



# Seasonal habitat use of three predatory fishes in a freshwater ecosystem

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**Abstract** To understand the spatiotemporal overlap in the habitat use of sympatric predators, we studied longitudinal activity and reservoir section and depth use of pike (*Esox lucius*), pikeperch (*Sander lucioperca*) and catfish (*Silurus glanis*) in the Římov Reservoir, using an autonomous telemetry system for 11 months. We found significant differences among these species in studied parameters that varied considerably over tracked period. Pike consistently used the same sections of the reservoir, while pikeperch and catfish frequently visited a tributary during the warm season (late spring and early autumn), and

moved closer to the dam during the cold season (late autumn to early spring). Pike longitudinal activity was highest in the cold season, pikeperch in the warm season, and catfish activity peaked in both seasons. Overlap in the depth use among species was higher in the warm season, when all species used the upper layer of the water column, and lower in the cold season, when pikeperch and catfish used deeper areas. These results demonstrated overlay and temporal variation of habitat use among these predators, as well as potential spatiotemporal space for their direct ecological interactions.

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## Introduction

Predators are an essential component of ecosystems because of their regulatory function through top-down control and behaviourally mediated effects on prey species (Carpenter et al., 1985; Kronfeld-Schor & Dayan, 2003; Pelinson et al., 2021). In addition, they are often economically important species. This makes them highly relevant to a variety of stakeholders, including ecosystem service managers, the scientific community and the general public. However, despite the great interest in freshwater predators and their ecology, there is relatively little information on their movement ecology and habitat use, because

tracking their movements in large lentic waters is challenging (Říha et al., 2021; Westrelin et al., 2022).

The spatial distribution of freshwater fish predators and their temporal dynamics are determined by numerous abiotic and biotic factors, as well as individual and species-specific characteristics and stages (Giske et al., 1998). In general, predators should prefer to seek habitats with favourable hunting conditions and prey availability (Hugie & Dill, 1994). These conditions vary among species depending on their hunting strategies and adaptations (Pavlov & Kasumyan, 2002), leading to differences in predator activity and distribution. These interspecific differences reduce competition among sympatric predators and ultimately lead to spatiotemporal interspecific habitat partitioning, with consequences for both predators and prey (Werner et al., 1977; Hughes & Grabowski, 2006).

Knowledge of the spatial and temporal overlap in the distribution of sympatric predators is critical to understanding their interspecific interactions and their effects on prey (Kronfeld-Schor & Dayan, 2003; Guzzo et al., 2016; Lear et al., 2021). Examining where and when different predators spatially overlap can provide information about the space and environmental conditions in which they can potentially interact, as well as the degree of their ecological niche differentiation. Such information is particularly important for understanding the niche partitioning mechanisms that drive coexistence of predator populations (Kronfeld-Schor & Dayan, 2003; Westrelin et al., 2022). Knowledge of the spatial overlap of predators also allows prediction of the ecological consequences of predator coexistence for their prey. Using this information, predation risk in different habitats mediated by various predators can be determined, and the response of prey to different predators can be studied (Gaynor et al., 2019). Knowledge of all this information can ultimately contribute to better management and protection of predator populations (Lear et al., 2021). However, studies demonstrating habitat overlap and its temporal dynamics among sympatric predators are rare in freshwater systems, and spatial overlap among predators therefore remains largely unexplored.

In an ecosystem that provides habitats with different prey availability and different environmental conditions, predators habitat partitioning can be expected according to species-specific environmental

requirements. Canyon-shaped reservoirs are a good example of aquatic ecosystems that provide a wide range of conditions for predators and provide an opportunity to study predator habitat use and their spatial overlap. Canyon-shaped reservoirs are complex systems with characteristic morphological and limnological features. These water bodies usually exhibit longitudinal gradients (from an inlet of an inflowing river to the dam) in various abiotic and biotic factors (Vašek et al., 2016). The most important ones are gradually increasing depth (from shallow, non-stratified tributary to deep, stratified sections near the dam) and decreasing nutrient concentration towards the dam. Such productivity gradients affect the entire system by producing similar gradients in primary producers (algae) and consumers (zooplankton and fish), as well as a wide range of environmental and foraging conditions, from highly trophic, turbid, and prey-rich sections near tributaries to lower trophic and more transparent sections with low prey abundance closer to the dam (Prchalová et al., 2009; Vašek et al., 2016). Thus, different predators with different hunting strategies may be favoured in different longitudinal parts of the reservoir, which can lead to spatial segregation among predator species.

The apex predators pike (*Esox Lucius* Linnaeus, 1758), pikeperch [*Sander lucioperca* (Linnaeus, 1758)], and wels catfish (*Silurus glanis* Linnaeus, 1758) are among the most abundant piscivorous predators in European freshwaters and have high ecological and economic value (Overton et al., 2015; Cucherousset et al., 2018; Skov & Nilsson, 2018). Previous studies have shown that the hunting conditions and movement patterns of these species considerably differ in several aspects of their ecology: (i) in the degree of site fidelity, with fidelity being highest for wels catfish and lowest for pikeperch (Keskinen et al., 2005; Sandlund et al., 2016; Cucherousset et al., 2018), (ii) in preferred hunting conditions, since pike is a visually oriented predator (Skov & Nilsson, 2018), whereas pikeperch and wels catfish hunt at low light intensity (Cucherousset et al., 2018; Jokela-Määttä et al., 2019), and (iii) in temperature preference, with pikeperch and wels catfish being warm-water species, while pike is considered a cool-water species (Feiner & Höök, 2015; Cucherousset et al., 2018; Skov & Nilsson, 2018). In addition, changes in seasonal activity and habitat use have been reported for all three species (Jepsen et al., 1999;

Slavík et al., 2007; Baktoft et al., 2012). Hence, when these three apex predators live in sympatry in a reservoir, a spatial and temporal partitioning driven by the longitudinal environmental gradient and very different ecological traits should be expected. However, the occurrence of longitudinal and vertical partitioning and their temporal dynamics are poorly studied in these important predators (but see Westrelin et al., 2022), and their overlap in longitudinal and vertical reservoir use is not well understood.

To understand whether and how longitudinal movements and depth use differ between pike, pikeperch, and wels catfish in sympatry, we deployed an autonomous telemetry system in the Římov Reservoir (Czech Republic) for 11 months to track the movements of tagged individuals of these species. We hypothesize that (i) pikeperch and wels catfish spend more time in the high-turbidity area near the tributary than pike; (ii) longitudinal space use will be highest for pikeperch and lowest for wels catfish; (iii) pikeperch and wels catfish should prefer shallower depths than pike due to their preference for higher temperatures; (iv) differences among species in the studied parameters should vary temporally, with significant seasonal changes. In this study, we focus exclusively on longitudinal use between the tributary and dam, and use of depth, neglecting horizontal, inshore–off-shore movement, and the diurnal aspect.

## Materials and methods

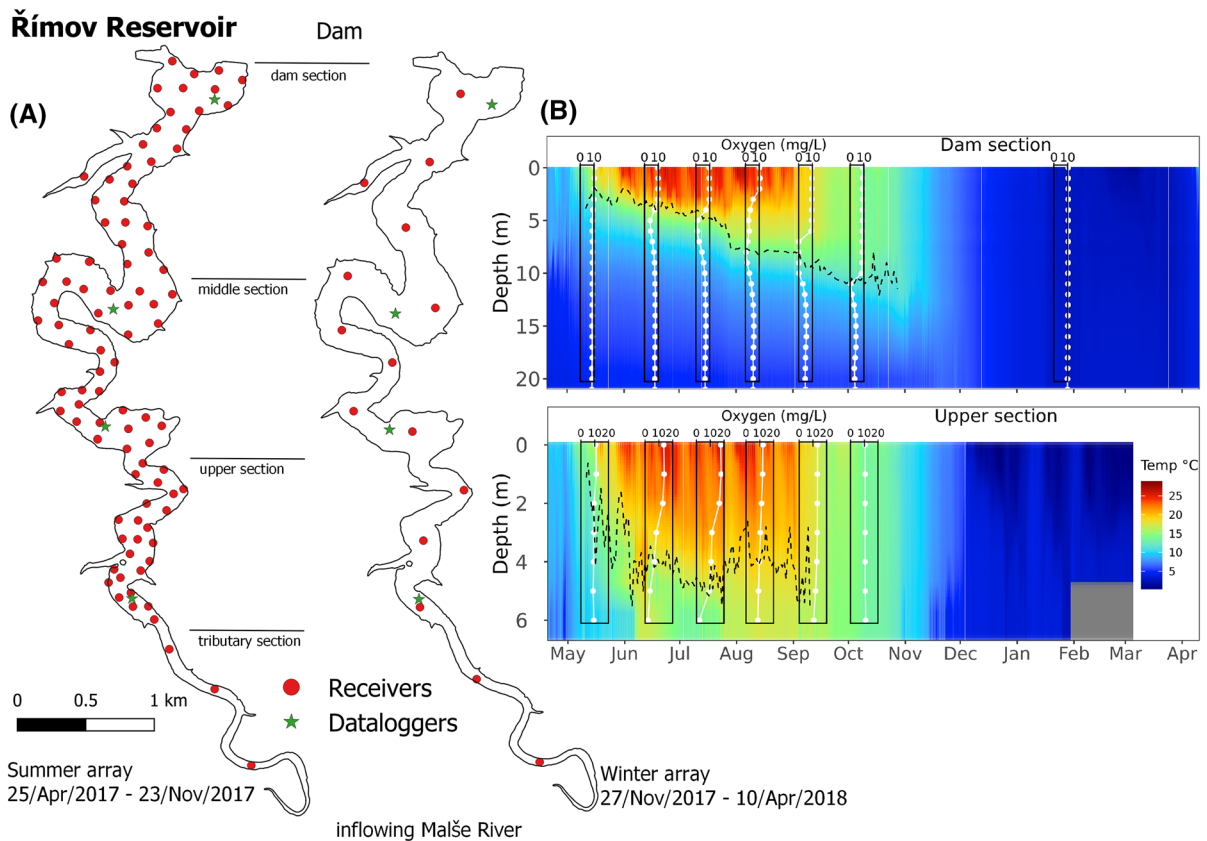
### Study site

This study was conducted in the deep, narrow, canyon-shaped Římov Reservoir, a frequently studied site (Znachor et al., 2016) with a single river inflow and stable abiotic conditions, as well as a well-developed longitudinal productivity gradient (Vašek et al., 2016). The reservoir is located in South Bohemia, Czech Republic (N 48°51.00978', E 14°29.47462'; Fig. 1), and was built for drinking-water storage and flood control. The reservoir was built in 1978 by damming the Malše River. The maximum area of the Římov Reservoir is 210 ha, the maximum volume is 33,106 m<sup>3</sup>, and the maximum depth is 45 m with an average depth of 16 m. The length of the reservoir is about 8.5 km (measured along the central longitudinal axis of

the reservoir) and the maximum surface elevation is 471 m a.s.l. The theoretical mean retention time is about 92 days. The reservoir is dimictic, with summer stratification normally lasting from April to September. Due to steep banks and water-level fluctuations, there are no submerged aquatic macrophytes in the littoral zone. The water-level fluctuations in the reservoir had a rather seasonal character with low day-to-day water-level fluctuation. The difference between the highest and lowest water levels was 1.6 m during the studied period, but the range and mean of day-to-day water-level fluctuation was 0–0.25 m and 0.04 m, respectively. The trophic state of the reservoir is mesotrophic to eutrophic, with phosphorus and chlorophyll-a concentrations decreasing towards the dam (Seda & Devetter, 2000). Algal, zooplankton, and fish densities, as well as turbidity, follow the trophic gradient, with the highest values near the tributary and decreasing towards the dam (Vašek et al., 2016).

