ± standard deviation [SD] = 6 ± 0.7 lx), night (LI = 0 lx) and night with artificial light (LI ± SD = 4 ± 0.17 lx), corresponding to levels close by but not directly under a typical street light source (Gaston et al., 2014), were included as treatments with overhead cover. Daytime trials took place between 1 and 5 p.m., while night time ones after 5 p.m. (when dark outside). The complete experiment lasted over three consecutive days. Treatment order was randomized within blocks with the following restrictions: daylight trials need to take place during the day and night trials at night, a fish/group is only tested once in a day and all fish/groups experience all treatments once over the course of the experiment. Also, the last group of the previous day was not allowed to be the first on the day after, to give all groups a minimum recovery time of 12 h between trials. No group of fish (and hence no individual fish) experienced the same light treatment twice.

To test the passage behaviour, a group of fish was netted from the holding box, placed in a small bucket and gently released into the flume on the downstream side of the weir. Based on passage behaviour in pre-experimental trials, European gudgeon was given 90 min to pass before the experiment was ended, whereas the trial was ended after 1 h for Italian riffle dace. By the end of the trial, the weir opening was blocked and fish were captured separately from upstream and downstream the weir, scanned for PIT-ID (HPR Plus PIT Tag handheld reader, Biomark, USA) and then returned to their holding box.

2.3.2 | Experiment II

After the initial set of trials, a subset of 40 fish per species were randomly selected for a follow-up experiment (Experiment II) under higher level light conditions (i.e. keeping the same setup but without overhead cover). This experiment followed the same protocol as the first, but only night (LI = 0 lx) and night with artificial light (LI ± SD = 118 ± 10 lx), corresponding to levels directly under an

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artificial light source (Gaston et al., 2014), were included as treatments. The complete experiment lasted over two consecutive days. Treatment order was randomized within blocks, a fish/group was only tested once in a day and all fish/groups again experienced all treatments once over the course of the experiment.

2.4 | Statistical analysis

PIT-data and video were used to define passage success (yes/no) and passage time (time since start of the trial) for each fish. For some fish, PIT-tag detection data did not allow a direct assignment of passage time (e.g. when many fish upstream the weir caused tag collisions). In such cases, video recordings were used to confirm passage times. Some individuals passed the weir multiple times, but only the first of these passages were included in the analysis.

Generalized linear mixed effects models (GLMM) were used to test for treatment effects on passage success (yes/no) and time to passage for fish passing (removing the non-passers from the dataset). Variable Night was assigned as a baseline variable to the GLMMs and hence tested statistically against Day and ALAN. In addition to treatment, fish length was included in all models, to control for potential effects of size. As individual fish experienced repeated trials, the experimental design allowed to test for effects of prior experience (learning) on the passage performance. This was done by adding trial day to all models. To control for repeated measures (of the same individual) and non-independence within groups, individuals nested in groups were included as a random intercept in all models (Dingemanse & Dochtermann, 2013).

For the categorical data—passage success (yes/no)—a Laplace approximation method was used. In case of passage times, the choice of the analysis depended on their statistical distribution. If passage times followed a normal distribution, linear mixed model (LMM) was applied, whereas, if they did not, penalized quasilikelihood method (PQL) was used (Bolker et al., 2009).

Data management, plotting and statistical tests were performed in *R* (R Foundation for Statistical Computing, Vienna, Austria, URL https://www.R-project.org), involving the following packages: *ggplot2* (ver. 3.4.0), *tidyverse* (ver. 1.3.2), *plotly* (ver. 4.10.1) and *car* (ver. 3.1–1) for plots and visual analysis, *dplyr* (ver. 1.0.10) and *plyr* (ver. 1.8.7) for data management, *MASS* (ver. 7.3–58.1) and *lme4* (ver. 1.1–31) for application of GLMM.

3 | RESULTS

A very large proportion of both Italian riffle dace (100%) and European gudgeon (98.3%) successfully passed the obstacle at least once.

3.1 | European gudgeon

3.1.1 | Experiment I

European gudgeon were more likely to pass at night than in daylight, and ALAN reduced passage success at night (Figure 2, Table 2). No effect of treatment on passage times was detected (Table 2). Mean passage times were 35.6 min (±20.1) at night, 35.6 min (±23.4) under

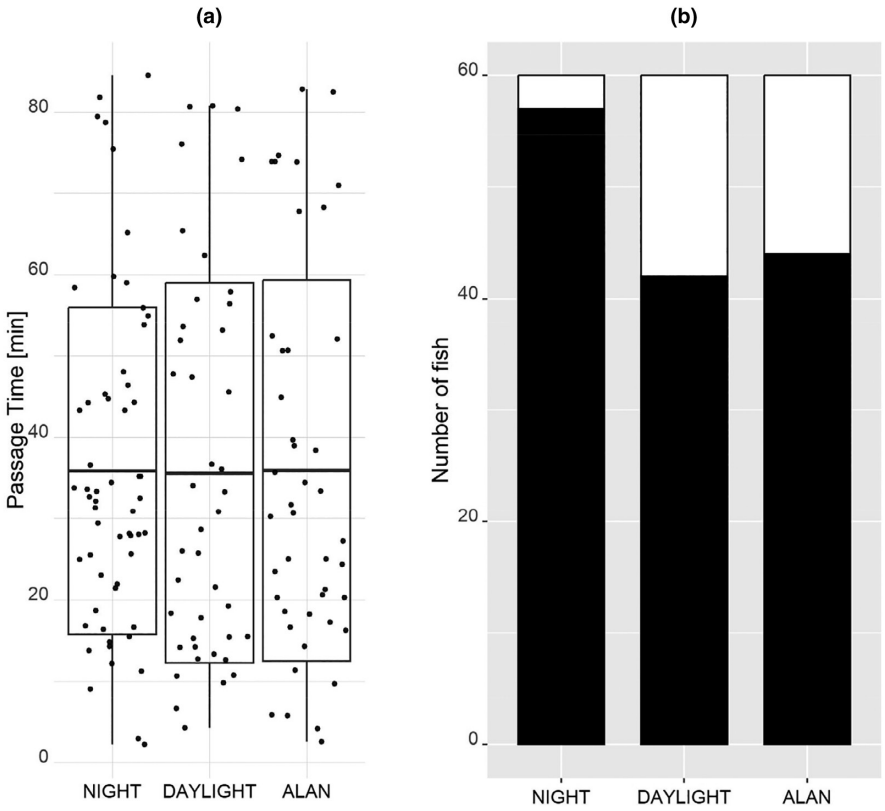


FIGURE 2 Passage success for European gudgeon (*Gobio gobio*; 60 fish per treatment) under night, daylight and ALAN treatments. (a) boxplots of passage times (min) per light treatment, (b) histograms with the proportion of passers (black) and non-passers (white) per light treatment.

