

Bigger than expected: Species- and size-specific passage of fish through hydropower screens

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ARTICLE INFO

Keywords:

Bar rack
Downstream migration
Fish guiding structure
Screening
Sustainable hydropower
Turbine entrainment

ABSTRACT

Mitigating the adverse ecological impacts on stream ecosystems caused by hydropower expansion is a major challenge. To prevent fish from turbine entrainment and to reduce injury and mortality risk, physical barriers such as fine screens with horizontally or vertically oriented bars are frequently installed at turbine inlets. In this study, the species- and size-dependent protection from turbine entrainment of different types of fish protection screens (FPSs) were investigated at five hydropower sites by a net-based monitoring of downstream moving wild fish and hatchery-reared test fish during different seasons (15,223 individuals from 40 species). Across different screen types and fish species, considerably larger individuals were able to pass the FPSs than what would have been expected from common models estimating the physical passability of these mechanical barriers. The examined FPSs with 15 mm and 20 mm bar spacing could be passed by adult barbel (*Barbus barbus* L.), brown trout (*Salmo trutta* L.) and European perch (*Perca fluviatilis* L.) up to a total length (TL) of 32 cm (15 mm FPSs) and 34 cm (20 mm FPSs), respectively. In addition, the 20 mm FPSs could be passed by Danube salmon (*Hucho hucho* L.) up to 39 cm TL. Consequently, thresholds from modelling and rules of thumb for estimating maximum TLs capable of passing 15 mm and 20 mm FPSs were exceeded by up to 135% for these species. The results of this study suggest that fish species other than eel can also squeeze through physical barriers narrower than body dimensions. No physical fish protection was realised by the investigated 15 mm and 20 mm FPSs for many small-bodied species such as bullhead (*Cottus gobio* L.), gudgeon (*Gobio gobio* L.) and spirin (*Alburnoides bipunctatus* Bloch) with maximum TLs smaller than 20 cm. This also holds true for juveniles and sub-adults of larger species, which can pass these physical barriers. Since a large part of the downstream moving fish generally consists of small species or small individuals, these fish sizes must be given greater consideration in physical fish protection concepts at hydropower plants.

1. Introduction

The global expansion of hydropower and associated adverse ecological impacts on stream habitat and aquatic organisms pose a major challenge to the conservation of freshwater biodiversity (Geist, 2021; Zarfl et al., 2015). Particularly fish are affected by habitat loss and degradation, disruption of migration routes and the injury and mortality risk during turbine passage (e.g. Agostinho et al., 2008; Kuriqi et al., 2021; Mueller et al., 2022).

Fish predominantly follow the main current during their downstream migration (Lundström et al., 2010; Williams et al., 2012). As the majority of the river discharge flows through the turbines at most hydropower plants, a large proportion of active or passive downstream moving fish also use this corridor (Fjeldstad et al., 2018). Since the

turbine passage usually involves a high injury and mortality risk to fish (Algera et al., 2020; Mueller et al., 2022; Pracheil et al., 2016), efforts are being made to prevent fish from turbine entrainment by means of physical or behavioural barriers. According to scientific literature, physical barriers with bar structure and bar spacings between 10 mm to 30 mm are classified as ‘fish protection screens’ (FPSs), ‘fish exclusion barriers’, ‘fish protection barriers’ or ‘fish-friendly trash racks’ (c.f. Albayrak et al., 2020; David et al., 2022; Raynal et al., 2013; Szabo-Mezaros et al., 2018). These are installed upstream of the turbine inlet and are intended to exclude specific fish sizes from passing through the turbine due to small bar spacing. There is a great variability of the screen bar types in terms of arrangement (horizontal vs. vertical), shape (e.g. flat, triangular, rounded) and orientation to the flow direction (e.g. acute-angled, obtuse-angled, perpendicular) (David et al., 2022). It is

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<https://doi.org/10.1016/j.ecoleng.2022.106883>

Received 11 November 2022; Received in revised form 21 December 2022; Accepted 24 December 2022

Available online 4 January 2023

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intended that fish with a body width greater than the bar spacing should physically not be able to pass the FPS (Ebel, 2013; Schwevers and Adam, 2020). Due to the shape of FPSs (e.g. plane or semi-circular), different inclinations to the stream bed or the arrangement of the bars (horizontal vs. vertical), these physical barriers are also intended to have a behavioural effect and guide downstream moving fish to bypasses (Larinier and Travade, 2002; Meister et al., 2022).

There are a number of scientific studies that have investigated the technical and hydraulic advantages and disadvantages of different types of FPSs (e.g. Albayrak et al., 2020; Raynal et al., 2013). Although there is a growing body of literature on the effectiveness of different mechanical barriers to prevent turbine entrainment, the majority of available studies are on few economically valuable species such as salmon and eel (e.g. Amaral et al., 2003; Boubée and Williams, 2006; Økland et al., 2016; Russon et al., 2010). There are large knowledge gaps regarding the effectiveness of different types of FPSs for less economically important

fish species, some of which are also endangered and protected by law (e.g. Danube salmon, *Hucho hucho* L.; European Commission, 1992). However, this information is highly relevant since it often forms the basis for deducing legal requirements and decisions on the installation of fish protection measures at hydropower plants. It has so far been underestimated that also many potamodromous fish species, which are not known as medium- or long-distance migrators, also migrate or drift downstream in large numbers and consequently have to pass hydro-power facilities (Katopodis, 2005; Knott et al., 2020).