### Fish tagging

A total of 15 pike and 20 pikeperch individuals were caught by electrofishing and 15 wels catfish individuals by long-lining. Electrofishing was performed using a boat electrofisher system similar to that described by Miranda & Kratochvíl (2008). Electro-fishing was conducted by steering the boat at slow speed along the shoreline. Pike were caught along the entire reservoir shore; pikeperch were caught at two locations in the reservoir (Supplementary Material Fig. S1). Long-lining was performed at four locations in the reservoir (Supplementary Material Fig. S1) following the methodology described by Vejřík et al. (2017). After capture, all individuals were anaesthetized with 2-phenoxy-ethanol (SIGMA Chemical Co., USA, 0.7 ml l<sup>-1</sup>, mean residence time in an anaesthetic bath 3.75 min), measured, weighed, and tagged. A 1–1.5 cm incision was made on the ventral surface posterior to the pelvic girdle and a transmitter (Lotek Wireless Inc., MM-M-11-28-TP, 65 × 12 mm, mass in air 13 g, including pressure and temperature sensors, burst rate 15 s) was inserted through the incision and advanced into the body cavity. The incision was closed with two separate sutures. The mean surgery time was 3 min. All fish were released immediately after recovery from the anaesthesia at the site where



**Fig. 1** **A** Positions of the two telemetry arrays and dataloggers deployed in the Římov Reservoir. **B** Development of water column temperature and oxygen stratification at the dam and upper sections throughout the whole tracking period (note that,

at the dam, where maximum depth is 42 m, the data loggers were deployed at 20 m depth). The thermocline is represented by a dashed line

they were captured. Fish were caught and tagged between April 18 and 25, 2017. Details of the tagged and analysed fish are summarized in Table 1.

**Fish tracking**

MAP positioning system (Lotek Wireless Inc., Canada) was deployed in the reservoir to locate tagged fish. Two different arrays of receivers were deployed

**Table 1** Description of tagged fish in the Římov Reservoir

Species	NTa/NAn	TL (cm)/W (kg) of analysed individuals (individuals excluded prior to analyses)				Ratio of tag weight to body weight (%)		
		Mean	SD	Min	Max	Mean	Min	Max
Pike	15/10	70/2.9 (62/2.0)	17/2.8 (14.9/2.0)	50/0.8 (49/0.7)	116/10.9 (88/6.3)	0.5	0.1	1.8
Pikeperch	20/7	49/1.0 (51/1.2)	6/0.4 (8.8/0.7)	40/0.5 (39/0.4)	56.5/1.6 (66/2.7)	1.1	0.5	2.9
Wels catfish	15/14	117/12.3 (81/3.4)	26/9.5	86/3.8 (81/3.4)	166/35 (81/3.4)	0.1	0.03	0.3

NTa stands for the number of tagged individuals, NAn for the number of analysed individuals (5 pike, 13 pikeperch, and 1 wels catfish tagged were not included into analyses, as their positions remained constant with no movement and those individuals died or expelled tag). Ratio of tag weight to body weight was calculated for all tagged individuals

sequentially in the reservoir during the tracking period to address the unique challenges of tracking fish in different seasons.

The first array was deployed in the reservoir from the start of tracking on April 18, 2017, through November 20, 2017 (hereafter referred to as the summer array). This array consisted of a total of 90 receivers (Lotek Wireless Inc., WHS3250) deployed to provide complete coverage and fine-scale positioning of the entire reservoir (86 receivers), with the exception of the near tributary and the small bay near the dam (Fig. 1). Individual receivers were placed in the near tributary area (3 receivers) and in the small bay (1 receiver) to obtain presence data from these areas. The distance between neighbouring receivers throughout the array was 80–300 m. The exact positions of the deployed receivers were measured using a differential instrument GPS, Spectra Precision, Promark 220 (USA). Based on range tests conducted prior to the reservoir survey (November 2016), this receiver array was arranged to provide fine-scale position data from the entire reservoir area, with the exception of the nearby tributary and small bay, which were monitored by individual receivers. Range tests also indicated that the detection range of these individual receivers was approximately 265–410 m. The accuracy of the system was monitored using 22 stationary reference tags (Lotek Wireless Inc., Canada, model MM-M-16-50-TP, burst rate 25 s) placed at 7 locations (at depths of 1, 5, and 10 m at all sites and additionally at 20 m depth near the dam). In addition, the accuracy of the entire system was tested after deployment (July 2017) and before final recovery of the system (November 2017) by dragging the reference tags across the reservoir by boat. Reference tags were dragged in three depths of 1, 3, and 8 m by an average speed of 0.7 m/sec.

The second arrangement of the receiver array was deployed from 27 November 2017 to 10 April 2018 (referred to here as the winter array, Fig. 1). The winter array consisted of 15 receivers (of the same type as in the summer array) distributed along the centre line of the reservoir to track fish movement along the longitudinal axis of the reservoir at a lower resolution. The reason for the lower resolution in winter was the inability to maintain the entire summer array when the reservoir was covered by ice. The performance and detection capability of the winter array were tested in December 2017 by dragging 3 reference tags

(at a depth of 3 m with an average speed of 1.2 m/sec) across the reservoir from a boat. The test showed that the detection range of the receivers was between 343 and 1234 m, with a mean range of  $750 \pm 261$  m. Individual and total yield of fish locations during the study period is provided in the Supplementary material (Table S1).

#### Temperature and oxygen monitoring

To obtain abiotic parameters that could influence the spatial distribution of the tracked species, we monitored water temperature and oxygen concentration in the reservoir. Water temperature was monitored using 60 data loggers (Onset, USA, HOBO Pendant temp/light 64 K). The data loggers were placed at four locations to cover the longitudinal axis of the reservoir (Fig. 1). At each location, the data loggers were attached at 1-m intervals to a rope that extended from the surface to a depth of 13 m (data logger locations in the dam and middle section) and down to 6 m (data logger in the upper section). An additional data logger was located at a depth of 20 m (data logger locations in the dam and middle sections). The rope was attached to a floating buoy anchored to the bottom. This arrangement ensured both dense coverage at depths with rapid temperature changes and, with a 5-min measurement interval, high spatial and temporal resolution of the temperature profile. The depth of the thermocline was calculated using the R package *rLakeAnalyzer* (Read et al., 2019), specifically the *thermo.depth* function.

Oxygen concentration was measured at every data logger location each week during the summer array deployment and once during the winter array deployment (February 2018) using a calibrated YSI 556 MPS probe (YSI Incorporated, USA).

#### Data processing

For the fine-scale summer array, individual horizontal fish locations were first calculated using the manufacturer's proprietary positioning software UMAP v.1.4.3 (Lotek Wireless Inc., Canada). Fish depth was recorded from the tag's internal sensor, which has a resolution of 0.7 m. In the next step, raw horizontal locations were filtered using a series of general additive models (GAM) and only locations that exceeded a threshold of 75 m beyond the final GAM

were included in the analysis (details in Říha et al., 2021). The next step was to visually inspect the location estimates (unfiltered and filtered) and depth profiles of each fish. If both horizontal and vertical positions remained constant with no fish movement, this was interpreted as either a dead individual or a tag that was expelled, which was the case for 5 pike, 13 pikeperch, and 1 wels catfish that were removed from further analyses.

In the final step, horizontal locations were projected onto the longitudinal centre line of the reservoir by the shortest distance from the position to the line. The longitudinal distance from the dam to the projected point along the centre line was then calculated. For individual summer receivers (i.e. those near the tributary and a small bay), the position of each receiver was projected onto the centre line of the reservoir, and the distance from the dam along the centre line to these projected points was used as the longitudinal distance from the dam for individual fish detected by these receivers.

For the winter array, the distance of fish from the dam was calculated similarly to the individual receivers in summer. However, in some cases, receiver detection ranges overlapped and duplicate detections occurred, i.e. an individual was detected by two or three receivers at the same time. In such cases, the detection with the highest power value (detected in RSSI units, Received Signal Strength Indicator) was included in the analyses and the remaining detections were discarded because we assumed that the distance between the fish and the receiver was inversely related with signal power.

### Statistical analyses

Three space use parameters were calculated: use of different parts of the reservoir, use of depth and longitudinal activity. To calculate the use of reservoir sections, fish horizontal locations were discretized using the categories developed for the Římov Reservoir by Prchalová et al. (2009), with the reservoir divided into dam (0–1800 m from dam), middle (1800–5200 m), upper (5200–6600 m), and tributary area (6600–8650 m; Fig. 1; for more details about characteristics of each section see Prchalová et al., 2009). Fish depth locations were discretized from 0–1 to greater than 10 m (0–1, 1–2, 2–3, 3–5, 5–7, 7–10, > 10 m). Although our time series contains

data points 15 s apart, we use daily averages for both use of reservoir section and depth. This is a fairly acceptable proxy that still ensures a high number of repeated measurements across all individuals and allows us to focus on seasonal patterns of daily use when daily trends are relevant. Data were grouped by the identity of the individual (fishID) and whether they were in a particular section of the reservoir or at a particular depth, and the daily average was calculated. Both average daily use of reservoir sections and daily residence time of individual fish at a given depth were calculated by season, categorically coded (spring I—late spring: April 27–June 21, 2017; summer: June 21–September 22, 2017; autumn: September 22–December 21, 2017; winter: December 21, 2017–March 20, 2018; spring II—early spring: March 20, 2018–April 10, 2018), and species (pike, pikeperch, and wels catfish). Longitudinal activity was defined as the difference between the maximum and minimum distance from the dam, for each individual per day separately, thus indicating the daily range of longitudinal movement. All analyses were performed using R software version 3.6.3 (R Development Core Team, 2020).

### *Reservoir section and depth use*

Cumulative link mixed-effects models (CLMMs) were used to examine the effects of seasonality and temperature on reservoir section (CLMM<sub>res</sub>) and depth (CLMM<sub>depth</sub>) use by the three species. CLMMs are a special class of general linear mixed-effects models that account for the effects of predictors on an ordered categorical outcome fitted with a logit link function (see Supplementary Material for more details on CLMM parameterization). The response variables analysed were (1) reservoir section use (res\_sec\_use) and (2) depth use (depth\_use), both categorised as given above and coded as ordinal variables. CLMMs were fitted using the *clmm* function of the R package “ordinal” (Christensen, 2019).

To estimate the differential effects of season and species on reservoir section use and depth, we first used a likelihood-ratio test to compare a model with the interaction between the categorical variables season and species (to a main effects only model without the interaction that was eventually included in the model when supported). The fish identity (fishID)

was included as a random intercept value to account for variability among fish.

From the two fitted CLMMs, we calculated the probability of using a particular reservoir section or depth according to the odds ratio (OR) between levels of the dependent variable (see Supplementary Material for more details on the parameterization of the CLMMs and the calculation and interpretation of OR).

The Ivlev electivity index  $E_i$  (Ivlev 1961) was used to evaluate the preference of the three species for each reservoir section and the seasonal changes in this preference in a spatially standardised manner among reservoir sections according to  $E_i = (r_i - p_i)/(r_i + p_i)$ , where  $r_i$  represents the relative utilization of reservoir section  $I$ , derived from the probabilities estimated by the CLMMres model, and  $p_i$  represents the relative availability of the section, given by the ratio of the section area to the total area of the reservoir. The range of values of  $E_i$  is from  $-1$ , indicating less use of reservoir section  $I$  than its availability relative to the total area of the reservoir, to  $1$ , indicating excessive use of the reservoir section, with intermediate values indicating proportional use of the section relative to its area.