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TABLE 2 Passage success and passage times analysis for European gudgeon (*Gobio gobio*). Statistical parameters of generalized linear mixed effects models (GLMM) are reported: estimate (*E*), standard error (SE), Student-*t* (*t*), *z*-value (*z*) and *p*-value (*p*).

	Passage success				Passage times			
	Estimate (*E*)	Std Error (SE)	*z*-Value (*z*)	*p*-Value (*p*)	Estimate (*E*)	Std Error (SE)	Student-test (*t*)	*p*-Value (*p*)
Experiment I								
Daylight	−2.89	0.84	−3.42	6×10^{-3}	−0.04	0.11	−0.34	.74
ALAN	−2.65	0.83	−3.20	1.4×10^{-3}	−0.04	0.11	−0.34	.74
Length	0.39	0.5	0.78	.43	0.16	0.1	1.72	.092
Trial day	0.53	0.32	1.69	.09	−0.16	0.06	−2.71	.008
Random effect	/	0.07	/	/	/	3.99×10^{-6}	/	/
Experiment II								
High-ALAN	−15.83	7.16	−2.21	.03	0.48	0.11	4.48	1×10^{-3}
Length	−0.11	2.77	−0.041	.97	−0.1	0.15	−0.66	.52
Trial day	−1.04	3.35	−0.31	.76	−0.18	0.11	−1.7	.1
Random effect	/	5.98	/	/	/	0.04	/	/

Note: Covariates included inside the model are reported: treatment daylight, treatment ALAN, treatment high-ALAN, fish length, experimental day number (trial day) and random effect. For passage success (categorical response variable), the Laplace approximation method was applied. For passage times, since they did not follow a normal distribution, a penalized quasilikelihood method was applied. Night treatment serves as baseline for all models.

daylight and 35.9 min (±23.4) under ALAN. Passage time decreased with trial day, indicating faster passage with experience, and fish length did not show significant effects on neither passage success or passage times (Table 2).

3.1.2 | Experiment II

In the higher light level treatment, passage success showed a similar trend as for the first experiment, higher passage success at night compared to high-ALAN (Figure 3; Table 2). Under higher light intensities, European gudgeon also passed faster in darkness compared to ALAN (Figure 3; Table 2). Mean passage time in darkness (19.23 ± 10.88 min) was lower than in high-ALAN (28.44 ± 19.41 min). No effect of fish length or trial day on either passage success or passage time ($p < .05$) was detected.

3.2 | Italian riffle dace

3.2.1 | Experiment I

Italian riffle dace displayed high passage success regardless of treatment and no effect on passage success of time of day or artificial light was observed (Figure 4; Table 3). No effect of any of the main treatments was detected ($p > .05$), while larger fish passed faster than shorter fish (Figure 4, Table 3). Time to passage decreased with the progression of the experiment, with individual fish passing faster with experience ($p < .05$, for variable trial day).

3.2.2 | Experiment II

Also in the higher light level treatment, after removing the overhead cover, Italian riffle dace passed at high proportions under all conditions (Figure 5; Table 3). An effect of treatment emerged, as fish passed substantially faster under high-ALAN compared to unlit nights (Figure 5; Table 3). Again, larger fish passed faster than smaller fish (Table 3). No effect of trial day on either passage success or passage time was seen ($p < .05$).

4 | DISCUSSION

The success of a fish passage solution is the product of the physical conditions in the fishway and fish's behaviour and capability (Williams et al., 2012). Here we studied the fish passage behaviour of European gudgeon and Italian riffle dace in relation to artificial light within a flume. Both species passed the obstacle at high efficiencies under all light conditions, but their passage behaviours were influenced by artificial light. While ALAN reduced passage success and resulted in delayed passage for gudgeon, riffle dace passed at higher rates under the artificial light compared to night treatments. For both species, the behaviour under artificial light did not differ from the behaviour under lit conditions during the day.

For European gudgeon, ALAN caused a reduction in passage success with fewer fish passing under artificial light conditions at night compared to the dark night treatment. At higher light intensities, ALAN also delayed passage raising the time to passage for successful

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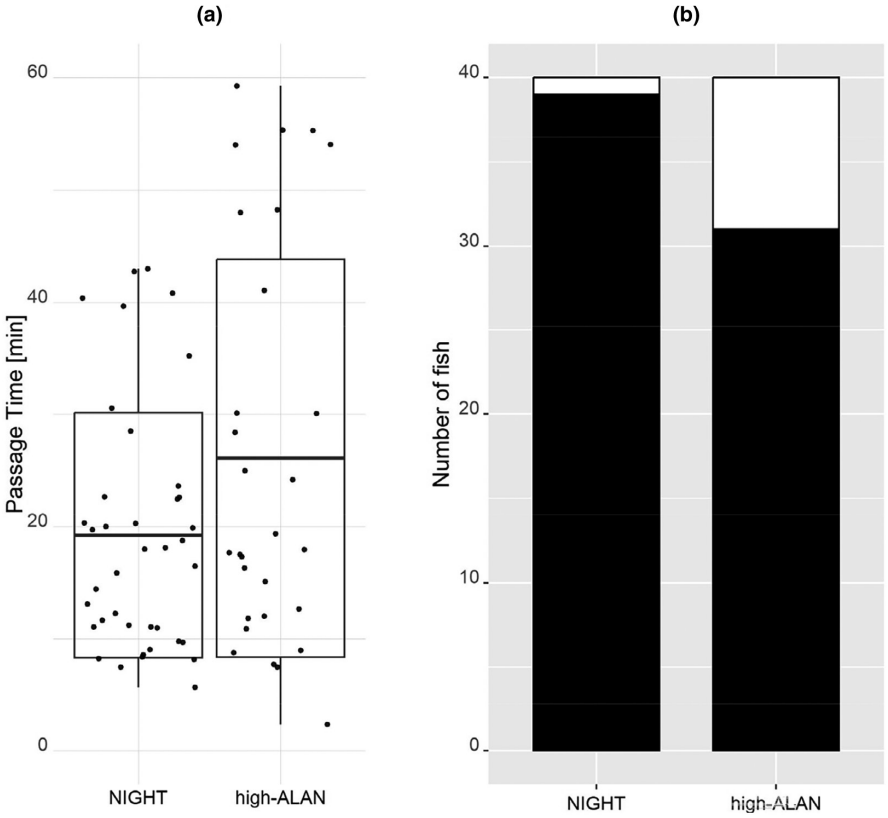


FIGURE 3 Passage success for European gudgeon (*Gobio gobio*; 40 fish per treatment) under night and high-ALAN treatments. (a) boxplots of passage times (min) per light treatment, (b) histograms with the proportion of passers (black) and non-passers (white) per light treatment.