The information available in the peer-reviewed and grey literature on the species-specific total length (TL) up to which a fish can pass a FPS is mostly based on numerical modelling (e.g. Ebel, 2013; Schwevers and Adam, 2020). It is assumed that a fish cannot pass a FPS if its maximum body width is greater than the distance between the screen bars. However, modelling approaches cannot fully account for potential behavioural and morphological differences within a species and between

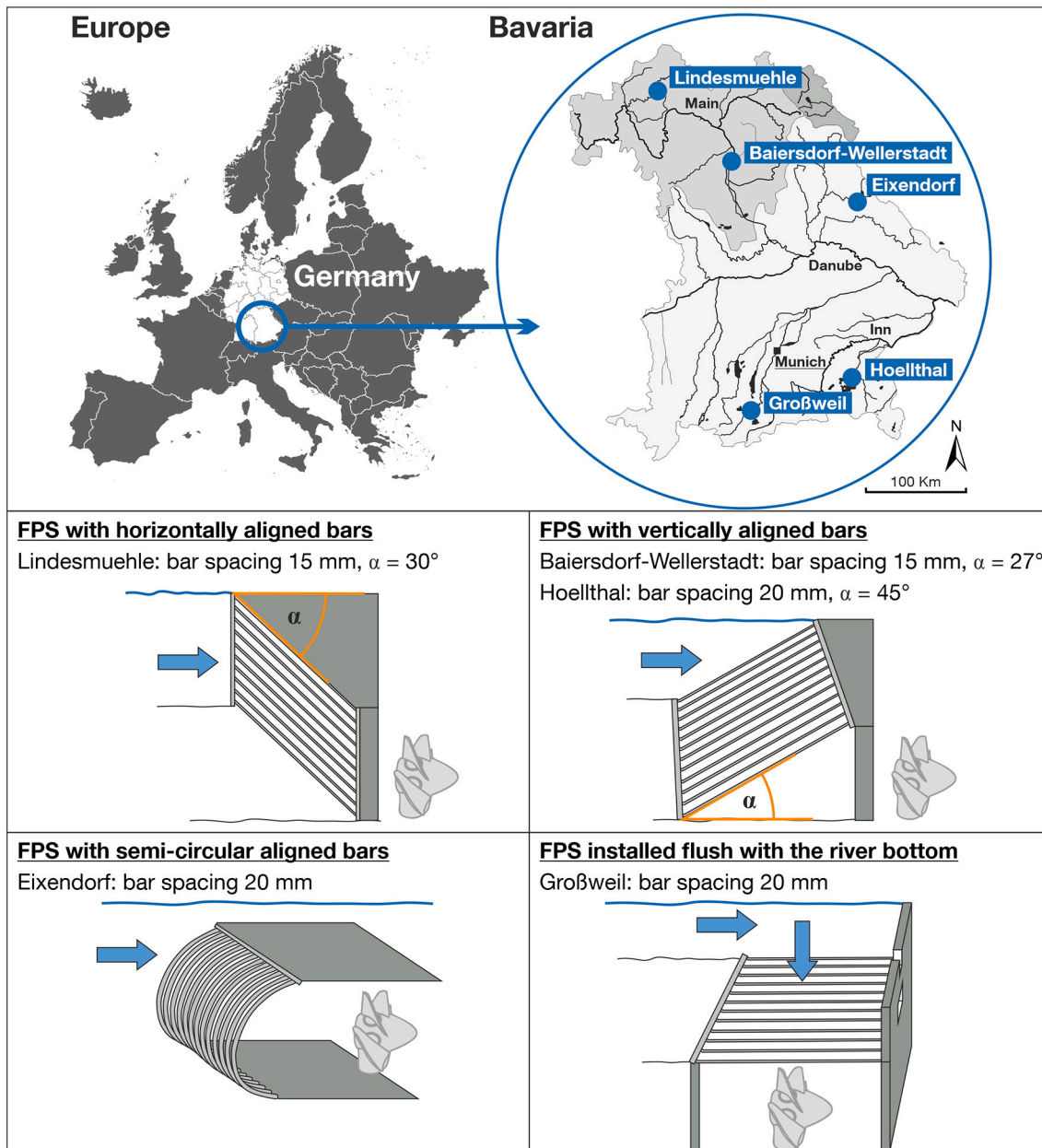


Fig. 1. Location of the study sites in Bavaria, Germany (upper part of the figure) and schematics of the different types of assessed fish protection screens (FPS) (lower part). Blue arrows in FPS schematics indicate the main flow direction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species. In contrast, field studies that consider the effectiveness of FPSs including intra- and interspecific differences for the entire downstream moving fish community are, to the best of our knowledge, currently not available in international peer-reviewed literature. Yet, field studies under realistic environmental conditions are crucial in order to verify the knowledge gained in laboratory experiments or to improve modelling approaches (Geist, 2021; Spears et al., 2021).