### Longitudinal movement

We examined differences in longitudinal movements of pike, pikeperch, and wels catfish from April 2017 to April 2018 and the effects of body length. Because our data span was only one year and due to the lack of variability among years, we modelled the time series as a long-term trend based on a daily basis to keep quite a good accuracy of fish locations. The resolution of these locations would have been coarse if we had chosen a seasonal basis. Therefore, the time series included observations over the day of the year (with day 1 on 27 April 2017), while seasonality was graphically interpolated from the corresponding data. To trend the data for each species, we used a generalized additive mixed-effects model (GAMM) with a smooth function for time and a random smooth function for fish identity as  $\text{random} = \text{list}(\text{fishID} \sim 1)$  to account for individual repeated measures over time. All GAMMs were fitted separately as  $\text{GAMM}_{\text{pike}}$ ,  $\text{GAMM}_{\text{pikeperch}}$ , and  $\text{GAMM}_{\text{catfish}}$  using Restricted Maximum Likelihood Estimation (REML) with Gaussian error distribution and identity linkage

function with the *gamm* function from the package “mgcv” (Mixed GAM Computation Vehicle with Automatic Smoothness Estimation, Wood, 2021). The equation of this model can be expressed as follows:

$$g(E[\text{range}_i]) = \beta_0 + f(\text{time}_i) + f(\text{bl}) + \text{fish ID}_i + \varepsilon_i, \varepsilon_i \sim WN(0, \sigma^2), y_i \sim EF(\mu, \phi). \quad (1)$$

### Identification of periods with significant changes

We performed a functional data analysis to examine how the longitudinal range changed over time. To identify periods with significant upward and downward trends, i.e. the rate of change (slope) of the nonlinear time trend, the periods with statistically significant changes were determined using the finite difference method. In this approach, the value of the fitted spline function for the trend component is determined by calculating the first derivative at a time  $t$ , i.e. the slope between each two closely spaced time points is given by

$$f'(t_1) \approx \frac{f(t_1 + t_2) - f(t_1)}{t_2}. \quad (2)$$

The first derivative gives an idea of the change in response relative to the change between these two adjacent time points, which would represent the expected differences in longitudinal trends (see Supplementary Material for more details on first-derivative calculations).

### Smooth differences between species

Using the entire dataset, we created a new GAMM ( $\text{GAMM}_{\text{sp\_diffs}}$ ) to examine the variation in horizontal movement from the dam among the three species at different times of the year. The “species” factor was included in the model for the time-spline function with the argument “by” ( $s(\text{time}, \text{by} = \text{species})$ ), which denotes a smoothing factor interaction ( $\text{time} \times \text{species}$ ). This interaction fits a separate smoothing for each species with its own smoothing parameter ( $\lambda_i$ ) and penalty term, and allows us to estimate the difference between the fitted trends. Because each estimated smoothing function is subject to identifiable constraints (i.e. each with a separate penalty that

shrinks it towards the null effect) to identify periods with significant differences in longitudinal movement, we also included the “species” factor as a parametric term to estimate the mean of the longitudinal range for each species. By expanding Eq. (1), the formula of this model is expressed as follows:

$$g(E[\text{range}_i]) = \beta_0 + \beta_j(\text{species}_j) + f(\text{time}_i \times \text{species}_j) + f(b) + \text{fish ID}_i + \varepsilon_i, \quad (3)$$

where  $\beta_j$  is the mean intercept value of the response for a given level of species<sub>*j*</sub>.

The *plot\_diff* function from the package “itsadug” (van Rij et al., 2017) was applied to the model to determine the differences between each pair of the three estimated smoothings (see Supplementary Material for more details).

## Results

### Use of reservoir sections

Considering the average use of reservoir sections over time for the three species, there were significant changes between seasons, except between winter and early spring (least-squares means, LSM, of pairwise comparisons across seasons  $\pm$  SE:  $0.20 \pm 0.12$ ,  $z=1.71$ ,  $P=0.43$ ) and between autumn and winter (LSM:  $-0.15 \pm 0.06$ ,  $z=-2.57$ ,  $P=0.08$ ; Table 2; and S2, S5 in Supplementary Material). The pattern of reservoir section use was similar for pikeperch and wels catfish (Fig. 2), and both species preferred the middle section in autumn, winter, and early spring, although wels, unlike pikeperch, also used the upper section in early spring. However, as predicted by the model, the upper section and tributary were more heavily used in late spring ( $P(Y_j \geq 3) \pm$  SE: upper reservoir-pikeperch:  $0.38 \pm 0.09$ , wels catfish:  $0.32 \pm 0.08$ ; tributary-pikeperch:  $0.15 \pm 0.10$ , wels catfish:  $0.10 \pm 0.05$ ) and in summer (upper reservoir-pikeperch:  $0.30 \pm 0.12$ , wels catfish:  $0.28 \pm 0.09$ ; tributary-pikeperch:  $0.09 \pm 0.06$ , wels catfish:  $0.08 \pm 0.04$ ; Table 3). The change in preference for middle and upper (upper and tributary) sections with a significant trend of change between these two seasons was significant for pikeperch (LSM of seasonal differences  $\pm$  SE:  $0.53 \pm 0.12$ ,  $z=4.42$ ,  $P=0.001$ ), but not for wels catfish (LSM:  $0.22 \pm 0.08$ ,  $z=2.89$ ,

$P=0.20$ ). Pike used sections of the reservoir similarly throughout the tracking period, except in early spring (Fig. 2). From late spring through winter, pike preferred the middle section and tended to avoid the dam and upper sections. In early spring, they preferred both the dam and middle section (LSM over season  $\times$  species:  $1.14 \pm 0.20$ ,  $z=5.57$ ,  $P<0.001$ ; Figs. 2; and S2, S5 in Supplementary Material).

### Longitudinal movement

The range of the total explored reservoir area throughout the tracking period did not differ significantly among species (ANOVA,  $P=0.92$ ). Most individuals of all three species ranged from 50 to 75% of the reservoir extent (4.2–6.4 km). Intraspecific differences were greater than interspecific differences and slightly higher for pike (15–91%; 1.3–7.8 km) and wels catfish (17–91%; 1.5–7.8 km) than for pikeperch (37–94%; 3.2–8 km).

The temporal pattern of longitudinal activity differed among species (smooth functions of long-term trends were significant in all fitted models and significantly varied among species; Tables 3, 4; Fig. 3A). Body length had no effect on longitudinal activity of any species (Likelihood-ratio test,  $\chi^2_{27, 13}=2.03$ ,  $P=0.67$ ), so it was ultimately not included in the final models. Wels catfish covered the greatest average longitudinal distance per day (mean  $\pm$  SE:  $0.99 \pm 0.09$  km/day,  $t=10.55$ ,  $P<0.001$ ), followed by pike ( $0.90 \pm 0.11$  km/day,  $t=8.045$ ,  $P<0.001$ ) and finally pikeperch ( $0.77 \pm 0.13$  km/day,  $t=5.75$ ,  $P<0.001$ ).

Analysis of the first derivative of the rate of change of longitudinal movements over time revealed several periods of significant (decreasing or increasing) change (Fig. 3B). Pike longitudinal activity decreased significantly in late spring (April 27–May 30), increased slightly at the beginning of summer (June 18–27), and increased again significantly in autumn (October 3–November 19) before decreasing for nearly two weeks (January 4–16). This was followed by an increase from mid-winter to early spring (February 5–March 13) before declining significantly (March 27–April 11; Fig. 3B). It is worth noting that the increase was much stronger in winter than in autumn, peaking around February 25.

Pikeperch activity increased significantly in late spring and early summer (May 23–June 27), peaked



**Table 2** Summary of the cumulative link mixed model predicting differences in use of reservoir sections by pike, pikeperch, and wels catfish across seasons from April 2017 to April 2018

Variable	OR [95% CI]	z value	P value
Res_sec (thresholds)			
$\theta_1$ (dam/middle)	0.23 [0.06–0.95]	– 2.02	<b>0.043</b>
$\theta_2$ (middle/lupper)	5.21 [1.27–21.36]	2.29	<b>0.022</b>
$\theta_3$ (upper/tributary)	33.43 [8.14–137.37]	4.87	<b>&lt; 0.001</b>
Species			
$\beta_1$ (pike) (ref.)	–	–	–
$\beta_1$ (pikeperch)	5.81 [0.75–45.05]	1.68	0.092
$\beta_1$ (wels catfish)	3.72 [0.61–22.74]	1.42	0.154
Season			
$\beta_2$ (spring I) (ref.)	–	–	–
$\beta_2$ (summer)	0.95 [0.78–1.17]	– 0.47	0.640
$\beta_2$ (autumn)	1.13 [0.91–1.39]	1.09	0.273
$\beta_2$ (winter)	1.07 [0.86–1.33]	0.58	0.56
$\beta_2$ (spring II)	0.34 [0.23–0.52]	– 5.12	<b>&lt; 0.001</b>
Species × Season			
$\beta_3$ (Northern pike × spring I) (ref.)	–	–	–
$\beta_3$ (pikeperch × summer)	0.62 [0.45–0.84]	– 3.04	<b>0.002</b>
$\beta_3$ (wels catfish × summer)	0.84 [0.66–1.08]	– 1.33	0.183
$\beta_3$ (pikeperch × autumn)	0.12 [0.09–0.17]	– 11.93	<b>&lt; 0.001</b>
$\beta_3$ (wels catfish × autumn)	0.21 [0.16–0.27]	– 11.68	<b>&lt; 0.001</b>
$\beta_3$ (pikeperch × winter)	0.18 [0.13–0.26]	– 9.33	<b>&lt; 0.001</b>
$\beta_3$ (wels catfish × winter)	0.26 [0.20–0.34]	– 9.84	<b>&lt; 0.001</b>
$\beta_3$ (pikeperch × spring II)	0.58 [0.31–1.11]	– 1.65	0.099
$\beta_3$ (wels catfish × spring II)	1.36 [0.82–2.26]	1.19	0.240
Random Effects			
$\sigma^2$	3.29		
$\tau_{00}$ fishID	3.99		
ICC	0.55		
$N_{\text{fishID}}$	31		
Marginal $R^2$ /Cond. $R^2$	0.052/0.572		