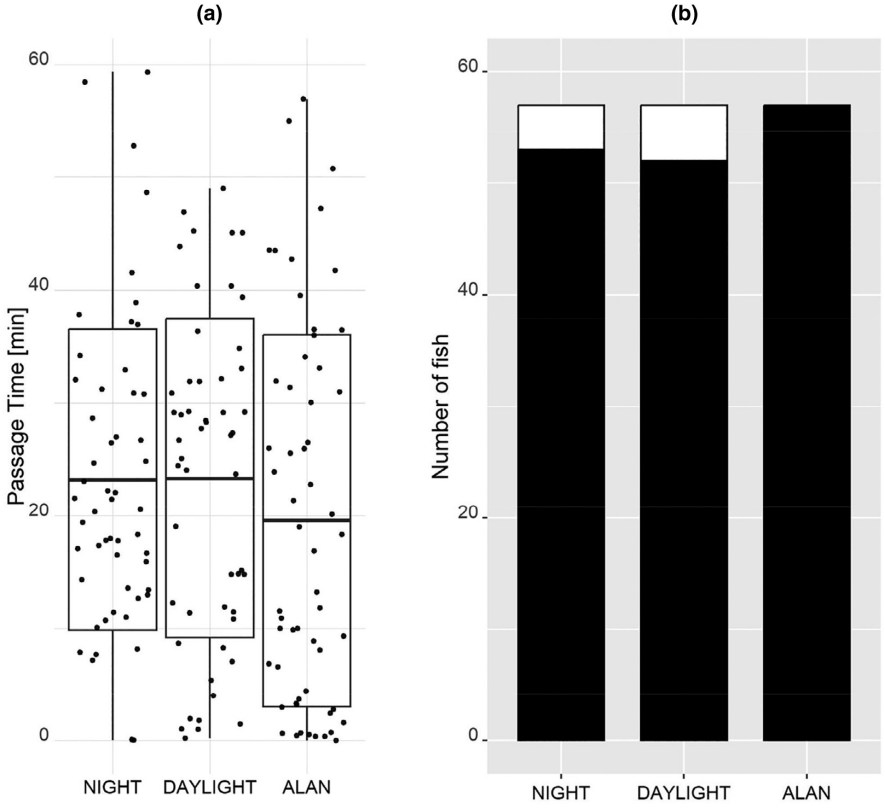


FIGURE 4 Passage success for Italian riffle dace (*Telestes muticellus*; 60 fish per treatment) under night, daylight and ALAN treatments. (a) boxplots of passage times (min) per light treatment, (b) histograms with the proportion of passers (black) and non-passers (white) per light treatment.

passers compared to the night treatment. As similar passage behaviour was observed under daylight and ALAN, the fish were likely predominantly reacting to the prevailing light conditions. For a range of different species, higher light levels are associated with higher predation risk, inducing lower activity levels as a predator avoidance behaviour (Contor & Griffith, 1995; Lima & Dill, 1990). Gudgeon, in addition, can deploy a freezing behaviour (Eilam, 2005) to avoid predator detection. Both lower activity and freezing may have contributed to

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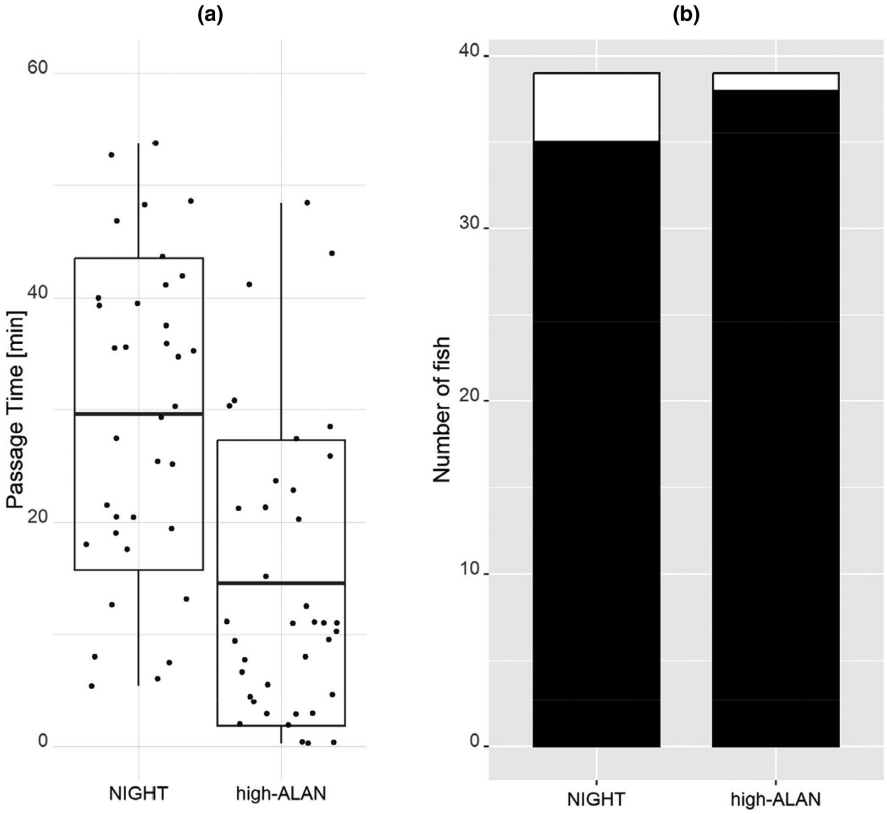


FIGURE 5 Passage success for Italian riffle dace (*Telestes muticellus*; 40 fish per treatment) under night and high-ALAN treatments. (a) boxplots of passage times (min) per light treatment, (b) histograms with the proportion of passers (black) and non-passers (white) per light treatment.