In this study, we investigated the species- and size-dependent protection from turbine entrainment of different commonly used types of FPSs at five hydropower sites by a net-based monitoring during different seasons. For this purpose, downstream moving wild fish and hatchery-reared test fish (subsequently referred to as 'test fish') of different size classes released in the headwaters of the hydropower plants were captured and assessed after passing through the screen and turbine. Specifically, we hypothesized that FPSs with bar spacings of 15 mm and 20 mm prevent sub-adult and adult fish from turbine passage according to common models estimating the physical passability of FPSs (cf. Ebel, 2013; Schwevers and Adam, 2020).

2. Materials and methods

2.1. Study sites

The study was conducted at five small-scale (< 1 MW) run-of-the-river hydropower plants in Bavaria, Germany (Fig. 1). The study sites differ in terms of hydropower plant technology and concepts for fish protection (Fig. 1). The hydropower plants studied include both conventional hydropower plants (CHPPs) with Kaplan bulb turbines and the innovative concepts 'shaft hydropower plant' (SHPP) and 'movable hydropower plant' (MHPP).

The CHPP at the River Regnitz in Baiersdorf-Wellerstadt (N 49.6706, E 11.0424) is equipped with two identical horizontal Kaplan bulb turbines. As a fish protection measure, a vertical screen with a bar spacing of 15 mm is installed in front of the turbine inlet (inclination to the streambed 27°). Another CHPP is located at the River Franconian Saale in Bad Kissingen (N 50.1879, E 10.0744) and is operated with a horizontal Kaplan bulb turbine. To hinder fish from passing the turbine, a horizontal screen (bar spacing 15 mm) is installed in front of the turbine inlet at an angle of 30° to flow direction. The third CHPP is located at the River Alz in Hoellthal (N 47.9780, E 12.5027) and is also operated with a horizontal Kaplan bulb turbine. A vertical screen inclined towards the stream bed (angle of inclination 45°) with a bar spacing of 20 mm should prevent fish from turbine entrainment. The MHPP at the River Schwarzach in Eixendorf (N 49.3396, E 12.4799) is equipped with a horizontal Kaplan bulb turbine. To protect fish from turbine entrainment, a semi-circular screen with a bar spacing of 20 mm is installed in front of the turbine inlet. The SHPP at the River Loisach in Großweil (N 47.6819, E 11.3002) is operated with two identical horizontal Kaplan bulb turbines. Horizontally arranged FPSs with 20 mm bar spacing, installed flush with the river bottom, should prevent downstream moving fish from turbine passage (Fig. 1).

2.2. Experimental design

In order to assess for which species-specific TL the FPSs with bar spacings of 15 mm and 20 mm are passable, naturally downstream moving wild fish as well as test fish released upstream of the hydropower plants were captured by stow nets after passing the FPSs and the turbines. By using test fish, it was possible to ensure for a set of representative species with different morphological and behavioural characteristics that they encountered the assessed FPSs in high numbers and at a broad range of sizes. The data set comprises captured wild and released test fish at the study sites Lindesmuehle, Baiersdorf-Wellerstadt, Großweil and Hoellthal as well as data on released test fish at the Eixendorf MHPP.

Fish were caught with tapering stow-nets with decreasing mesh size

(mesh sizes: 30 mm, 20 mm, 15 mm, 10 mm and 8 mm) and a fyke-net at its end. In order to cover the entire turbine discharge, the nets were attached to metal frames and inserted into the u-profiles at the turbine outlets (cf. Knott et al., 2020). To minimise catch-related injuries, knotless polyamide netting material was used and nets were emptied every 1–2 h (Pander et al., 2018) both during the day and at night. Each individual fish was determined to species level and its TL was measured. The investigations were carried out between 2015 and 2021. Each site was sampled over several weeks in spring and autumn (Table 1). The net sampling took place over a period of 1947 h on a total of 189 study days (Table 1).

During the study period, a total of 36,803 test fish of eight species in different size classes (Table 2) were released immediately upstream of the hydropower plants in front of the FPSs. Before release, all test fish were marked with fin clips to distinguish them from wild fish when recaptured. These animal experiments were approved by the ethics committee of the Bavarian government (permit numbers ROB-55.2-2532.Vet_02–15-31 and ROB-55.2-2532.Vet_02–19-160) and complied with national animal welfare laws and regulations. In accordance with European standards (European Parliament, 2010) and national guidelines (Adam et al., 2013) for the use of fish in scientific experiments, discomfort or pain of the test fish were minimised as far as possible.

2.3. Statistical analyses

To assess the size selectivity of different types of FPSs, individual TLs of the different species of wild and test fish that were captured after screen passage were compared. Statistical analyses were performed with the statistics software R (version 4.1.2; R Core Team, 2021). Since data were not normally distributed, Wilcoxon tests (comparison of two groups) or non-parametric Kruskal-Wallis tests and Bonferroni-corrected post-hoc pairwise Mann-Whitney *U* tests (comparison of more than two groups) were used. Statistical test results were classified as significant at an error probability of $p \leq 0.05$.