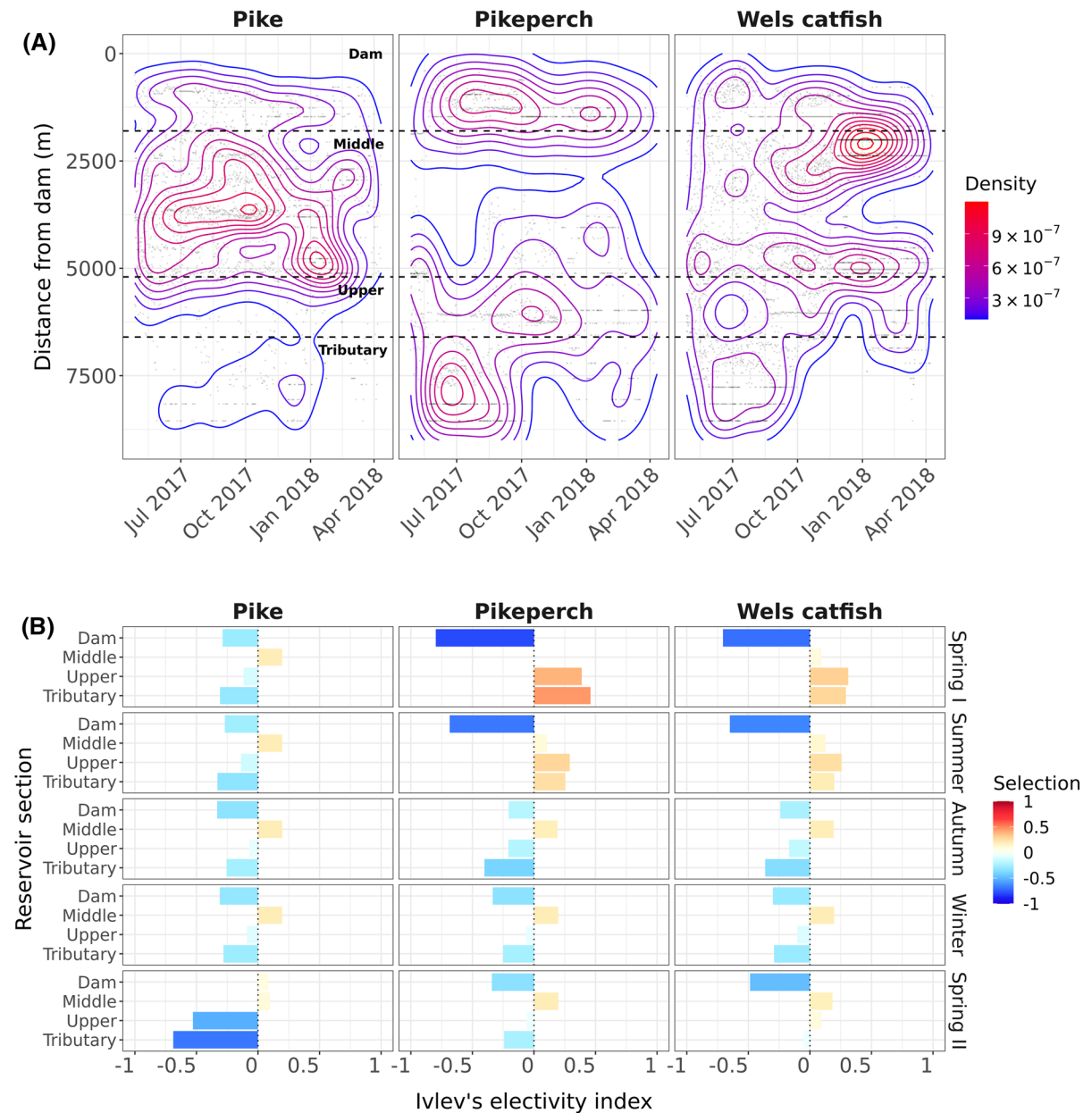
Numbers represent odds ratios (OR) and 95% confidence intervals (95% CI) (see supplemental material for odds ratio calculation and interpretation). res\_sec is an ordinal dependent variable used to fit the CLMMres model, with  $k=4$  categories related to different reservoir sections, where  $\theta_k$  is the cumulative probability of using each category (dam, middle reservoir, upper reservoir, and tributary).  $\beta_1$ – $\beta_3$  are exponentials of the estimated fixed effects regression coefficients for each of the interaction covariates species × season (see main text and Supplementary Information for a description of the variables and model fit). Random effects are represented by the individual intercepts for fish identity tag (fishID) ( $\tau_{00}$ ) and residual variance ( $\sigma^2$ ). ICC is the intraclass correlation coefficient, which measures the degree of repeatability at the individual level. Marginal  $R^2$ /Cond.  $R^2$  are marginal and conditional r-squared values that refer to the proportion of variation explained by fixed effects and the variance explained by fixed and random effects, respectively

In bold,  $P < 0.05$

in July, and then declined significantly and steadily during a month in summer (July 4–August 4) and during a longer period from late summer through mid-autumn (August 31–November 26). Pikeperch activity increased significantly during mid-autumn (November 12–December 5), but remained

consistently low during winter and early spring, and increased again during a month from late winter to early spring (March 10–April 11; Fig. 3B).

Wels catfish activity showed a significant downward trend in late spring through the beginning of summer (May 14–June 25), followed by a significant



**Fig. 2** **A** Density of locations of all tagged individuals as a function of distance from the dam and time. **B** Seasonal preference for different sections of the Římov reservoir by Northern pike, pikeperch, and wels catfish, estimated with the Ivlev's electivity index as a function of the proportion of a section used (on the y-axis) and the relative availability of the section with respect to the total area of the reservoir. Relative use of a section was estimated from cumulative probabilities using

a cumulative link mixed-effects model analysis (CLMM<sub>res</sub>), which sets the dam as the starting point of the measured longitudinal migration distance. Negative  $E_i$  values indicate that a reservoir section is avoided relative to its proportional availability, positive values indicate that this section is preferred, with 1 indicating overuse, and zero values indicate proportional use of the section relative to its area

**Table 3** Results of generalized additive mixed model analysis of differences in longitudinal movements of pike, pikeperch, and wels catfish from April 2017 to April 2018. The model(GAMM<sub>sp\_diffs</sub>) was fitted with a separate smoothing trend for each species by including a factor smoothing interaction term in the time-spline function (s(Time))

A. Parametric coefficients	Estimate	Std. Error	<i>t</i> value	<i>P</i> value
(Intercept)	0.90	0.11	8.04	<b>&lt; 0.001</b>
Pikeperch	− 0.13	0.17	− 0.75	0.453
Wels catfish	0.10	0.15	0.65	0.514
B. Smooth terms	edf	Ref.df	F value	<i>P</i> value
s(Time) × pike	7.20	8.00	92.95	<b>&lt; 0.001</b>
s(Time) × pikeperch	5.74	8.00	116.86	<b>&lt; 0.001</b>
s(Time) × wels catfish	7.61	8.00	42.47	<b>&lt; 0.001</b>
s(fishID)	27.44	28.00	52.55	<b>&lt; 0.001</b>
R <sup>2</sup> adj	0.21			
Deviance explained (%)	21			
Scale parameter ( $\phi$ )	0.64			

To avoid limitations in model identifiability, species was also included as a parametric term in the analysis. Fish identity (fishID) was included as random smooth intercepts to account for variability among fish (see Statistical analysis for more details on model fit). R<sup>2</sup> adj, adjusted r-squared.  $\phi$  is the estimated scale parameter associated with the variance of random effects

In bold,  $P < 0.001$

**Table 4** GAMM analysis of longitudinal data on pike, pikeperch, and wels catfish movements from April 2017 to April 2018

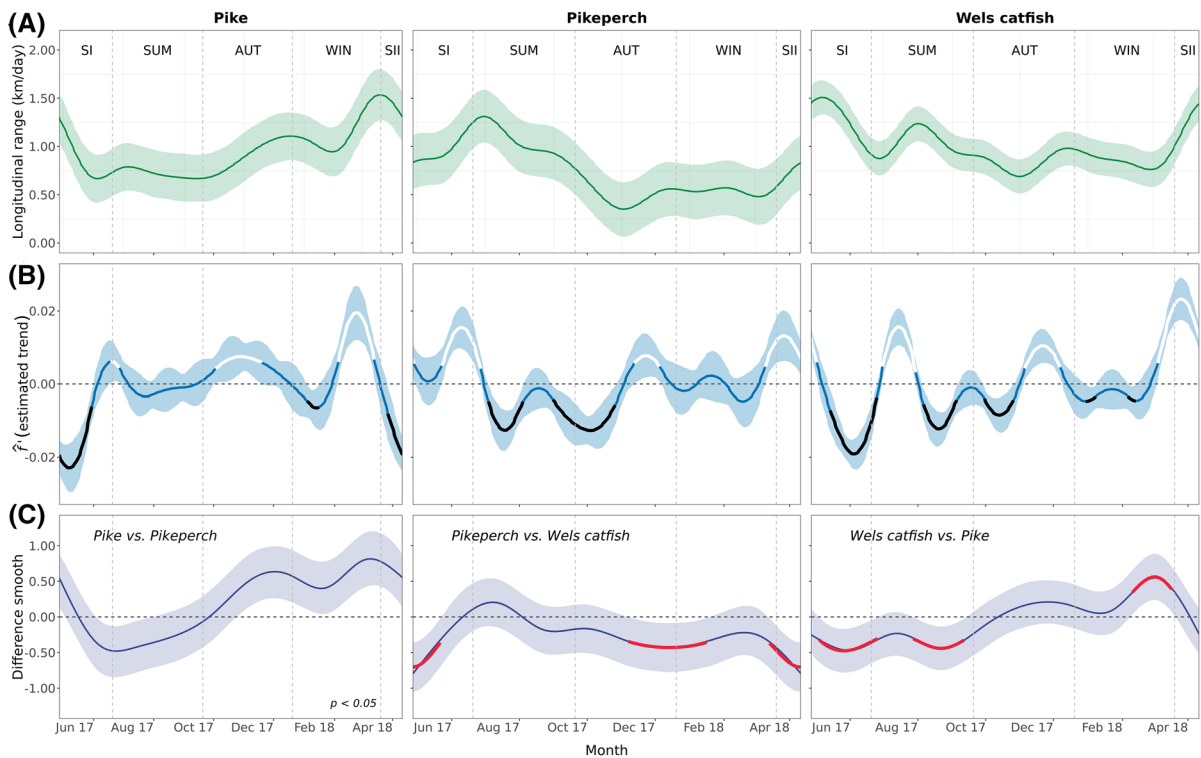
Model	Intercept	s(Time)	s(fishID)	R <sup>2</sup> adj	Scale est. ( $\phi$ )
GAMM <sub>pike</sub>	0.89* (0.12)	7.16*	8.79*	0.21	0.71
GAMM <sub>pikeperch</sub>	0.79*(0.13)	6.43*	5.89*	0.26	0.54
GAMM <sub>catfish</sub>	0.99* (0.08)	7.51*	12.69*	0.16	0.65

Models (GAMM<sub>pike</sub>, GAMM<sub>pikeperch</sub>, GAMM<sub>catfish</sub>) were fitted separately for each species dataset using a cubic regression spline for the smooth function of time trend (s(Time)) and a random smooth function for fish tag identity (s(fishID)) (see Statistical Analysis for more details on model fitting). Numbers for the parametric components (intercept) refer to estimates (standard errors). The numbers for the smoothing components refer to the estimated effective degrees of freedom (edf), which reflect the degree of nonlinearity/complexity of the relationship between a covariate and the response.  $\phi$  is the estimated scale parameter estimated from a GAMM in conjunction with the random effects variance. R<sup>2</sup> adj, adjusted r-squared. \* $P < 0.01$

increase in July (June 30–July 30). Thereafter, activity declined significantly and bottomed out during two consecutive periods (August 6–September 5 and September 30–October 26). Activity resumed in early November (November 5–December 7), followed by two short periods of about a week with significantly lower activity (December 30–January 8 and February 6–February 12). Finally, there followed a period of significantly increased activity from late winter to late spring (March 5–April 11), peaking in April (Fig. 3B).