TABLE 3 Passage success and passage times analysis for Italian riffle dace (*Telestes muticellus*). Statistical parameters of generalized linear mixed effects models (GLMM) are reported: estimate (*E*), standard error (SE), Student-*t* (*t*), z-value (*z*) and *p*-value (*p*).

	Passage success				Passage times			
	Estimate (*E*)	Std Error (SE)	*z*-Value (*z*)	*p*-Value (*p*)	Estimate (*E*)	Std Error (SE)	Student-*t* (*t*)	*p*-Value (*p*)
Experiment I								
Daylight	0.08	2.11	0.04	.97	0.12	2.43	0.05	.29
ALAN	29.22	2.84×10^{-6}	0	1	−3.14	2.37	−1.32	.29
Length	0.24	2.13	0.11	.91	−4.08	0.93	−4.38	1.17×10^{-5}
Trial day	−2.4	1.98	−1.21	.23	−4.58	1.2	−3.81	1×10^{-3}
Random effect	/	0.56	/	/	/	0.34	/	/
Experiment II								
High-ALAN	1.54	1.17	1.32	.19	−0.69	0.15	−4.63	1×10^{-3}
Length	−0.4	0.35	−1.17	.24	−0.15	0.06	−2.49	.02
Trial day	1.54	1.17	1.32	.19	0.14	0.14	1.02	.31
Random effect	/	0	/	/	/	1.95×10^{-6}	/	/

Note: Covariates included inside the model are reported: treatment daylight, treatment ALAN, treatment high-ALAN, fish length, experimental day number (trial day) and random effect. For passage success (categorical response variable), the Laplace approximation method was applied. For passage times, since they did not follow a normal distribution, a penalized quasilikelihood method was applied. Night treatment serves as baseline for all models.

lower passage rates under lit conditions. Higher passage rates during night have also been reported for lamprey (*Petromyzon marinus*) (Hard & Kynard, 1997), barbel (*Barbus barbus*) and other cyprinids (Lucas & Frear, 1997; Prchalová et al., 2006), and ALAN can directly disrupt the nocturnal movement of eels and salmons (Hadderingh et al., 1999; Tabor et al., 2004; Vøllestad et al., 1986).

Italian riffle dace, on the other hand, passed faster under ALAN compared to unlit nights, but only in the second high light level experiment. In the low-intensity ALAN experiment, Italian riffle dace passed at high rates regardless of light treatment. In fish passage situations, fish often rely on both visual and hydrodynamic cues (Kemp & Williams, 2009), and passage might be impeded in the

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lack of light, especially in hydrodynamically demanding situations (Jones et al., 2017; Nyqvist, Nilsson, et al., 2017). The flow in our experiment, however, did not seem to constitute a challenging environment for Italian riffle dace and few fish failed to pass in all treatments. Instead, it is likely that the higher passage rates under high ALAN treatment compared to unlit night is due to the fish striving to move away from an exposed situation, trying to avoid the light. Avoidance of lit parts of arenas is known for both cyprinids and eels (Hadderingh et al., 1999; Lin et al., 2021). Light levels under the low- and high-intensity treatments correspond to the environment directly under or at some distance from a light source respectively (Gaston et al., 2014).

An alternative explanation for the difference in response to the high ALAN treatment between European gudgeon (decreased passage rate) and Italian riffle dace (increased passage rate) may lie in the reaction to ALAN related to natural diel activity of the respective species. Many fish have evolved to be active mainly during the night or the day (Jones & Hale, 2020), and these adaptation may also affect fish passage behaviour and movement in relation to prevailing light conditions (Keep et al., 2021). For example, European catfish (*Siluris glanis*), European eel and a range of Iberian cyprinids have been observed to predominantly pass fishways at night, whereas bream (*Abramis brama*), asp (*Leuciscus aspius*) and striped mullet (*Mugil cephalus*) pass mainly during day (Ovidio et al., 2023; Santos et al., 2005). Even within the same species, however, behavioural response to light levels may differ between sites, and with environmental conditions (Ovidio et al., 2023; Rimmer & Paim, 1990; Santos et al., 2005). Neither illumination preferences nor natural diurnal activity patterns have, to our knowledge, been described for gudgeons or riffle daces. For neither species, however, did the passage behaviour during daytime differ from the behaviour under similar light (ALAN) conditions at night in our experiments, indicating that light conditions rather the time of day itself influenced the behaviours.

Interestingly, for both European gudgeon and Italian riffle dace, there was an effect of ALAN on time to passage at the higher ALAN treatment (Experiment II) but not under the lower ALAN treatment (Experiment I). Fewer European gudgeon also passed under both low and high ALAN compared to in darkness but with a stronger effect under the high light intensity treatment. The smaller, or lack of effect, at the lower light levels might constitute a dose-dependent response to ALAN (Lin et al., 2021). Although even lower light levels than the ones used in our experiment have also affected fish behaviour (Czarnecka et al., 2019; Foster et al., 2016; Perkin et al., 2011), for Italian riffle dace the lower light levels could have been too low to elicit a response. Light intensity thresholds for behavioural effects have been identified for shade avoiding species (Keep et al., 2021), and ALAN effects on both feeding and movement can be modulated by light intensity level (Lin et al., 2021; Tabor et al., 2004), making light level-dependent ALAN effects a relevant avenue for future research. The light level differences in our experiment, however, were achieved by the removal of an overhead cover, and it cannot be ruled out that the stronger reaction under higher light intensities was due also to the absence of overhead cover (Watz et al., 2015).