3. Results

During the study period, a total of 15,223 downstream moving wild and test fish from 40 species were caught after passing the different FPSs of the investigated hydropower plants. The data set of downstream moving wild fish comprises 4781 individuals from 39 species. The most frequently caught wild fish species were spiralin (*Alburnoides bipunctatus* Bloch), roach (*Rutilus rutilus* L.) and bleak (*Alburnus alburnus* L.), summing up to 48% of the total catch of wild individuals. TLs of all captured wild fish that passed the FPSs ranged from 2 cm (Rudd, *Scardinius erythrophthalmus* L.; Topmouth gudgeon, *Pseudorasbora parva* Temminck & Schlegel) to 61 cm (European eel, *Anguilla anguilla* L.; arithmetic mean 9.9 cm) (Table A.1). Besides European eel, the largest wild fish species were European catfish (*Silurus glanis* L., max. TL 41 cm) and lake trout (*Salvelinus namaycush* Walbaum, max. TL 38 cm). 98% of the downstream moving wild fish that passed the FPSs were < 20 cm in TL (89% < 15 cm).

A total of 10,442 individuals of the eight test fish species were recaptured after passing the FPSs and the turbines. TLs of recaptured test fish ranged from 3 cm (Brown trout, *Salmo trutta* L.) to 69 cm (European eel). Besides European eel, the largest recaptured test fish species were Danube salmon (max. TL 39 cm) and brown trout (max. TL 34 cm). 84% of the recaptured test fish that passed the FPSs were < 20 cm in TL (73% < 15 cm).

Significantly larger wild and test fish (without European eel) were able to pass the 20 mm FPSs than the 15 mm FPSs (Wilcoxon test: $W = 13,355,067$; $p < 0.001$). For the 15 mm FPSs, the proportion of fish ≥ 15 cm (without European eel) passing was 9% (≥ 20 cm: 1%). In contrast, 18% of the fish that were able to pass the 20 mm FPSs (without European eel) were ≥ 15 cm and 6% were ≥ 20 cm.

The TL of fish (without European eel) passing the horizontal 15 mm

Table 1

Seasonal study period, catch numbers for wild and hatchery-reared test fish and size range (min–max) of total lengths (TL) at the investigated hydropower sites; hrs = catch period in hours, Ind. released = number of released test fish, Ind. recaptured = number of recaptured test fish.

		Lindesmuehle	Baiersdorf-Wellerstadt	Eixendorf	Großweil	Hoellthal
Sampling period	Spring	28 Apr to 09 May 2015	28 Apr to 08 May 2015	24 Apr to 23 May 2017	09 Mar to 31 Mar 2021	30 Mar to 16 Apr 2019
	(hrs)	(246)	(174)	(293)	(187)	(126)
Autumn	14 Sep to 05 Oct 2015	16 Sep to 30 Sep 2015	08 Sep to 02 Oct 2017	15 Sep to 06 Oct 2020	12 Sep to 06 Oct 2018	
	(hrs)	(363)	(138)	(116)	(146)	(158)
Wild fish	No. of species	21	32	n.a.	11	24
	No. of individuals	544	1864	n.a.	198	2175
	TL min–max [cm]	2.4–24.0	2.0–35.0	n.a.	4.6–37.6	3.0–61.0
Hatchery-reared test fish	Ind. released	2472	13,845	10,749	7265	7265
	TL min–max [cm]	4.0–64.5	3.5–64.3	4.0–71.4	2.9–66.7	4.1–71.2
	Ind. recaptured	50	1296	3230	2950	2916
	TL min–max [cm]	5.8–38.0	5.0–44.1	4.0–69.3	3.4–57.7	4.4–64.7

Table 2

Number (n) and range (min–max) of total lengths (in cm) of hatchery-reared test fish that were released in the headwaters of the investigated hydropower plants. The arithmetic mean (am) and standard deviation (sd) are given in parentheses.

	Lindesmuehle		Baiersdorf-Wellerstadt		Eixendorf		Großweil		Hoellthal	
	n	min–max (am ± sd)	n	min–max (am ± sd)	n	min–max (am ± sd)	n	min–max (am ± sd)	n	min–max (am ± sd)
European eel (<i>Anguilla anguilla</i> L.)	618	19.6–64.5 (39.9 ± 9.5)	618	20.0–64.3 (38.0 ± 9.0)	824	22.0–71.4 (43.0 ± 7.8)	931	23.1–66.7 (41.4 ± 7.8)	619	24.5–71.2 (41.8 ± 8.6)
Common nase (<i>Chondrostoma nasus</i> L.)	618	4.0–12.6 (7.9 ± 1.7)	618	3.5–12.4 (8.1 ± 1.6)	3178	6.0–20.4 (11.3 ± 2.5)	1648	7.2–29.7 (13.2 ± 4.1)	773	10.1–26.4 (16.7 ± 3.2)
Brown trout (<i>Salmo trutta</i> L.)	618	9.0–24.0 (14.6 ± 2.4)	618	8.2–16.1 (12.9 ± 1.1)	2163	4.2–41.0 (17.8 ± 7.7)	1442	2.9–38.8 (13.4 ± 8.4)	927	4.1–42.0 (17.8 ± 7.5)
European perch (<i>Perca fluviatilis</i> L.)	618	6.7–15.0 (10.1 ± 1.3)	618	7.0–14.5 (10.0 ± 1.2)	824	5.4–14.7 (10.6 ± 1.1)	1232	6.6–25.8 (13.0 ± 5.1)	412	5.1–16.1 (11.5 ± 1.2)
Barbel (<i>Barbus barbus</i> L.)					1545	4.0–22.6 (10.6 ± 4.2)	1376	6.2–37.4 (12.7 ± 6.0)	1648	5.0–21.0 (10.6 ± 3.4)
Roach (<i>Rutilus rutilus</i> L.)					2266	4.8–21.7 (13.3 ± 2.0)	1648	5.2–19.5 (13.1 ± 1.6)	1030	6.1–16.0 (9.5 ± 1.1)
European grayling (<i>Thymallus thymallus</i> L.)					1545	6.5–30.0 (16.0 ± 6.5)	1030	4.8–20.3 (11.5 ± 3.2)	1090	7.5–29.8 (16.4 ± 5.9)
Danube salmon (<i>Hucho hucho</i> L.)					1500	9.0–51.3 (23.3 ± 11.0)	1442	9.2–59.3 (20.1 ± 8.4)	766	7.8–60.0 (21.0 ± 11.1)