Trend analysis (GAMM<sub>sp\_diffs</sub>) revealed exact periods of significant differences among species in their longitudinal activity (Fig. 3C). Pike had

significantly higher activity than pikeperch from mid-autumn (October 27) to late spring (April 11) and lower activity from the end of late spring (June 4) to mid-summer (July 31) (difference smooth: 5.70,  $F = 116.34$ ,  $P < 0.001$ ). Pike had significantly lower activity than wels catfish from late spring (May 4) to the beginning of summer (June 25) and from mid-summer (July 27) to the end of summer (September 11) and higher activity from mid-winter (February 10) to the end of winter (March 17) (difference smooth: 7.60,  $F = 41.77$ ,  $P < 0.001$ ). Lastly, pikeperch was significantly less active than wels catfish in late spring (April 27 to May 21), from mid-autumn 2017 (November 6) to mid-winter 2018 (January 16)



**Fig. 3** **A** Effect of smooth time functions on longitudinal movement ( $\text{km day}^{-1}$ ) of pike, pikeperch, and wels catfish in Římov Reservoir in different seasons. The fitted spline with 95% confidence interval (CI, shaded area) represents the average trend effect from April 2017 to April 2018 based on the additive mixed-effects models (Table 4). **B** Rate of change in longitudinal movements over time, determined from the estimated first derivative of the fitted trend spline function from each of the above GAMMs. The periods of statistically signifi-

cant increasing (thick white) and decreasing (thick black) rates of change in the trend series are depicted. The shaded area is the 95% simultaneous confidence interval calculated using posterior Bayesian simulations for the data predicted from the models. **C** Estimation of smooth differences (95% CI, shaded area) in longitudinal movement trends among species using the  $\text{GAMM}_{\text{sp\_diffs}}$  model (Table 3). Periods where the value zero (horizontal line) is not included in the 95% CI indicate significant differences between two species (outlined by a red line)

and from end of winter (March 13) to beginning of spring (April 11), (difference smooth: 7.20,  $F=92.95$ ,  $P<0.001$ ).

### Depth use

Thermal stratification of water column was well developed from May to end of October. The thermocline developed in the depths of 3–4 m in May and July, ranged from 4 (July) to 8 m (end of August) in summer and declined to depths from 9 m (September) to 11 m (end of October) in early autumn (Fig. 1).

Considering the average use of depth over time for the three species, no significant differences were found in late spring (spring I) and summer (LSM over

season  $\times$  species: all,  $P>0.1$ ), i.e. when they used more intensively the epilimnetic part of the water column up to 5 m (Table 5 and S3, Supplementary Material; Fig. 4). However, within this range, the near-surface region (depth 0–2 m) was used more in late spring than in summer (LSM across seasons  $\pm$  SE:  $-1.5 \pm 0.05$ ,  $z=-21.85$ ,  $P<0.001$ ), as predicted by the model ( $P(Y_j \leq 2) \pm$  SE: spring I:  $0.35 \pm 0.02$  vs. summer:  $0.27 \pm 0.02$ ) and use of the shallowest waters (up to 1 m depth) decreased significantly from late spring to summer for all species [OR 6.2 (5.09–7.55),  $P<0.001$ ]. A similar pattern to late spring was observed in early spring for pike and pikeperch, while wels catfish showed a gradually increasing probability of using greater depths up to 10 m in early spring [OR 161.09 (94.84–273.62),  $P<0.001$ ], with 7–10 m

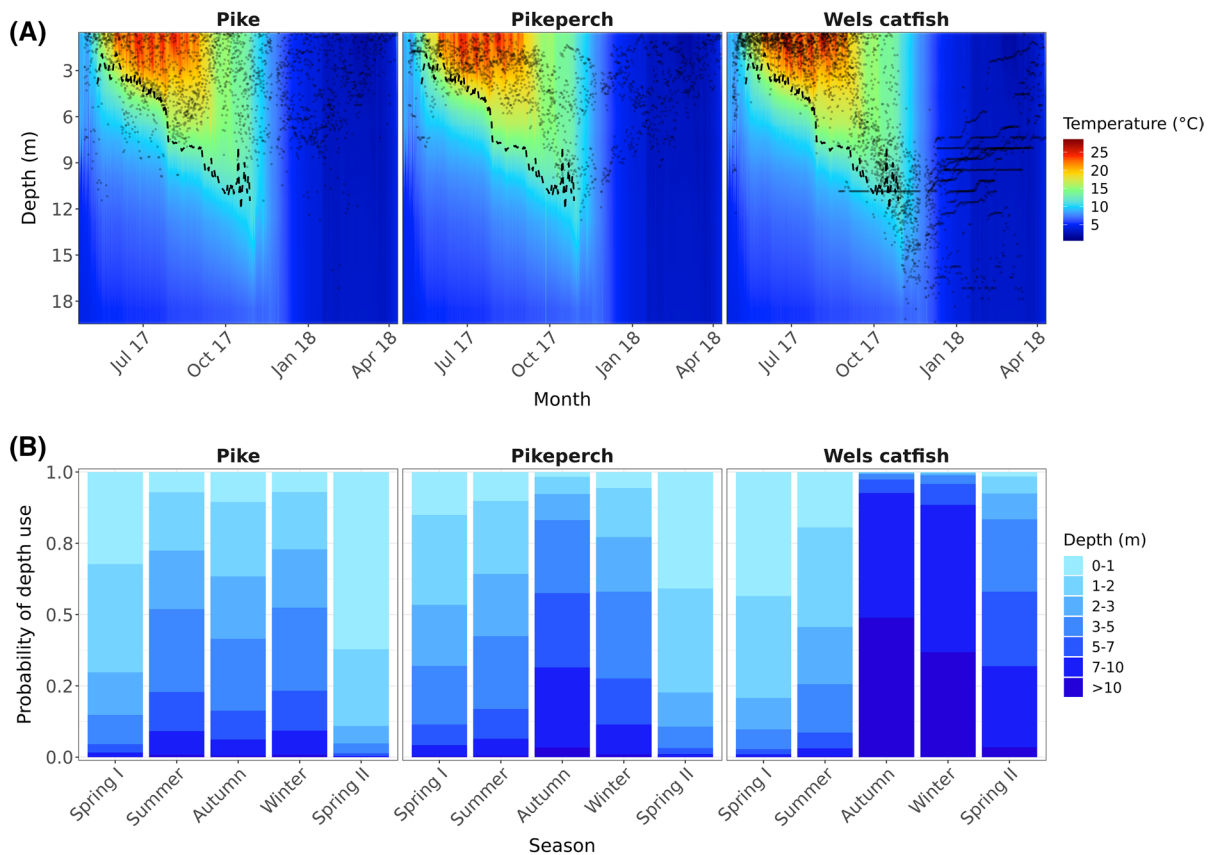
**Table 5** Summary of cumulative link mixed model predicting differences in depth use by Northern pike, pikeperch, and wels catfish across seasons from April 2017 to April 2018

Variable	OR [95% CI]	Z value	P value
Depth_use (thresholds)			
$\theta_1$ (0-1 m 1-2 m)	0.48 [0.25–0.89]	– 2.31	<b>0.021</b>
$\theta_2$ (1-2 m 2-3 m)	2.36 [1.26–4.42]	2.67	<b>0.008</b>
$\theta_3$ (2-3 m 3-5 m)	5.75 [3.06–10.80]	5.44	<b>&lt;0.001</b>
$\theta_4$ (3-5 m 5-7 m)	20.9 [11.11–39.32]	9.43	<b>&lt;0.001</b>
$\theta_5$ (5-7 m 7-10 m)	61.68 [32.72–116.25]	12.75	<b>&lt;0.001</b>
$\theta_6$ (7-10 m > 10 m)	814.86 [428.79–1548.54]	20.46	<b>&lt;0.001</b>
Species			
$\beta_1$ (pike) (ref.)	–	–	–
$\beta_1$ (pikeperch)	2.7 [1.01–7.21]	1.98	<b>0.047</b>
$\beta_1$ (wels catfish)	0.62 [0.27–1.41]	– 1.14	0.254
Season			
$\beta_2$ (spring I) (ref.)	–	–	–
$\beta_2$ (summer)	6.2 [5.09–7.55]	18.15	<b>&lt;0.001</b>
$\beta_2$ (autumn)	4.08 [3.32–5.01]	13.45	<b>&lt;0.001</b>
$\beta_2$ (winter)	6.35 [5.12–7.86]	16.89	<b>&lt;0.001</b>
$\beta_2$ (spring II)	0.29 [0.19–0.45]	– 5.43	<b>&lt;0.001</b>
Species × Season			
$\beta_3$ (pike × spring I) (ref.)	–	–	–
$\beta_3$ (pikeperch × summer)	0.25 [0.19–0.33]	– 10.02	<b>&lt;0.001</b>
$\beta_3$ (wels catfish × summer)	0.51 [0.41–0.65]	– 5.45	<b>&lt;0.001</b>
$\beta_3$ (pikeperch × autumn)	2.57 [1.91–3.46]	6.25	<b>&lt;0.001</b>
$\beta_3$ (wels catfish × autumn)	308.81 [234.43–406.79]	40.77	<b>&lt;0.001</b>
$\beta_3$ (pikeperch × winter)	0.46 [0.34–0.63]	– 4.92	<b>&lt;0.001</b>
$\beta_3$ (wels catfish × winter)	120.92 [92.20–158.59]	34.66	<b>&lt;0.001</b>
$\beta_3$ (pikeperch × spring II)	0.88 [0.47–1.63]	– 0.41	0.686
$\beta_3$ (wels catfish × spring II)	161.09 [94.84–273.62]	18.80	<b>&lt;0.001</b>
Random effects			
$\sigma^2$	3.29		
$\tau_{00}$ fishID	0.99		
ICC	0.23		
$N_{\text{fishID}}$	31		
Marginal $R^2$ /Cond. $R^2$	0.594/0.688		

Numbers represent OR and 95% CI (see supplemental material for odds ratio calculation and interpretation). Depth\_use is an ordinal dependent variable used to fit the CLMMdepth model, with  $k=7$  categories related to different depth ranges, where  $\theta_k$  is the cumulative probability of using each category (from 0–1 to > 10 m).  $\beta_1$ – $\beta_3$  are exponentials of the estimated fixed effects regression coefficients for each of the interaction covariates species × season. Random effects are represented by the individual intercepts for the fish identity (fishID) ( $\tau_{00}$ ) and the residual variance ( $\sigma^2$ ). ICC is the intraclass correlation coefficient, which measures the degree of repeatability at the individual level. Marginal  $R^2$ /Cond.  $R^2$  are marginal and conditional r-squared values that refer to the proportion of variation explained by fixed effects and the variance explained by fixed and random effects, respectively

In bold,  $P < 0.05$

being the most used depth range ( $P(Y_j \leq 6) \pm \text{SE}$ ):



**Fig. 4** **A** Mean daily depths of all tracked individuals (black dots) as a function of temperature (colours) and time. The thermocline is represented by a dashed line; **B** Cumulative probabilities of depth use in Řimov Reservoir by Northern pike, pikeperch, and wels catfish at different times of the year from April 2017 to April 2018, estimated using a cumulative link

mixed-effects model analysis (CLMM<sub>depth</sub>). Depth was divided into seven levels corresponding to increasing depth in the water column, from 0–1 to >10 m. The y-axis represents the probability of using the depth in each season (x-axis). Depth 0–1 m was set as the reference category in the analysis

$0.29 \pm 0.05$ ; Fig. 4).