In a real fish pass, successful passage encompasses a series of events: approaching, entering, passing through and exiting the fishway (Castro-Santos et al., 2009; Nyqvist et al., 2016; Silva et al., 2018). All these events may, in theory, be differently affected by environmental variables, including ALAN (Nyqvist et al., 2016). In our study, fish were directly inserted into the lit or dark flume, and only the 'passing through the obstacle' phase was evaluated. In nature, however, ALAN would also include entering and exiting the lit area, with avoidance or attraction behaviour affecting passage success (Hadderingh et al., 1999; Lin et al., 2021). Abrupt change in light intensity is known to affect fish behaviour and to even change movement trajectories (Greenberg et al., 2012; Hard & Kynard, 1997). From this perspective, even the increased passage rate for Italian riffle dace under ALAN in our study may suggest potential negative effects on passage in real fishways. For example, eels—that are known to display higher passage rates at night (Russon et al., 2010)—tended to avoid a lit channel but once in the channel they passed faster if the channel was lit (Vowles & Kemp, 2021). Future studies need to evaluate approach, enter and exit phases of fish passage in relation to ALAN, but also to artificial shade caused by bridges and culverts, which could also affect fish behaviour (Jones et al., 2017; Keep et al., 2021).

Both species passed the obstacle at a higher rate on subsequent trial days but only within the first experiment. This indicates an effect of learning and experience on passage performance; experience resulted in faster passage over the first three consecutive days of trials (Experiment I), whereas no difference was seen between the fourth and fifth day of trial (Experiment II). Learning is important for a range of fish behaviours, including orientation, avoidance and predator–prey interactions (Kieffer & Colgan, 1992; Odling-Smee & Braithwaite, 2003). For example, learning can improve shelter finding as well as the interpretation of the hydrodynamic environment (Aronson, 1971; Markel, 1994; von Campenhausen et al., 1981), but has been surprisingly little explored in relation to fish passage. Juvenile eels were found to climb at a faster rate after having climbed before, but, as the experienced eels consisted of successful passers, this experiment could not distinguish learning from selection (Podgorniak et al., 2016). Hagelin et al., 2021, in contrast, observed lower passage performance in experienced Atlantic salmon and brown trout (*Salmo trutta*), but here experience was intertangled with energy expenditure and handling stress. Interestingly, in our experiment, fish did not only pass faster with experience, but also appeared to learn to better negotiate the complex hydrodynamics in the downstream arena as time progressed, both within and between trials. Bearing in mind the common occurrence of systems with a series of fish passes (e.g. Keefer et al., 2021; Nyqvist, McCormick, et al., 2017), future experiments should further explore learning in relation to fish passage and hydrodynamics.

To conclude, artificial light at night accelerated passage for Italian riffle dace while reducing passage rates for European gudgeon, indicating a risk of negative effects from ALAN on passage performance at real fishways—or movement rates in lit areas of natural streams—for both species. Although these particular species are not considered highly migratory, both may display substantial dispersal

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movements, and at least riffle daces have been described to migrate shorter distances to seek shelter or reproduce (Schiavon et al., 2023; Stott, 1967; Wocher & Rösch, 2006). Future studies need to explore the full series of events associated with successful fish passage in relation to ALAN, including entering and exiting lit areas, for these and other species. Further exploring effects of different levels of light intensities, as well as the interaction between visual and other sensory cues, constitute other pressing research needs.

AUTHOR CONTRIBUTIONS

Fabio Tarena, Claudio Comoglio and Daniel Nyqvist conceived of the presented idea. Fabio Tarena, Daniel Nyqvist and Alessandro Candiotto ran the experiments. Fabio Tarena wrote the manuscript with support from Daniel Nyqvist and final edits from Claudio Comoglio. All authors discussed the results and contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Aronson, L. R. (1971). Further studies on orientation and jumping behavior in the gobiid fish, bathygobius soporator. *Annals of the New York Academy of Sciences*, *188*, 378–392. https://doi.org/10.1111/j.1749-6632.1971.tb13110.x

Bassi, A., Love, O. P., Cooke, S. J., Warriner, T. R., Harris, C. M., & Madliger, C. L. (2022). Effects of artificial light at night on fishes: A synthesis with future research priorities. *Fish and Fisheries*, *23*(3), 631–647. https://doi.org/10.1111/faf.12638

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., … Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*(7838), 436–441. https://doi.org/10.1038/s41586-020-3005-2

Bermúdez, M., Puertas, J., Cea, L., Pena, L., & Balairón, L. (2010). Influence of pool geometry on the biological efficiency of vertical slot fishways. *Ecological Engineering*, *36*(10), 1355–1364. https://doi.org/10.1016/j.ecoleng.2010.06.013

Blanchet, S., Rey, O., Etienne, R., Lek, S., & Loot, G. (2010). Species-specific responses to landscape fragmentation: Implications for management strategies. *Evolutionary Applications*, *3*(3), 291–304. https://doi.org/10.1111/j.1752-4571.2009.00110.x

Blaxter, J. H. S., & Batty, R. S. (1987). Comparisons of herring behaviour in the light and dark: Changes in activity and responses to sound. *Journal of the Marine Biological Association of the United Kingdom*, *67*(4), 849–859. https://doi.org/10.1017/S0025315400057088

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Brown, R. S., Cooke, S. J., Anderson, W. G., & McKinley, R. S. (1999). Evidence to challenge the "2% rule" for biotelemetry. *North American Journal of Fisheries Management*, *19*(3), 867–871. https://doi.org/10.1577/1548-8675(1999)019<0867:ETCTRF>2.0.CO;2

Bunt, C. M., Castro-Santos, T., & Haro, A. (2012). Performance of fish passage structures at upstream barriers to migration. *River Research and Applications*, *28*(4), 457–478. https://doi.org/10.1002/rra.1565

Castro-Santos, T., Cotel, A. L., & Webb, P. W. (2009). Fishway evaluations for better bioengineering: An integrative approach. *Challenges for Diadromous Fishes in a Dynamic Global Environment*, *American Fisheries Society*, Symposium (Vol. 69, pp. 557–575).

Cinzano, P., Falchi, F., & Elvidge, C. D. (2001). The first world atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, *328*(3), 689–707. https://doi.org/10.1046/j.1365-8711.2001.04882.x

Clay, C. H., & Eng, P. (1995). *Design of fishways and other fish facilities* (1st ed.). CRC Press. https://doi.org/10.1201/9781315141046

Contor, C. R., & Griffith, J. S. (1995). Nocturnal emergence of juvenile rainbow trout from winter concealment relative to light intensity. *Hydrobiologia*, *299*(3), 179–183. https://doi.org/10.1007/BF00767324

Cullen, P., & Mccarthy, T. (2000). The effects of artificial light on the distribution of catches of silver eel, *Anguilla anguilla* (L.), across the Killaloe eel weir in the lower river Shannon. *Biology and Environment: Proceedings of the Royal Irish Academy*, *100B*, 165–169.