FPS in Lindesmuehle (am ± sd: 8.3 ± 4.0 cm) was significantly lower

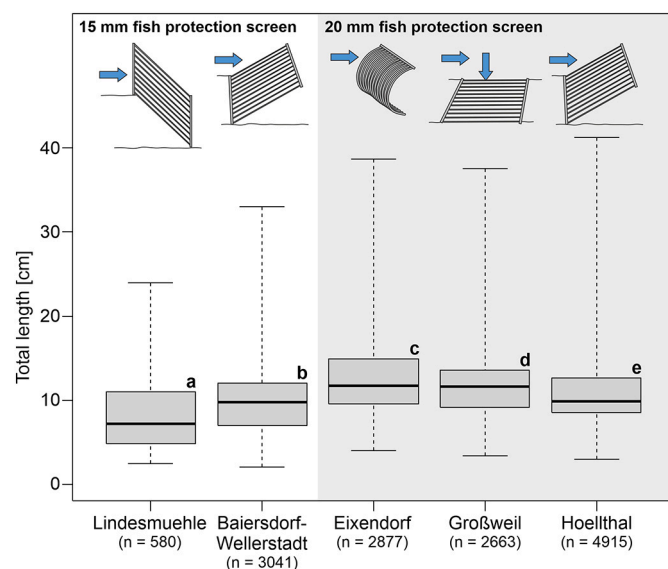


Fig. 2. Comparison of the total lengths of captured wild and test fish that passed the different types of fish protection screens (excluding European eel). Different lowercase letters indicate significant differences between screen types ($p \leq 0.05$) according to Bonferroni-corrected post-hoc pairwise Mann-Whitney U test. Box: 25% quantile, median, 75% quantile; whisker: minimum, maximum values; n = sum of captured wild and test fish.

than for the vertical 15 mm FPS in Baiersdorf-Wellerstadt (9.8 ± 3.4 cm) (Fig. 2). At the vertical FPS with 20 mm bar spacing in Hoellthal (11.2 ± 4.6 cm), the TL of fish (without European eel) with screen passage was significantly lower than at the 20 mm FPSs in Eixendorf (12.5 ± 4.4 cm) and Großweil (11.8 ± 3.6 cm) (Fig. 2).

The species-specific TLs of fish that passed the FPSs were different between the investigated screen types as illustrated for four exemplary fish species (Fig. 3). These species were selected because they are representatives of different ecological guilds and differ in body shape (e.g. elongated, fusiform, laterally compressed) and behaviour (e.g. bottom-, open water-oriented). TLs of European eels which were able to pass the 15 mm FPSs were significantly lower than of European eels that passed the 20 mm FPSs (Wilcoxon test: $W = 15,790$; $p < 0.001$). No significant differences in TLs of European eels passing the FPSs were found between the horizontal 15 mm FPS in Lindesmuehle (33.7 ± 2.9 cm) and the vertical 15 mm FPS in Baiersdorf-Wellerstadt (32.1 ± 4.2 cm) (Fig. 3). There were also no significant differences in TLs of European eels that were able to pass the different types of 20 mm FPSs in Eixendorf (42.1 ± 7.5 cm), Großweil (40.2 ± 6.4 cm) and Hoellthal (40.7 ± 8.1 cm) (Fig. 3). For other species such as common nase (*Chondrostoma nasus* L.), brown trout and European perch (*Perca fluviatilis* L.), significant differences in TL of fish with screen passage between the different FPS types were also detected (Fig. 3).