During water column destratification (early autumn), species differed markedly in their use of depth. In autumn, pike used shallower water than in summer (mean depth 3 m) (LSM across seasons  $\pm$  SE:  $0.42 \pm 0.08$ ,  $z = 4.95$ ,  $P < 0.001$ ) but, in winter, was found significantly deeper again (autumn–winter:  $-0.44 \pm 0.09$ ,  $z = -4.90$ ,  $p < 0.001$ ) and reached a level similar to summer with a similar pattern of depth use in these two seasons (summer–winter:  $-0.02 \pm 0.09$ ,  $z = -0.26$ ,  $P = 1.00$ ). Pikeperch and wels catfish used deeper water in autumn than in winter, with the former more likely to use depths of 5 to 10 m in autumn [OR 2.57 (1.91–3.46),  $P < 0.001$ ] and 3 to 5 m in winter [OR 0.46 (0.34–0.63),  $P < 0.001$ ], while the second were significantly more likely to

use depths greater than 10 m in autumn [OR 308.81 (234.43–406.79),  $P < 0.001$ ] and 7 to 10 m depth in winter [OR 120.92 (92.20–158.59),  $P < 0.001$ ] (Figs. 4; and S4, S6 in Supplementary Material).

## Discussion

Our study revealed significant differences in habitat use among the three predatory species—pike, pikeperch, and wels catfish, in terms of their use of different sections, longitudinal activity, and use of depth in an 8.5 km long reservoir. Interspecific differences in these parameters varied considerably over time, with the greatest differences between the warm season (late spring and early autumn) and the cold season

(late autumn to early spring). Use of different reservoir sections was stable for pike, while pikeperch and wels catfish frequently visited the tributary and upper sections of the reservoir during the warm season and moved closer to the dam during cold season. Overall longitudinal activity was similar for all species, but pike activity was highest in the cold season, pikeperch activity peaked in the warm season, and wels catfish activity had several peaks in both the warm and cold seasons. Overlap in depth use among species was the greatest in the warm season, when all species used the upper layers of the water column, and the lowest in the cold season, when pikeperch and especially wels catfish used deeper areas. The results therefore supported our hypothesis that pikeperch and wels catfish use the area near tributaries to a greater extent than pike. Our second hypothesis, that longitudinal activity would be the highest in pikeperch and the lowest in wels catfish, was not confirmed because activity was similar in all species. Our hypothesis that pikeperch and wels catfish used shallower depths than pike was also not confirmed, as all species used the same depths during water column temperature stratification.

#### Use of particular reservoir sections

Our results showed that the use of reservoir sections depended on species and season. The strongest changes in pikeperch and wels catfish were observed in the sections close to the inflow of the Malše River (upper and tributary sections). These two species frequently visited these reservoir sections in late spring and summer, and then gradually moved closer to the dam as the stratification of the water column disappeared. Wels catfish avoided the upper and especially the tributary sections of the reservoir more than pikeperch during the cold season. Wels catfish gradually moved closer to the dam throughout January and then gradually retreated towards the tributary for the remainder of the winter and early spring. For pikeperch, the section near the tributary was completely avoided only in October and November, after which some individuals occasionally returned to this section. For both species, the timing of these changes corresponded to changes in their depth use (as described above). Overwintering in deeper areas near the dam has been documented previously for pikeperch (Jepsen et al., 1999), but to our knowledge,

such behaviour has not been documented for wels catfish in lentic environments.

Previous studies in the Římov Reservoir described a stable longitudinal gradient in productivity closely associated with turbidity and distribution of prey fish during the warm season (Prchalová et al., 2009; Vašek et al., 2016). These gradients make the sections near the tributary of the Malše River rich in prey fish, but also eutrophic and thus turbid. Pikeperch and wels catfish are species well adapted to turbid conditions (Cucherousset et al., 2018; Jokela-Määttä et al., 2019), so their higher use of these sections may be related to the presence of favourable conditions and higher prey density. Their avoidance of this area during the cold season could be related to their preference for greater depths during this time, which are not present in the shallow upper sections and tributary. However, other factors could also be responsible for these behavioural differences, such as seasonal changes in prey density or other intra- and interspecific interactions that need to be further investigated. Pike seemed to avoid the upper sections of the reservoir. Moreover, higher use of reservoir sections was stable across seasons, changing only in early spring when they moved nearer to the dam. The timing of changes in pike and higher use of particular sections of the reservoir correspond to spawning activity (Pauwels et al., 2014) and it is very likely that these changes in sections use are related to the location of suitable spawning habitats. Since shallow beaches with submerged terrestrial macrophytes were available in the main body of the reservoir in early spring.

#### Longitudinal activity

Our 11-month tracking showed that the upper reach of the reservoir was much less used by pike than by wels catfish and pikeperch, although the longitudinal extent visited was generally similar for all species, covering 50–75% (4–6.5 km) of the reservoir length. These results are consistent with previous studies of pikeperch (Fickling & Lee, 1985; Koed, 2001; Vehanen & Lahti, 2003), but show greater movement ability for pike and wels catfish than is usually documented (Cucherousset et al., 2018), and confirm recent studies showing greater spatial use and movement by these species (Capra et al., 2018; Nyqvist et al., 2020; Lenhardt et al., 2021; Říha et al., 2021).

It shows that these species were able to survey a relatively large portion of the reservoir and select suitable locations to reside during different parts of the annual cycle. This partially challenges the view of pike and wels catfish as stationary species with a relatively restricted home range (Craig, 2008; Cucherousset et al., 2018; Skov et al., 2018), while pikeperch is a species with low site fidelity (Fickling & Lee, 1985; Koed, 2001; Vehanen & Lahti, 2003).

Despite the similarities in overall longitudinal coverage, we found large differences among species in the temporal pattern of longitudinal activity. Telemetry studies of pike reported ambiguous differences in locomotor activity in the warm and cold seasons. They showed similar or higher winter activity (Jepsen et al., 2001; Koed et al., 2006; Baktoft et al., 2012; Nordahl et al., 2020) with a peak in activity in early spring (Pauwels et al., 2014; Monk et al., 2020) and lower activity in the cold season (Cook & Bergersen, 1988; Rogers & Bergersen, 1995; Kobler et al., 2008). Our results support studies showing higher winter activity, as pike longitudinal activity was low in summer, gradually increased in the cold season, and peaked in early spring.

Longitudinal activity of pikeperch peaked in summer (July and August) and was relatively low in other seasons, which is consistent with other results from lentic waters (Jepsen et al., 1999; Vehanen & Lahti, 2003) and contrasts with observations of riverine pikeperch, which were more active in spring and autumn (Koed, 2001; Horký et al., 2008). We expected a similar temporal pattern for wels catfish, as it has been previously documented that they have their highest activity in spring and summer and are inactive (or even hibernate) during the cold season (Daněk et al., 2014, 2016; Cucherousset et al., 2018; Kuzishchin et al., 2018). However, our results showed that activity of wels catfish was similar throughout the tracking period, with several peaks in late spring, summer, and at the transition between autumn and winter. These results corroborate those of recent studies indicating lower but persistent wels catfish activity even during the cold season (Lenhardt et al., 2021; Santis & Volta, 2021; Monk et al., 2020).

Seasonal changes in activity are related to different phases of the annual life cycle, such as feeding, spawning, or overwintering, and during their transitions (Horký et al., 2006; Slavík et al., 2007; Baktoft et al., 2012). The transition between feeding and

overwintering could explain the differences between warm and cold seasons and the changes in pikeperch activity. Previous studies have found that pikeperch stop feeding at lower temperatures. Pikeperch have been found to feed significantly less below 8 °C and barely at all below 4 °C (Malinovskyi et al., 2019); however, Teletchea et al. (2009) showed that feeding rate during the cold season may depend on body fat content. A similar reduction in activity between feeding and hibernation was expected in wels catfish (Cucherousset et al., 2018). Wels catfish in aquaculture have been documented to stop feeding at temperatures below 7–10 °C (David, 2006; Copp et al., 2009), or have been suspected to do so based on stomach studies (Wysujack & Mehner, 2002) and their reduced catches (Britton et al., 2007). However, a recent study by Santis & Volta (2021) documented that they continue to feed in winter at temperatures below 10 °C, and our results showed that wels catfish were longitudinally active in winter and that these movements were related to depth use (see below) and differences in use of specific reservoir sections. These changes in winter activity cannot be explained by changes in abiotic conditions (i.e. temperature, oxygen concentration, or lack of currents) because they were uniform throughout the reservoir in winter. A more likely explanation is that wels catfish winter activity was driven by feeding or other interactions with conspecifics (social interaction) or other predators (e.g. direct competition; Cucherousset et al., 2018). However, the winter ecology of freshwater fishes is generally poorly understood, and very little information is available on the winter movements and habitat use of species and their prey (Marsden et al., 2021).

Spawning activity of these species could explain the changes in activity in late spring and early summer. Pikeperch spawn from mid to late April at sites with latitudes similar to those in Římov Reservoir (Lappalainen et al., 2003). Wels catfish spawn when water temperature rises to 18–22 °C (Copp et al., 2009), and the temperature was this high in late May in Římov Reservoir. Our results showed that longitudinal activity was low from the end of April to the end of May for pikeperch and from mid-May to the end of June for catfish. After these periods, the activity of both species increased significantly. A decrease in activity during spawning and a subsequent increase in activity can be expected as males guard nests after



spawning and remain inactive for several weeks in both species (Lappalainen et al., 2003; Copp et al., 2009). Sex was not examined in our study, but we can assume that some proportion of the marked individuals were males, which contributes significantly to the observed activity patterns.

In pike, reduced but persistent food intake has been documented even in winter (Diana, 1979), and it has been suggested that this is related to energy requirements for ovarian recruitment and early spring spawning (Baktoft et al., 2012). Based on these results, we can hypothesize that the increased movement of pike along the reservoir during the cold season may be related to foraging activity. The highest peak in longitudinal activity of pike was recorded in early spring in Římov Reservoir. High early spring activity has been documented previously (Pauwels et al., 2014) and is thought to be caused by spawning activity, as the species spawns in early spring (Skov & Nilsson, 2018) and the high activity might be linked with search of suitable spawning ground or partner.

#### Depth use

Concerning the depth use, our results showed a large overlap among species in spring and summer, but a partitioning in autumn and winter. During the warm season, all three species used the upper part of the water column, which agrees well with the extent of the thermocline and confirms previous results (Copp et al., 2009; Nordahl et al., 2020; Říha et al., 2021; Westrelin et al., 2022). There could be several explanations for a depth use in summer that are not mutually exclusive and may interact. The strong temperature stratification of the water column meant that optimal temperatures for all three species (Feiner & Höök, 2015; Cucherousset et al., 2018; Skov & Nilsson, 2018) occurred only in the epilimnetic surface layer (up to 5–7 m during the period from late spring to early autumn). In addition, anoxic conditions prevailed in most of the reservoir below the thermocline from late August, making the depths below the thermocline inaccessible to fish. In addition to abiotic factors, prey distribution could also play a crucial role in the distribution of aquatic predators (Brodersen et al., 2015; Říha et al., 2021). Previous studies on the Římov Reservoir have shown that almost all prey species are restricted to the epilimnion in summer (Prchalová et al., 2009; Vašek et al., 2016). Therefore,

the reason for the strong overlap in the use of depth by predators in summer and early autumn was likely to be a result of the combined effects of temperature profile, oxygen availability, and prey distribution.