Czarnecka, M., Kakareko, T., Jermacz, Ł., Pawlak, R., & Kobak, J. (2019). Combined effects of nocturnal exposure to artificial light and habitat complexity on fish foraging. *Science of the Total Environment*, *684*, 14–22. https://doi.org/10.1016/j.scitotenv.2019.05.280

Davies, T. W., Duffy, J. P., Bennie, J., & Gaston, K. J. (2014). The nature, extent, and ecological implications of marine light pollution. *Frontiers in Ecology and the Environment*, *12*(6), 347–355. https://doi.org/10.1890/130281

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39–54. https://doi.org/10.1111/1365-2656.12013

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

DWA-German Association for Water, Wastewater and Waste. (2014). Fischaufstiegsanlagen und fisch-passierbare bauwerke—gestaltung, bemessung, qualitätssicherung—stand: Korrigierte fassung februar 2016 (isbn: 978-3-942964-91-3).

Eilam, D. (2005). Die hard: A blend of freezing and fleeing as a dynamic defense—Implications for the control of defensive behavior.

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Neuroscience & Biobehavioral Reviews, *29*(8), 1181–1191. https://doi.org/10.1016/j.neubiorev.2005.03.027

Elvidge, C. K., Ford, M. I., Pratt, T. C., Smokorowski, K. E., Sills, M., Patrick, P. H., & Cooke, S. J. (2018). Behavioural guidance of yellow-stage American eel *Anguilla rostrata* with a light-emitting diode device. *Endangered Species Research*, *35*, 159–168. https://doi.org/10.3354/esr00884

Fortini, N. (2016). *Nuovo atlante dei pesci delle acque interne italiane: guida completa ai pesci, ciclostomi e crostacei decapodi di acque dolci e salmastre*. Aracne.

Foster, J. G., Algera, D. A., Brownscombe, J. W., Zolderdo, A. J., & Cooke, S. J. (2016). Consequences of different types of Littoral zone light pollution on the parental care behaviour of a freshwater teleost fish. *Water, Air, & Soil Pollution*, *227*(11), 404. https://doi.org/10.1007/s11270-016-3106-6

Gaston, K. J., Duffy, J. P., Gaston, S., Bennie, J., & Davies, T. W. (2014). Human alteration of natural light cycles: Causes and ecological consequences. *Oecologia*, *176*(4), 917–931. https://doi.org/10.1007/s00442-014-3088-2

Gouskov, A., Reyes, M., Wirthner-Bitterlin, L., & Vorburger, C. (2016). Fish population genetic structure shaped by hydroelectric power plants in the upper Rhine catchment. *Evolutionary Applications*, *9*(2), 394–408. https://doi.org/10.1111/eva.12339

Greenberg, L., Calles, O., Andersson, J., & Engqvist, T. (2012). Effect of trash diverters and overhead cover on downstream migrating brown trout smolts. *Ecological Engineering*, *48*, 25–29. https://doi.org/10.1016/j.ecoleng.2011.05.001

Hadderingh, R. H., Van Aerssen, G. H. F. M., De Beijer, R. F. L. J., & Van Der Velde, G. (1999). Reaction of silver eels to artificial light sources and water currents: An experimental deflection study. *Regulated Rivers: Research & Management*, *15*(4), 365–371. https://doi.org/10.1002/(SICI)1099-1646(199907/08)15:4<365::AID-RRR552>3.0.CO;2-K

Hagelin, A., Museth, J., Greenberg, L., Kraabøl, M., Calles, O., & Bergman, E. (2021). Upstream fishway performance by Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) spawners at complex hydropower dams—Is prior experience a success criterion? *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(2), 124–134. https://doi.org/10.1139/cjfas-2019-0271

Hard, A., & Kynard, B. (1997). Video evaluation of passage efficiency of American Shad and sea lamprey in a modified Ice Harbor fishway. *North American Journal of Fisheries Management*, *17*(4), 981–987. https://doi.org/10.1577/1548-8675(1997)017<0981:VEOPEO>2.3.CO;2

Helfman, G. S. (1986). Fish behaviour by day, night and twilight. In T. J. Pitcher (Ed.), *The behaviour of teleost fishes* (pp. 366–387). Springer US. https://doi.org/10.1007/978-1-4684-8261-4_14

Hesthagen, T., & Garnås, E. (1986). Migration of Atlantic Salmon smolts in river Orkla of Central Norway in relation to management of a Hydroelectric Station. *North American Journal of Fisheries Management*, *6*(3), 376–382. https://doi.org/10.1577/1548-8659(1986)6<376:MOASSI>2.0.CO;2

Hölker, F., Wolter, C., Perkin, E., & Tockner, K. (2010). Light pollution as a biodiversity threat. *Trends in Ecology & Evolution*, *25*, 681–682. https://doi.org/10.1016/j.tree.2010.09.007

Jones, M. J., Baumgartner, L. J., Zampatti, B. P., & Beyer, K. (2017). Low light inhibits native fish movement through a vertical-slot fishway: Implications for engineering design. *Fisheries Management and Ecology*, *24*(3), 177–185. https://doi.org/10.1111/fme.12205

Jones, M. J., & Hale, R. (2020). Using knowledge of behaviour and optic physiology to improve fish passage through culverts. *Fish and Fisheries*, *21*(3), 557–569. https://doi.org/10.1111/faf.12446

Keefer, M. L., Jepson, M. A., Clabough, T. S., & Caudill, C. C. (2021). Technical fishway passage structures provide high passage efficiency and effective passage for adult Pacific salmonids at eight large dams. *PLoS One*, *16*(9), e0256805. https://doi.org/10.1371/journal.pone.0256805

Keep, J. K., Watson, J. R., Cramp, R. L., Jones, M. J., Gordos, M. A., Ward, P. J., & Franklin, C. E. (2021). Low light intensities increase avoidance behaviour of diurnal fish species: Implications for use of road culverts by fish. *Journal of Fish Biology*, *98*(3), 634–642. https://doi.org/10.1111/jfb.14604

Kemp, P. S., & Williams, J. G. (2009). Illumination influences the ability of migrating juvenile salmonids to pass a submerged experimental weir. *Ecology of Freshwater Fish*, *18*(2), 297–304. https://doi.org/10.1111/j.1600-0633.2008.00347.x