The largest fish that passed through the examined FPSs with a bar spacing of 15 mm were European eels up to 44 cm TL (Fig. 4). Comparatively large individuals of barbel (*Barbus barbus* L.; max. TL 32 cm), brown trout (max. TL 26 cm) and European perch (max. TL 20 cm) were also able to pass the 15 mm FPSs. The assessed FPSs with 20 mm bar spacing could be passed by European eels up to 69 cm TL. Danube

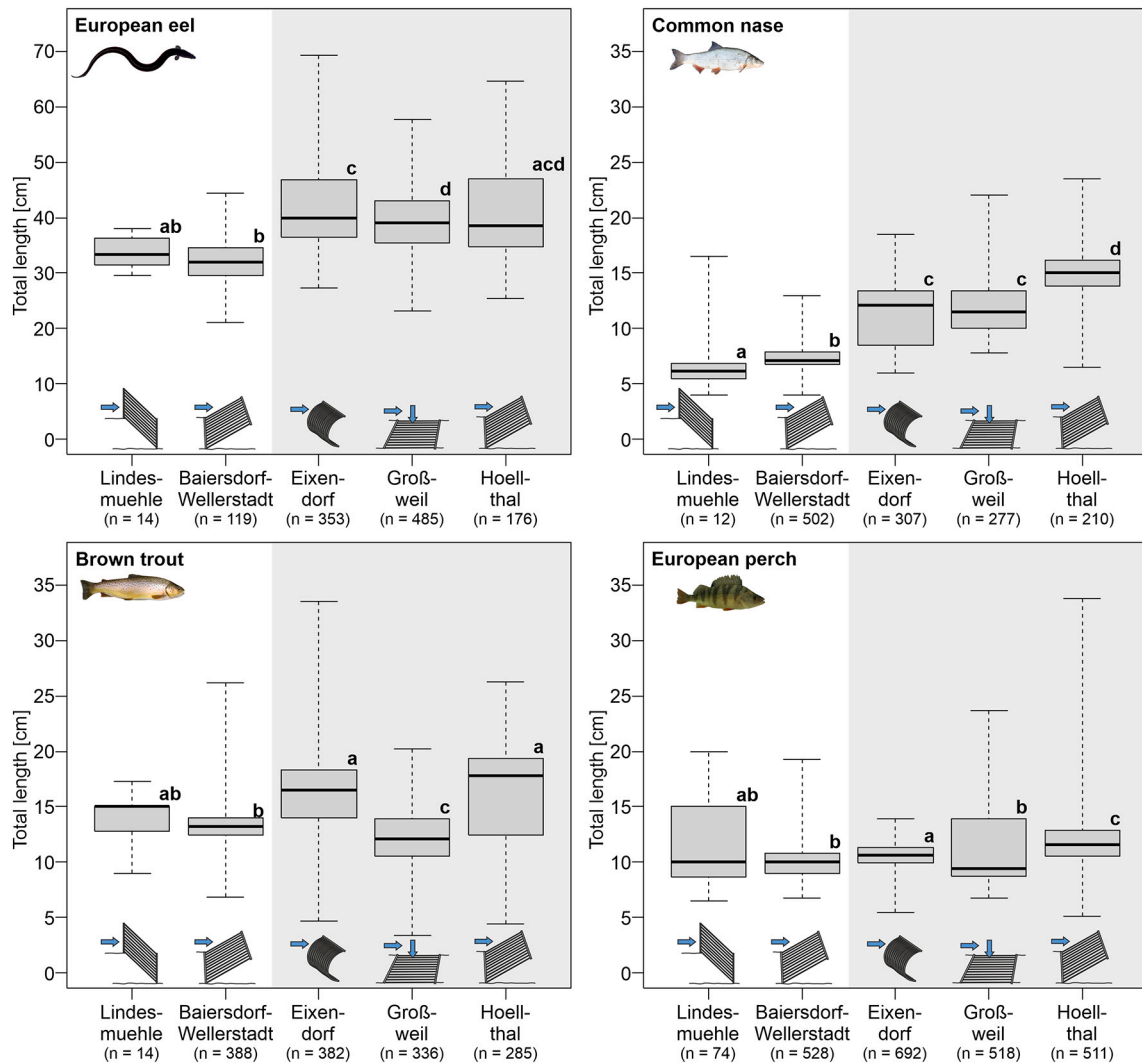


Fig. 3. Comparison of species-specific total lengths of captured wild and test fish that have passed the different types of fish protection screens (FPSs) for four exemplary species. Study sites with 15 mm FPSs are shown in the light part of the figure, sites with 20 mm FPSs in the grey part. Different lowercase letters indicate significant differences between screen types ($p \leq 0.05$) according to Bonferroni-corrected post-hoc pairwise Mann-Whitney U test. Box: 25% quantile, median, 75% quantile; whisker: minimum, maximum values; n = sum of captured wild and test fish.

salmon up to 39 cm TL, brown trout and European perch up to 34 cm TL and barbel up to 31 cm TL could also pass the FPSs with 20 mm bar spacing (Fig. 4).

4. Discussion

Based on a dataset of >15,000 wild and test fish from 40 species caught after passing through different types of FPSs that are intended to prevent fish from turbine entrainment, this study provides new insights into species-specific TLs that can pass through these physical barriers under realistic field conditions.