Pikeperch and wels catfish responded similarly to the autumnal mixing of the water column, preferring greater depths after the thermocline receded. Pikeperch used the deepest parts of the reservoir only in the autumn, while wels catfish gradually descended and reached the greatest depths in January. The use of greater depths during the cold season for overwintering has been documented previously for these two species (Nyberg et al., 1996; Jepsen et al., 1999; Daněk et al., 2014; Kuzishchin et al., 2018). However, previous studies generally documented static behaviour of both species when overwintering in deep holes and assumed that this was a response to oxygen availability or currents (Nyberg et al., 1996; Jepsen et al., 1999; Daněk et al., 2014; Cucherousset et al., 2018; Kuzishchin et al., 2018). Such explanations cannot be applied to the Římov Reservoir (no current, homogeneous oxygen concentration in winter, see Fig. 1), and we can hypothesize that use of deeper areas may be a species-specific behavioural trait that is independent of conditions, at least in wels catfish. In pikeperch, not all individuals descended to greater depths, and some remained at the same depth during the cold period. However, other factors such as changes in prey distribution could play a role in both pikeperch and wels catfish, as use of deeper river holes has been documented for different species in a riverine environment (Rakowitz et al., 2014). In addition, pikeperch observed in the study could be preyed upon by the largest pike or wels catfish present in the reservoir (Adánek et al., 2019; Santis & Volta 2021). In other studies, this species has been observed to prefer the deepest parts of a water body in winter (Jepsen et al., 1999; Vehanen & Lahti, 2003), and pikeperch use of depths that do not overlap with those of pike or wels catfish could be related to the risk of their predation. In the absence of a vertical temperature gradient (which has been suggested as a major factor in summer vertical distribution), the gradual ascent of wels catfish to shallower depths in late winter and early spring must be explained by other factors, such as photoperiod duration or changes in prey distribution.

## Caveats

Our study has several potential limitations that must be considered when interpreting the results. The sample size and body size range were limited for all three species. Therefore, statistical evidence for detecting differences among species or for more detailed analyses of reservoir section use was limited. Furthermore, the three fish species differed in their body size and it could influence observed interspecies differences in overall longitudinal activity. However, if body length is an important factor for longitudinal activity, then we would expect a significant relationship between body size and longitudinal activity at least for pike and wels catfish for which we had quite a broad range of available body lengths (body range of analysed pike individuals 50–116 cm, wels catfish 86–166 cm, Tab. 1). Our modelling approach showed that body length did not have a significant effect on longitudinal activity for any species. Therefore, it seems that there is no simple relationship between longitudinal activity and body size in these predatory species in the Římov Reservoir. In addition, we did not examine fish sex. However, sex-specific differences in activity have been documented previously, particularly during spawning in all three species (Jepsen et al., 1999; Poulet et al., 2005; Copp et al., 2009; Pauwels et al., 2014). We did not include sex in the analyses, and it may therefore be another factor contributing to the high inter-individual variability observed. Differences in the accuracy of the summer and winter arrays may have resulted in a slight overestimation of activity in winter compared to summer at the individual species level. However, the design of the winter array was the same for all three species, so the results for winter should reflect interspecific differences well. Moreover, the seasonal changes in longitudinal activity of pikeperch and wels catfish agree well with the timing of their vertical movement (detected by the internal sensors on the tags, which were independent of the array deployment method) and confirm our conclusions about changes in their activity.

## Conclusions

Observed space use in three tracked predators can help us better understand their interspecific interactions, their effects on prey, and how to better

manage their populations. The three studied predator species have a large overlap in their prey in reservoirs with similar prey composition (Adámek et al., 2019; Vejřík et al., 2019). This suggests that there is a higher potential for direct interactions and competition in spring and summer in Římov Reservoir when they have high vertical spatial overlap. Furthermore, interactions between wels catfish and pikeperch are likely to be stronger during these seasons than between these two fish species and pike because pikeperch and wels catfish use narrow and spatially limited upper and tributary areas to a greater extent. During the cold season (autumn and winter), spatial overlap between all of three species was largely reduced as they preferred different depths. This reduced their potential interactions and may promote their coexistence in the reservoir (McMeans et al., 2020). A distinct seasonal pattern in the use of tributary and upper areas by wels catfish and pikeperch also suggests a strong fluctuation in predation risk to their prey in these parts of the reservoir, with high predation risk from multiple predators in spring and summer and lower predation risk mediated almost exclusively by pike in autumn and winter. However, information on how prey species cope with seasonal changes in predation risk and the seasonal evolution of predator–prey interactions is lacking because there is little information on the winter ecology of fish in general (McMeans et al., 2020). Predatory fish are released in Římov Reservoir for biomanipulation purposes, and protection from illegal fishing is an important tool for maintaining their populations (Vašek et al., 2013). Our results have shown that greater efforts should be made to protect predatory fish, namely wels catfish and pikeperch, in the upper and tributary parts during summer and spring, when these predators are more concentrated in these areas and are at a higher risk from fishing.

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**Author contributions** All authors contributed substantial comments during manuscript preparation. MŘ: Conceptualization. MŘ: Data curation. RRB, MŘ, KÖG: Formal analysis.

RRB: Statistical analysis. MŘ, JP, PB: Funding acquisition. MŘ, LV, IJ, ATS, LV, V.Draštík, PB, MH, TJ, PR, ZS, LK, MT, MP, MS, JP: Investigation. MŘ, KØG, IJ, AST: Methodology. RRB, MŘ: Visualization. MŘ, RRB: Writing—original draft. All authors: Writing—review & editing.

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**Data availability** The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Conflict of interest** The authors declare that they have no competing interests.

**Ethical approval** Animal treatment was performed in accordance with guidelines from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic and with permission (Ref. no. 310/7387) of the managers of the study sites, Povodí Vltavy s.p.

#### References

- Adámek, Z., L. Mikl, L. Šlapanský, P. Jurajda & K. Halačka, 2019. The diet of predatory fish in drinking water reservoirs – How can they contribute to biomanipulation efforts? *Folia Zoologica* 68: 215–224.
- Baktoft, H., K. Aarestrup, S. Berg, M. Boel, L. Jacobsen, N. Jepsen, A. Koed, J. C. Svendsen & C. Skov, 2012. Seasonal and diel effects on the activity of northern pike studied by high-resolution positional telemetry. *Ecology of Freshwater Fish* 21: 386–394.
- Britton, J. R., J. Pegg, R. Sedgwick & R. Page, 2007. Investigating the catch returns and growth rate of wels catfish, *Silurus glanis*, using mark–recapture. *Fisheries Management and Ecology* 14: 263–268.
- Brodersen, J., J. G. Howeth & D. M. Post, 2015. Emergence of a novel prey life history promotes contemporary sympatric diversification in a top predator. *Nature Communications* 6: 8115.
- Capra, H., H. Pella & M. Ovidio, 2018. Individual movements, home ranges and habitat use by native rheophilic cyprinids and non-native catfish in a large regulated river. *Fisheries Management and Ecology* 25: 136–149.
- Carpenter, S. R., J. F. Kitchell & J. R. Hodgson, 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634–639.
- Christensen, R. H. B., 2019. Regression models for ordinal data, R package:
- Cook, M. F. & E. P. Bergersen, 1988. Movements, habitat selection, and activity periods of northern pike in Eleven Mile Reservoir, Colorado. *Transactions of the American Fisheries Society* 117: 495–502.
- Copp, G. H., J. Robert Britton, J. Cucherousset, E. García-Berthou, R. Kirk, E. Peeler & S. Stakenas, 2009. Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries* 10: 252–282.
- Craig, J. F., 2008. A short review of pike ecology. *Hydrobiologia* 601: 5–16.
- Cucherousset, J., P. Horký, O. Slavík, M. Ovidio, R. Arlinghaus, S. Boulêtreau, R. Britton, E. García-Berthou & F. Santoul, 2018. Ecology, behaviour and management of the European catfish. *Reviews in Fish Biology and Fisheries* 28: 177–190.
- Daněk, T., L. Kalous, M. Petrtýl & P. Horký, 2014. Move or die: Change in European catfish (*Silurus glanis* L.) behaviour caused by oxygen deficiency. *Knowledge and Management of Aquatic Ecosystems* 414: 08.
- Daněk, T., P. Horký, L. Kalous, K. Filinger, V. Břicháček & O. Slavík, 2016. Seasonal changes in diel activity of juvenile European catfish *Silurus glanis* (Linnaeus, 1758) in Byšická Lake, Central Bohemia. *Journal of Applied Ichthyology* 32: 1093–1098.
- David, J. A., 2006. Water quality and accelerated winter growth of European catfish using an enclosed recirculating system. *Water and Environment Journal* 20: 233–239.
- Diana, J. S., 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). *Canadian Journal of Zoology* 57: 2121–2127.
- Feiner, Z. S. & T. O. Höök, 2015. Environmental biology of percid fishes. In Kestemont, P., K. Dabrowski & R. C. Summerfelt (eds), *Biology and culture of percid fishes principles and practices* Springer: 61–100.
- Fickling, N. J. & R. L. G. Lee, 1985. A study of the movements of the zander, *Lucioperca lucioperca* L., population of two lowland fisheries. *Aquaculture Research* 16: 377–393.
- Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power & J. S. Brashares, 2019. Landscapes of fear: Spatial patterns of risk perception and response. *Trends in Ecology and Evolution* 34: 355–368.
- Giske, J., G. Huse & Ø. Fiksen, 1998. Modelling spatial dynamics of fish. *Reviews in Fish Biology and Fisheries* 8: 57–91.
- Guzzo, M. M., P. J. Blanchfield, A. J. Chapelsky & P. A. Cott, 2016. Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. *Journal of Great Lakes Research* 42: 276–285.
- Horký, P., O. Slavík, L. Bartoš, J. Kolářová & T. Randák, 2006. The effect of the moon phase and seasonality on the behaviour of pikeperch in the Elbe River. *Folia Zoologica* 55: 411–417.
- Horký, P., O. Slavík & L. Bartoš, 2008. A telemetry study on the diurnal distribution and activity of adult pikeperch, *Sander lucioperca* (L.), in a riverine environment. *Hydrobiologia* 614: 151–157.