Kennedy, M., & Fitzmaurice, P. (2006). Some aspects of the biology of gudgeon *Gobio gobio* (L.) in Irish waters. *Journal of Fish Biology*, *4*, 425–440. https://doi.org/10.1111/j.1095-8649.1972.tb05690.x

Kieffer, J. D., & Colgan, P. W. (1992). The role of learning in fish behaviour. *Reviews in Fish Biology and Fisheries*, *2*(2), 125–143. https://doi.org/10.1007/BF00042881

Knaepkens, G., Maerten, E., & Eens, M. (2007). Performance of a pool-and-weir fish pass for small bottom-dwelling freshwater fish species in a regulated lowland river. *Animal Biology*, *57*, 423–432. https://doi.org/10.1163/157075607782232134

Kotusz, J., Witkowski, A., Baran, M., & Błachuta, J. (2006). Fish migrations in a large lowland river (Odra R., Poland)—Based on fish pass observations. *Folia Zoologica-Praha*, *55*, 386–398.

Larinier, M. (2002). Pool fishways, pre-barrages and natural bypass channels. *Bulletin Français de La Pêche et de La Pisciculture*, *364 supplément*, 54–82. https://doi.org/10.1051/kmae/2002108

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Lin, C., Dai, H., Shi, X., Deng, Z. D., Mao, J., Luo, J., Huang, W., Xu, J., Zhang, N., & Sun, S. (2021). Investigating feasible light configurations for fish restoration: An ethological insight. *Fisheries Research*, *234*, 105807. https://doi.org/10.1016/j.fishres.2020.105807

Lin, C., Deng, Z. D., Shi, X., Dai, H., Wang, J., Huang, W., Luo, J., & Huang, J. (2022). Mutually promoting or constraining? Disentangling the superimposed effect of velocity and illuminance on fish motion in low-velocity flows with a novel metric. *Freshwater Biology*, *67*(8), 1468–1480. https://doi.org/10.1111/fwb.13954

Lucas, M. C., & Baras, E. (2001). *Migration of freshwater fishes*. Blackwell Science.

Lucas, M. C., & Frear, P. A. (1997). Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology*, *50*(2), 382–396. https://doi.org/10.1111/j.1095-8649.1997.tb01366.x

Markel, R. W. (1994). An adaptive value of spatial learning and memory in the blackeye goby, *Coryphopterus nicholsi*. *Animal Behaviour*, *47*(6), 1462–1464. https://doi.org/10.1006/anbe.1994.1194

Marsden, T., & Stuart, I. (2019). Fish passage developments for small-bodied tropical fish: Field case-studies lead to technology improvements. *Journal of Ecohydraulics*, *4*, 1–13. https://doi.org/10.1080/24705357.2019.1646616

Montgomery, D. R. (2004). King of fish: The thousand-year run of Salmon. *Journal of Macromarketing*, *24*(1), 64–66. https://doi.org/10.1177/0276146704263930

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the World's large river systems. *Science*, *308*(5720), 405–408. https://doi.org/10.1126/science.1107887

Noatch, M. R., & Suski, C. D. (2012). Non-physical barriers to deter fish movements. *Environmental Reviews*, *20*(1), 71–82. https://doi.org/10.1139/a2012-001

Noonan, M. J., Grant, J. W. A., & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency: Effectiveness of fish passage

16000633, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/eff.12766 by CochraneItalia, Wiley Online Library on [09/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

facilities. *Fish and Fisheries*, *13*(4), 450–464. https://doi.org/10.1111/j.1467-2979.2011.00445.x

Nyqvist, D., Calles, O., Forneris, G., & Comoglio, C. (2022). Movement and activity patterns of non-native Wels catfish (*Silurus glanis* Linnaeus, 1758) at the confluence of a large river and its colder tributary. *Fishes*, *7*(6), Article 6. https://doi.org/10.3390/fishes7060325

Nyqvist, D., Greenberg, L. A., Goerig, E., Calles, O., Bergman, E., Ardren, W. R., & Castro-Santos, T. (2016). Migratory delay leads to reduced passage success of Atlantic salmon smolts at a hydroelectric dam. *Ecology of Freshwater Fish*, *26*(4), 707–718. https://doi.org/10.1111/eff.12318

Nyqvist, D., McCormick, S. D., Greenberg, L., Ardren, W. R., Bergman, E., Calles, O., & Castro-Santos, T. (2017). Downstream migration and multiple dam passage by Atlantic Salmon smolts. *North American Journal of Fisheries Management*, *37*(4), 816–828. https://doi.org/10.1080/02755947.2017.1327900

Nyqvist, D., Nilsson, P. A., Alenäs, I., Elghagen, J., Hebrand, M., Karlsson, S., Kläppe, S., & Calles, O. (2017). Upstream and downstream passage of migrating adult Atlantic salmon: Remedial measures improve passage performance at a hydropower dam. *Ecological Engineering*, *102*, 331–343. https://doi.org/10.1016/j.ecoleng.2017.02.055

Nyqvist, D., Schiavon, A., Candiotto, A., Mozzi, G., Eggers, F., & Comoglio, C. (2022). PIT-tagging Italian spined loach (*Cobitis bilineata*): Methodology, survival and behavioural effects. *Journal of Fish Biology*, *102*(3), 575–580. https://doi.org/10.1111/jfb.15289

Odling-Smee, L., & Braithwaite, V. A. (2003). The role of learning in fish orientation. *Fish and Fisheries*, *4*(3), 235–246. https://doi.org/10.1046/j.1467-2979.2003.00127.x

Ovidio, M., Dierckx, A., & Benitez, J.-P. (2023). Movement behaviour and fishway performance for endemic and exotic species in a large anthropized river. *Limnologica*, *99*, 126061. https://doi.org/10.1016/j.limno.2023.126061

Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C., & Tockner, K. (2011). The influence of artificial light on stream and riparian ecosystems: Questions, challenges, and perspectives. *Ecosphere*, *2*(11), art122. https://doi.org/10.1890/ES11-00241.1

Perkin, E. K., Hölker, F., Tockner, K., & Richardson, J. S. (2014). Artificial light as a disturbance to light-naïve streams. *Freshwater Biology*, *59*(11), 2235–2244. https://doi.org/10.1111/fwb.12426