It is remarkable that across different screen types and fish species, considerably larger individuals were able to pass the FPSs than would have been expected based on modelling (cf. Ebel, 2013; Schwevers and Adam, 2020). Physical barriers at hydropower inlets with a defined bar spacing should be physically impermeable for fish above a certain, species-specific varying TL. However, the assessed FPSs with 15 mm bar spacing could be passed by adult barbel, brown trout and European perch up to a maximum TL of 32 cm and by European eels up to 44 cm TL. The maximum TLs of fish caught after passing the FPSs with 20 mm bar spacing were 39 cm for Danube salmon and 69 cm for European eel. Consequently, the thresholds for the physical passability of FPSs with 15

mm and 20 mm bar spacing given in Ebel (2013) and Schwevers and Adam (2020) were clearly exceeded by 53–135% for barbel, brown trout, European perch and Danube salmon. To estimate which fish sizes can pass a physical barrier, the rule of thumb that the width of a fish is one tenth of its TL is also often used (except for eels) (David et al., 2022; Larinier and Travade, 2002). It is assumed that fish can only pass a physical barrier if the body width is less or equal to the opening. According to this rule of thumb, passage of the assessed 15 mm and 20 mm FPSs would only be possible for fish up to a maximum TL of 15 cm and 20 cm, respectively. These values were exceeded by 113% at the 15 mm FPSs examined in this study and by 94% at the 20 mm FPSs (without European eel).

In contrast, considerably smaller deviations from the modelled thresholds were found for European eel, common nase and roach. However, larger European eels than those recorded in this study can presumably also pass through FPSs with 15 mm and 20 mm bar spacing, as European eels up to 69 cm TL were able to pass through a vertical screen with 12 mm bar spacing in a laboratory experiment by Russon et al. (2010).

The deviations of the modelling from the results of this study may be explained by the fact that individual fish condition can vary, e.g. according to nutritional status and reproductive activity (e.g. Arslan et al.,

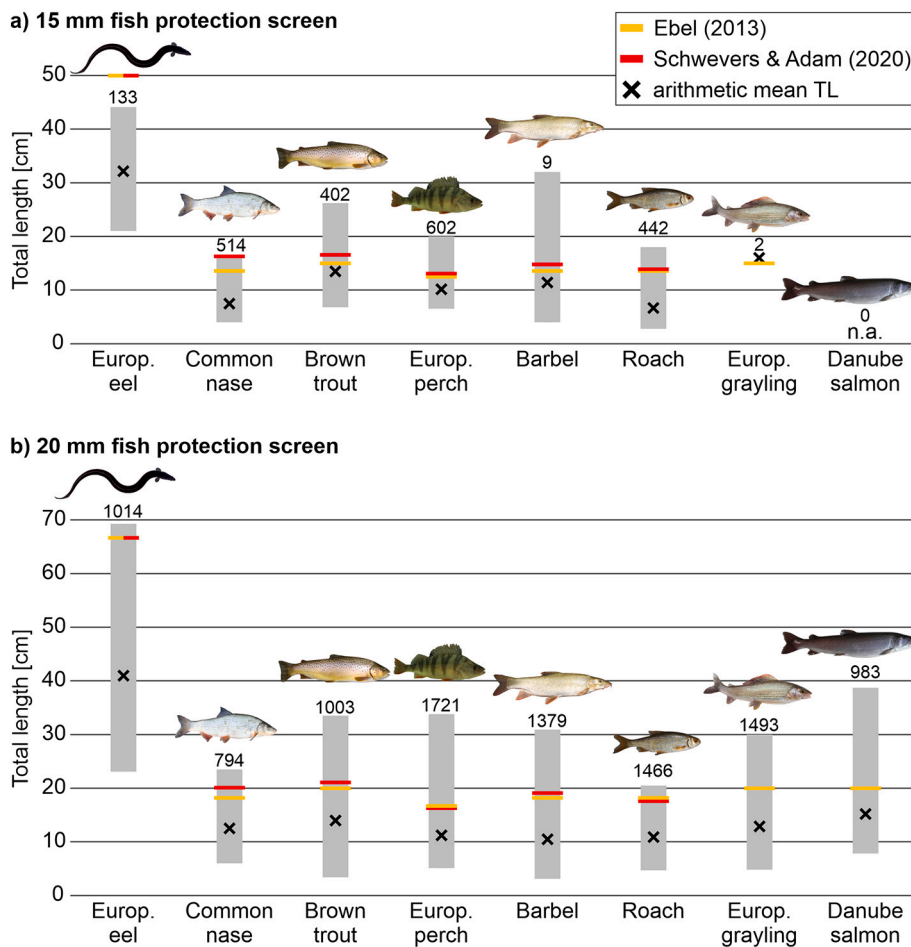


Fig. 4. Range of total lengths (TL) of the eight most frequently caught species of wild and test fish that passed the 15 mm (a) and 20 mm (b) fish protection screens (FPSs) at the investigated hydropower plants. Coloured bars symbolise the maximum species-specific TL determined in modelling by Ebel (2013) (orange) and Schwevers and Adam (2020) (red), up to which a fish should be physically able to pass a FPS with 15 mm or 20 mm bar spacing. The sum of captured wild and test fish is shown on the bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2004; Le Cren, 1951), which means that the body width and height can differ even at the same TL within one single species. Another reason for the deviations from the models is that in Ebel (2013), for example, identical threshold values were assumed for the salmonid species brown trout, European grayling and Danube salmon. However, the results of this study showed that considerably larger Danube salmon than brown trout and European grayling were able to pass the FPSs, which is probably due to the different morphology and behaviour of these species. For instance, Danube salmon usually have a smaller body width than brown trout at the same total length in the size classes investigated.