- Hughes, A. R. & J. H. Grabowski, 2006. Habitat context influences predator interference interactions and the strength of resource partitioning. *Oecologia* 149: 256–264.
- Hugie, D. M. & L. M. Dill, 1994. Fish and game: A game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology* 45: 151–169.
- Ivlev, V. S., 1961. *Experimental ecology of the feeding of fishes*, Yale University Press., 302.
- Jepsen, N., A. Koed & F. Økland, 1999. The movements of pikeperch in a shallow reservoir. *Journal of Fish Biology* 54: 1083–1093.
- Jepsen, N., S. Beck, C. Skov & A. Koed, 2001. Behavior of pike (*Esox lucius* L.) 50 cm in a turbid reservoir and in a clearwater lake. *Ecology of Freshwater Fish* 10: 26–34.
- Jokela-Määttä, M., M. Viljanen, N. Nevala, K. Donner & C. Brönmark, 2019. Photoreceptors and eyes of pikeperch *Sander lucioperca*, pike *Esox lucius*, perch *Perca fluviatilis* and roach *Rutilus rutilus* from a clear and a brown lake. *Journal of Fish Biology* 95: 200–213.
- Keskinen, T., J. P. J. Pääkkönen, J. Lilja, T. J. Marjomäki & J. Karjalainen, 2005. Homing behaviour of pikeperch (*Sander lucioperca*) following experimental transplantation. *Boreal Environment Research* 10: 119–124.
- Kobler, A., T. Klefoth, C. Wolter, F. Fredrich & R. Arlinghaus, 2008. Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake. *Hydrobiologia* 601: 17–27.
- Koed, A., 2001. Long-term effect of radio-tagging on the swimming performance of pikeperch. *Journal of Fish Biology* 58: 1753–1756.
- Koed, A., K. Balleby, P. Mejlhede & K. Aarestrup, 2006. Annual movement of adult pike (*Esox lucius* L.) in a lowland river. *Ecology of Freshwater Fish* 15: 191–199.
- Kronfeld-Schor, N. & T. Dayan, 2003. Partitioning of time as an ecological resource. *Annual Review of Ecology, Evolution, and Systematics* 34: 153–181.
- Kuzishchin, K. V., M. A. Gruzdeva & D. S. Pavlov, 2018. Traits of biology of European wels catfish *Silurus glanis* from the Volga-Ahtuba water system, the Lower Volga. *Journal of Ichthyology* 58: 833–844.
- Lappalainen, J., H. Dörner & K. Wysujack, 2003. Reproduction biology of pikeperch (*Sander lucioperca* (L.)) – A review. *Ecology of Freshwater Fish* 12: 95–106.
- Lear, K. O., N. M. Whitney, J. J. Morris & A. C. Gleiss, 2021. Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. *Proceedings of the Royal Society B* 288: 1954.
- Lenhardt, M. B., M. M. Smederevac-Lalić, S. Z. Spasić, Š Hont, M. Paraschiv, M. I. Iani, M. V. Nikčević, P. A. Klimley & R. Suci, 2021. Seasonal changes in depth position and temperature of European catfish (*Silurus glanis*) tracked by acoustic telemetry in the Danube River. *International Review of Hydrobiology* 106: 191–201.
- Malinovskyi, O., M. Blecha, J. Kristan & T. Policar, 2019. Feeding activity of pikeperch (*Sander lucioperca*) under winter and spring photothermal conditions of pre-spawning period. *Aquaculture Research* 51: 852–857.
- Marsden, J. E., P. J. Blanchfield, J. L. Brooks, T. Fernandes, A. T. Fisk, M. H. Futia, B. L. Hlina, S. V. Ivanova, T. B. Johnson, N. V. Klinard, C. C. Krueger, S. M. Larocque, J. K. Matley, B. McMeans, L. M. O'Connor, G. D. Raby & S. J. Cooke, 2021. Using untapped telemetry data to explore the winter biology of freshwater fish. *Reviews in Fish Biology and Fisheries* 31: 115–134.
- McMeans, B. C., K. S. McCann, M. M. Guzzo, T. J. Bartley, C. Bieg, P. J. Blanchfield, T. Fernandes, H. C. Giacomini, T. Middel, M. D. Rennie, M. S. Ridgway & B. J. Shuter, 2020. Winter in water: Differential responses and the maintenance of biodiversity. *Ecology Letters* 23: 922–938.
- Miranda, L. E. & M. Kratochvíl, 2008. Boat electrofishing relative to anode arrangement. *Transactions of the American Fisheries Society* 137: 1358–1362.
- Monk, C. T., B. Chéret, P. Czaplá, D. Hühn, T. Klefoth, E. Eschbach, R. Hagemann & R. Arlinghaus, 2020. Behavioural and fitness effects of translocation to a novel environment: Whole-lake experiments in two aquatic top predators. *Journal of Animal Ecology* 89: 2325–2344.
- Nordahl, O., P. Koch-Schmidt, P. Tibblin, A. Forsman & P. Larsson, 2020. Vertical movements of coastal pike (*Esox lucius*) – On the role of sun basking. *Ecology of Freshwater Fish* 29: 18–30.
- Nyberg, P., E. Degerman & B. Sers, 1996. Survival after catch in trap-nets, movements and growth of the pikeperch (*Stizostedion lucioperca*) in Lake Hjaelmaren, Central Sweden. *Annales Zoologici Fennici* 33: 569–575.
- Nyqvist, M. J., J. Cucherousset, R. E. Gozlan, W. R. C. Beaumont & J. R. Britton, 2020. Dispersal strategies of juvenile pike (*Esox lucius* L.): Influences and consequences for body size, somatic growth and trophic position. *Ecology of Freshwater Fish* 29: 377–383.
- Overton, J. L., D. Toner, T. Policar & D. Kucharczyk, 2015. Commercial production: Factors for success and limitations in European percid fish culture. In Kestemont, P., K. Dabrowski & R. C. Summerfelt (eds), *Biology and culture of percid fishes: principles and practices* Springer: 881–890.
- Pauwels, I. S., P. L. M. Goethals, J. Coeck & A. M. Mouton, 2014. Movement patterns of adult pike (*Esox lucius* L.) in a Belgian lowland river. *Ecology of Freshwater Fish* 23: 373–382.
- Pavlov, D. & A. Kasumyan, 2002. Feeding diversity in fishes: Trophic classification of fish. *Journal of Ichthyology* 42: S137–S159.
- Pelinson, R. M., M. A. Leibold & L. Schiesari, 2021. Top predator introduction changes the effects of spatial isolation on freshwater community structure. *Ecology* 102: e03500.
- Poulet, N., C. Arzel, S. Messad, S. Lek & C. Argillier, 2005. Diel activity of adult pikeperch *Sander lucioperca* (L.) in a drainage canal in the Mediterranean basin during spring. *Hydrobiologia* 543: 79–90.
- Prchalová, M., J. Kubečka, M. Čech, J. Frouzová, V. Draštík, E. Hohašová, T. Jůza, M. Kratochvíl, J. Matěna, J. Peterka, M. Říha, M. Tušer & M. Vašek, 2009. The effect of depth, distance from dam and habitat on spatial distribution of fish in an artificial reservoir. *Ecology of Freshwater Fish* 18: 247–260.
- R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rakowitz, G., B. Berger, E. Schludermann, M. Tritthart, H. Habersack & H. Keckeis, 2014. Deep pools of the Danube

- River: Ecological function or turbulent sink? *Hydrobiologia* 729: 143–159.
- Read, J. S., L. A. Winslow, R. Woolway, J. Brentrup, T. Leach, J. Zwart, S. Albers & D. Collinge, 2019. rLakeAnalyzer: Lake physics tools, R package.
- Říha, M., K. Gjelland, V. Děd, A. P. Eloranta, R. Rabaneda-Bueno, H. Baktoft, L. Vejřík, I. Vejříková, V. Draštík, M. Šmejkal, M. Holubová, T. Jůza, C. Rosten, Z. Sajdllová, F. Økland & J. Peterka, 2021. Contrasting structural complexity differentiate hunting strategy in an ambush apex predator. *Scientific Reports* 11: 17472.
- Rogers, K. B. & E. P. Bergersen, 1995. Effects of a fall draw-down on movement of adult northern pike and largemouth bass. *North American Journal of Fisheries Management* 15: 596–600.
- Sandlund, O. T., J. Museth & S. Øistad, 2016. Migration, growth patterns, and diet of pike (*Esox lucius*) in a river reservoir and its inflowing river. *Fisheries Research* 173: 53–60.
- Santis, V. & P. Volta, 2021. Spoiled for choice during cold season? Habitat use and potential impacts of the invasive *Silurus glanis* L. in a deep, large, and oligotrophic lake (Lake Maggiore, North Italy). *Water* 13: 2549.
- Seda, J. & M. Devetter, 2000. Zooplankton community structure along a trophic gradient in a canyon-shaped dam reservoir. *Journal of Plankton Research* 22: 1829–1840.
- Skov, C. & P. Nilsson, 2018. *Biology and ecology of pike*. CRC Press.
- Skov, C., M. C. Lucas & L. Jacobsen, 2018. Spatial ecology. In Skov, C. & P. A. Nilsson (eds), *Biology and ecology of pike* CRC Press: 91–128.
- Slavík, O., P. Horký, L. Bartoš, J. Kolářová & T. Randák, 2007. Diurnal and seasonal behaviour of adult and juvenile European catfish as determined by radio-telemetry in the River Berounka, Czech Republic. *Journal of Fish Biology* 71: 101–114.
- Teletchea, F., J. N. Gardeur, M. Psenicka, V. Kaspar, Y. Le Doré, O. Linhart & P. Fontaine, 2009. Effects of four factors on the quality of male reproductive cycle in pikeperch *Sander lucioperca*. *Aquaculture* 291: 217–223.
- van Rij, J., M. Wieling, R. Baayen & H. van Rijn, 2017. itsadug: Interpreting time series and autocorrelated data using GAMMs, R package.
- Vašek, M., M. Prchalová, J. Peterka, H. A. M. Ketelaars, A. J. Wagenvoort, M. Čech, V. Draštík, M. Říha, T. Jůza, M. Kratochvíl, T. Mrkvička, P. Blabolil, D. S. Boukal, J. Duras & J. Kubečka, 2013. The utility of predatory fish in biomanipulation of deep reservoirs. *Ecological Engineering* 52: 104–111.
- Vašek, M., M. Prchalová, M. Říha, P. Blabolil, M. Čech, V. Draštík, J. Frouzová, T. Jůza, M. Kratochvíl, M. Muška, J. Peterka, Z. Sajdllová, M. Šmejkal, M. Tušer, L. Vejřík, P. Znachor, T. Mrkvička, J. Sed'a & J. Kubečka, 2016. Fish community response to the longitudinal environmental gradient in Czech deep-valley reservoirs: Implications for ecological monitoring and management. *Ecological Indicators* 63: 219–230.
- Vehanen, T. & M. Lahti, 2003. Movements and habitat use by pikeperch (*Stizostedion lucioperca* (L.)) in a hydropeaking reservoir. *Ecology of Freshwater Fish* 12: 203–215.
- Vejřík, L., I. Vejříková, L. Kočvara, Z. Sajdllová, S. C. Hoang The, M. Šmejkal, J. Peterka & M. Čech, 2017. Thirty-year-old paradigm about unpalatable perch egg strands disclaimed by the freshwater top-predator, the European catfish (*Silurus glanis*). *PLoS ONE* 12: 1–9.
- Vejřík, L., I. Vejříková, L. Kočvara, P. Blabolil, J. Peterka, Z. Sajdllová, T. Jůza, M. Šmejkal, T. Kolařík, D. Bartoš, J. Kubečka & M. Čech, 2019. The pros and cons of the invasive freshwater apex predator, European catfish *Silurus glanis*, and powerful angling technique for its population control. *Journal of Environmental Management* 241: 374–382.
- Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsman & F. C. Funk, 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Board of Canada* 34: 360–370.
- Westrelin, S., J. Cucherousset, R. Roy, L. Tissot, F. Santoul & C. Argillier, 2022. Habitat partitioning among three predatory fish in a temperate reservoir. *Ecology of Freshwater Fish* 31: 129–142.
- Wood, S. N., 2021. mgcv: Mixed GAM computation vehicle with automatic smoothness estimation, R package.
- Wysujack, K. & T. Mehner, 2002. Comparison of losses of planktivorous fish by predation and seine-fishing in a lake undergoing long-term biomanipulation. *Freshwater Biology* 47: 2425–2434.
- Znachor, P., J. Hejzlar, J. Vrba, J. Sed'a, K. Šimek, J. Komárková, J. Kopáček, M. Šorf, J. Kubečka, M. Říha, J. Peterka & M. Vašek. (2016). Brief history of long-term ecological research into aquatic ecosystems and their catchments in the Czech Republic. Part I: manmade reservoirs. *Biology Centre CAS, České Budějovice*.

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