Podgorniak, T., Blanchet, S., De Oliveira, E., Daverat, F., & Pierron, F. (2016). To boldly climb: Behavioural and cognitive differences in migrating European glass eels. *Royal Society Open Science*, *3*(1), 150665. https://doi.org/10.1098/rsos.150665

Prchalová, M., Slavík, O., & Bartoš, L. (2006). Patterns of cyprinid migration through a fishway in relation to light, water temperature and fish circling behaviour. *International Journal of River Basin Management*, *4*(3), 213–218. https://doi.org/10.1080/15715124.2006.9635290

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. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*(3), 849–873. https://doi.org/10.1111/brv.12480

Rimmer, D. M., & Paim, U. (1990). Effects of temperature, photoperiod, and season on the photobehaviour of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology*, *68*(6), 1098–1103. https://doi.org/10.1139/z90-162

Romão, F., Branco, P., Quaresma, A. L., Amaral, S. D., & Pinheiro, A. N. (2018). Effectiveness of a multi-slot vertical slot fishway versus a standard vertical slot fishway for potamodromous cyprinids. *Hydrobiologia*, *816*(1), 153–163. https://doi.org/10.1007/s10750-018-3580-5

Russon, I. J., Kemp, P. S., & Calles, O. (2010). Response of downstream migrating adult European eels (*Anguilla anguilla*) to bar racks under experimental conditions. *Ecology of Freshwater Fish*, *19*(2), 197–205. https://doi.org/10.1111/j.1600-0633.2009.00404.x

Santos, J. M., Ferreira, M. T., Godinho, F. N., & Bochechas, J. (2005). Efficacy of a nature-like bypass channel in a Portuguese lowland river. *Journal of Applied Ichthyology*, *21*(5), 381–388.

Schiavon, A., Comoglio, C., Candiotto, A., Hölker, F., Ashraf, M. U., & Nyqvist, D. (2023). Survival and swimming performance of a small-sized Cypriniformes (*Telestes muticellus*) tagged with passive integrated transponders. *Journal of Limnology*, *82*(1), 25–31. https://doi.org/10.4081/jlimnol.2023.2129

Schiavon, A., Comoglio, C., Candiotto, A., Hölker, F., Spairani, M., Tarena, F., Watz, J., & Nyqvist, D. (2022). *Individual movement and behavior of Telestes muticellus and Barbus caninus of a small mountain stream*. [Poster presentation]. Vattendagarna 2022 med Fiskmarknad, Karlstad, Sweden.

Schmutz, S., & Mielach, C. (2013). Measures for ensuring fish migration at transversal structures. *ICPDR—International Commission for the Protection of the Danube River*.

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. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, *19*(2), 340–362. https://doi.org/10.1111/faf.12258

Solomon, O. O., & Ahmed, O. O. (2016). Fishing with light: Ecological consequences for coastal habitats.

Stott, B. (1967). The movements and population densities of roach (*Rutilus rutilus* (L.)) and gudgeon (*Gobio gobio* (L.)) in the river mole. *Journal of Animal Ecology*, *36*(2), 407–423. https://doi.org/10.2307/2922

Stuart, T. A. (1962). The leaping behavior of salmon and trout at falls and obstructions. https://www.semanticscholar.org/paper/The-leaping-behavior-of-salmon-and-trout-at-falls-Stuart/a5d89ab123bddb83228cdf920f72a2fcdb68fc18

Tabor, R. A., Brown, G. S., & Luiting, V. T. (2004). The effect of light intensity on sockeye Salmon fry migratory behavior and predation by Cottids in the Cedar River, Washington. *North American Journal of Fisheries Management*, *24*(1), 128–145. https://doi.org/10.1577/M02-095

Vøllestad, L. A., Jonsson, B., Hvidsten, N. A., Næsje, T. F., Haraldstad, Ø., & Ruud-Hansen, J. (1986). Environmental factors regulating the seaward migration of European silver eels (*Anguilla anguilla*). *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(10), 1909–1916. https://doi.org/10.1139/f86-236

von Campenhausen, C., Riess, I., & Weissert, R. (1981). Detection of stationary objects by the blind cave Fish *Anoptichthys jordani* (Characidae). *Journal of Comparative Physiology*, *143*(3), 369–374. https://doi.org/10.1007/BF00611175

Vowles, A., & Kemp, P. (2012). Effects of light on the behaviour of brown trout (*Salmo trutta*) encountering accelerating flow: Application to downstream fish passage. *Ecological Engineering*, *47*, 247–253. https://doi.org/10.1016/j.ecoleng.2012.06.021

Vowles, A. S., Anderson, J. J., Gessel, M. H., Williams, J. G., & Kemp, P. S. (2014). Effects of avoidance behaviour on downstream fish passage through areas of accelerating flow when light and dark. *Animal Behaviour*, *92*, 101–109. https://doi.org/10.1016/j.anbehav.2014.03.006

Vowles, A. S., & Kemp, P. S. (2021). Artificial light at night (ALAN) affects the downstream movement behaviour of the critically endangered European eel, *Anguilla anguilla*. *Environmental Pollution*, *274*, 116585. https://doi.org/10.1016/j.envpol.2021.116585

Watz, J., Bergman, E., Calles, O., Enefalk, Å., Gustafsson, S., Hagelin, A., Nilsson, P. A., Norrgård, J. R., Nyqvist, D., Österling, E. M., Piccolo, J. J., Schneider, L. D., Greenberg, L., & Jonsson, B. (2015). Ice cover

16000633, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/eff.12766 by CochraneItalia, Wiley Online Library on [09/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

alters the behavior and stress level of brown trout *Salmo trutta*. *Behavioral Ecology*, *26*(3), 820–827. https://doi.org/10.1093/beheco/arv019

Williams, J. G., Armstrong, G., Katopodis, C., Larinier, M., & Travade, F. (2012). Thinking like a fish: A key ingredient for development of effective fish passage facilities at river obstructions. *River Research and Applications*, *28*(4), 407–417. https://doi.org/10.1002/rra.1551

Wocher, H., & Rösch, R. (2006). Migrations of soufie (*Leuciscus souffia agassizii*, VAL. 1844) in a natural river and a tributary determined by mark-recapture. *Archiv für Hydrobiologie*, *165*, 77–87. https://doi.org/10.1127/0003-9136/2006/0165-0077

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