To date, it has been assumed that fish cannot pass through a physical barrier with bar structure if the maximum body width is greater than the bar spacing. There have only been observations of eels being able to squeeze through openings smaller than their body diameter (Sheridan et al., 2014). However, the findings of this study suggest that this may also hold true for other species. For some of them, it is thus most likely not the maximum body width or height that is decisive for the passability of a physical barrier, but instead skeletal structures with little or no flexibility such as the skull. In addition, manufacturer-related bar spacing tolerances, larger gaps at the connection between FPS and structural elements as well as operation-induced damages to the screen (e.g. widening of the bars due to dead wood or sediment), which were also observed in this study, can be an explanation why larger fish were able to pass the FPSs under realistic field conditions than calculated by modelling.

For small-bodied fish species such as bullhead (*Cottus gobio* L.), gudgeon (*Gobio gobio* L.) and spirilin with maximum TLs smaller than 20 cm the investigated FPSs with 15 mm and 20 mm bar spacing did not provide a physical barrier, as all size classes of these species were able to

pass through. Since small potamodromous fish species also migrate or drift downstream in large numbers (Knott et al., 2020; Pander et al., 2013), these species will inevitably encounter hydropower facilities and are thus exposed to the injury and mortality risk associated with turbine passage.

As expected, across all fish species, the TLs that were able to pass the assessed 15 mm FPSs (am: 9.6 cm, excluding European eel) were lower compared to the FPSs with 20 mm bar spacing (am: 11.7 cm, excluding European eel). The comparison between the examined 15 mm FPS with horizontally arranged bars (am: 8.3 cm, without European eel) and the 15 mm FPS with vertically arranged bars (am: 9.8 cm, without European eel) suggests that the horizontal arrangement provides slightly better fish protection (De Bie et al., 2021; Ebel, 2013). This is probably because fish with a body height larger than the bar spacing have to turn sideways to pass the horizontally arranged screen bars, which could also act as a behavioural barrier. However, it has to be considered that, in addition to the alignment of the screen bars, the site-specific hydraulic conditions at the screen (e.g. approach velocities, eddies, velocity vortices) can also influence the passability (Katopodis, 2005; Szabo-Meszaros et al., 2018). Whilst hatchery-reared fish may not have experienced the complex and dynamic hydraulic conditions like wild fish, and therefore may have different performance under challenging hydrodynamic conditions, their use allowed for a well-defined and systematic comparison among different species with high replication. In addition, fish protection at hydropower plants by bar screens is not solely based on physically preventing fish from turbine entrainment by small spacings. To allow safe passage without delay for downstream moving fish, other behaviour-influencing factors such as properly angled screens, adequate orientation and shape of the screen bars and, importantly, well-

functioning bypasses in spatial proximity to the screen are of decisive importance (Katopodis, 2005; Larinier and Travade, 2002).

In general, effective physical protection from turbine passage by 15 mm and 20 mm FPSs cannot be realised for a large part of freshwater fish populations (cf. Schwevers and Adam, 2020). This likely not only holds true for Europe, but globally since worldwide the majority of fish populations consists of small-bodied species and small juveniles (e.g. Fu et al., 2004; Kottelat and Freyhof, 2007; Olden et al., 2007) for which these physical barriers are passable. Previous assumptions in the scientific literature that FPSs with bar spacings of 10 to 30 mm can prevent a large proportion of the fish population from passing through (cf. Beck et al., 2019; David et al., 2022) must therefore be critically questioned and tested for plausibility. This is particularly relevant as recent studies indicated that fish mortality at small-scale hydropower plants is not only size-dependent, as suggested in modelling approaches, and injury and mortality rates can even be higher in small fish than in large fish, especially due to barotrauma, turbulence and stress (e.g. Boys et al., 2018; Mueller et al., 2022).

5. Conclusion

It has so far been underestimated that bigger than expected fish sizes can pass physical barriers at turbine inlets. The assessed FPSs with bar spacings of 15 mm and 20 mm could not prevent adult fish of medium-bodied species such as barbel, brown trout and European perch from entering the turbine corridor. In addition, physical fish protection with 15 mm and 20 mm FPSs was not possible for many small-bodied species and juvenile fish, as these physical barriers were passable for a wide range of size classes. As a large part of the downstream moving fish generally consists of small species or small individuals, these fish sizes must be given greater consideration in physical fish protection concepts at hydropower plants. However, since complete physical prevention of all size classes from turbine entrainment will not be feasible, low-harmful turbine technologies should be installed and operational management should be adapted to the locally occurring fish community (e.g. shutdown of turbines, opening of additional downstream corridors and/or increase of discharge to bypasses during peak fish migrations) to reduce the injury and mortality risk during hydropower plant passage.

CRedit authorship contribution statement

Josef Knott: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Visualization, Writing – review & editing. **Melanie Mueller:** Conceptualization, Methodology, Validation, Investigation, Writing – review & editing. **Joachim Pander:** Conceptualization, Methodology, Validation, Investigation, Writing – review & editing. **Juergen Geist:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

We are grateful to the Bavarian Environmental Agency, the hydro-power plant owners, the fisheries rights owners, the fisheries authorities, the TUM animal welfare officers and all field volunteers for their support. Funding: this work was supported by the Bavarian State Ministry of the Environment and Consumer Protection [grant numbers OelB-0270-

45821/2014, OelB-0270-88607/2018].

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2022.106883>.

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