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Research article

Understanding the temporal dynamics of a lowland river fish community at a hazardous intake and floodgate to inform safe operation

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A R T I C L E I N F O

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A B S T R A C T

Entrainment and mortality of freshwater fish at hazardous pumping station intakes used for Flood Risk Management (FRM) are of global concern. Although upstream and downstream passage of diadromous fish has received considerable attention, the ecological behaviours of river-resident fish at these structures and how to protect these species from entrainment is poorly-understood. At a lowland flood-relief pumping station and floodgate situated off-channel (River Foss) to the main-river Yorkshire Ouse (York, England), multi-beam sonar (Dual-Frequency Identification Sonar: DIDSON) was used over a pluriannual (three years) period to investigate diel movements of river-resident fish in response to the variations in temperature, hydrology and pump and floodgate operation, and to determine fish-friendly management options. Diel lateral movements of thousands of river-resident fish between the main-river, floodgate operated channel (River Foss) and off-channel pump forebay were predominantly during the crepuscular period and daytime, proposing important considerations for when managers should operate pumps and associated flood infrastructure. Seasonal diel movements increased throughout winter during a baseline year (no pump operation) and overwintering behaviour was influenced by cooling river temperatures. A Generalized Linear Mixed Model (GLMM) revealed fish entered the off-channel forebay when river levels were stable and not when they were rising or falling, suggesting hydrological stability was important for the ecological function of this fish community. Two years of impact data (pumps operated) then revealed pump operations severely disrupted the ecological functions of local fish populations, which was also uniquely quantified over two independent 24h periods during which temporal fish counts were reduced by 85%. A trial period where the floodgate was lowered ahead of dawn significantly reduced fish immigration into the hazardous forebay when compared to two different hydrological periods. Modifying when the floodgate and pumps operate, including lowering the floodgate ahead of fish immigration at dawn, and starting pumps during the night (but not day), are therefore promising non-engineered management options to prevent immigration of fish into the hazardous off-channel pump forebay and to reduce entrainment and mortality risk during pump operation.

1. Introduction

Anthropogenic modifications to freshwater ecosystems have significantly altered rivers through the construction of dams, weirs, culverts, gates and structures with water intakes, which include hydropower, water abstraction and pumping stations (PSs). The human demand for these structures cannot be understated; hydropower, for example, is responsible for almost 20% of all electricity produced worldwide (Moore, 2022), and PSs form a critical component of managing societal flood risks around the world. Many agricultural, industrial and residential properties in lowland regions are therefore reliant on PS operation to prevent inundation of flood water (Baumgartner et al., 2009; Buysse et al., 2014). Yet, these structures can severely impair longitudinal (Baker et al., 2021) and lateral (Tripp et al., 2016) fish migrations and movements. Indeed, there is a lack of information on how multi-species lowland river-resident fish communities interact with PSs year-round (but see Martins et al., 2014). The intake of PSs ('hazardous intake' hereafter) also presents a major hazard to fish where impingement against screens and entrainment through turbines and pumps can lead to injury and mortality of fish (Rytwinski et al., 2017;

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Bolland et al., 2019).

Legislation exists (e.g., the Eel Regulations 2009; Water Framework Directive, 2000/60/EEC) to protect fish at hazardous intakes, and has led to the use of physical (e.g., screens) and behavioural (e.g., sound, light and electricity) deterrents to prevent entrainment of fish (Sheridan et al., 2014; Adam and Schwevers, 2020; Jones et al., 2021). However, much of this work has focused on diadromous fish species of conservation interest, such as the catadromous European eel (*Anguilla anguilla*) (Sheridan et al., 2014; Fjeldstad et al., 2018; Piper et al., 2019) and anadromous Atlantic salmon (*Salmo salar*) (Perry et al., 2014; Tomanova et al., 2021). To date, there is a lack of information on the protection of river-resident fish communities. Physical and behavioural deterrents may be inefficient for multi-species protection because of highly variable species and life stage specific swimming capabilities and behaviours (Poletto et al., 2015). Further, retrofitting engineered fish protection is technically and financially challenging. As such, there is a need to develop cost-effective, non-engineered operational solutions informed by the ecology of the prevailing fish community.

Operational solutions for the protection of migratory fish include using spillway releases to limit fish passage through turbines at dams (Williams, 2008), opening sluice gates to facilitate downstream European eel movement at PSs (Egg et al., 2017; Baker *et al.*, 2021) and turbine and pump shutdown during seasonal migrations (Gilligan and Schiller, 2003; Trancart et al., 2013). In turn, turbine and pump shutdown could be used during diel movements of river-resident fish (Baumgartner et al., 2009; Reckendorfer et al., 2018). To do so requires knowledge on local multi-species community ecology, as the predictable temporal periods in fish activity at hazardous intakes are intrinsically linked with shifts in day and night light intensity, water temperature and hydrology, and predator avoidance. It is perhaps surprising, then, that the operational management of hazardous intakes rarely includes ecological considerations for river-resident fish (e.g., Harrison et al., 2019). Further, studies investigating the seasonal and diurnal movement patterns of river-resident fish at hazardous intakes are also scarce (but see Knott et al., 2019).

Lateral movements of fish into off-channel and backwater habitats are considered essential for the ecological functioning of fish communities, particularly with regards to temperature and hydrology (Tripp et al., 2016; Thurow, 2016). This is especially true during winter when macrophyte die-off reduces micro-habitat availability, river temperatures drop and main-river flows increase (Lyon et al., 2010). Furthermore, river level management during the winter requires increased pump operations, exacerbating harsh conditions for river-resident fish. Thus, this study took place during winter at the hazardous intake of an off-channel flood control PS on a lowland main-river. The connection between the main-river and off-channel PS was regulated by a floodgate which is lowered during pump operation, and thus prevents lateral movement of water and fish. Despite the management requirement of flood infrastructure, there are surprisingly few studies that have demonstrated how modifications to operations can successfully incorporate enhanced ecological opportunities for fish (but see Gordos, 2007; Seifert and Moore, 2017; Mel et al., 2020). Others have manipulated when floodgates open to improve fish passage (Perry et al., 2015; Wright et al., 2015). Thus, of additional importance in this study was to identify if floodgate operation prevented immigration of fish from the main-river into the off-channel PS.

Overall, if behaviour of river-resident fish communities around hazardous intake makes them more or less susceptible to entrainment, then a thorough understanding of fish ecology can be integrated into operational management to aid in fish protection. To do this requires the timing, frequency and abundance of the entire river-resident fish community movements in response to differing operational periods to be quantified. This was achieved here passively and non-invasively using a Dual frequency IDentification SONar (DIDSON) during a pluriannual investigation with highly contrasting inter-annual hydrology and pump operations, and also incorporated modifications to floodgate operations. Therefore, the overall aim of this study was to quantify the temporal dynamics of a lowland multi-species fish community at a hazardous intake, and to identify operational protection measures. In turn, this study addresses the following research questions; (1) What are the prevailing temporal dynamics in the frequency and magnitude of fish counts around a hazardous intake? (2) How does operation of a hazardous intake interact with the ecological functions of local fish communities? (3) How might the knowledge of temporal fish movements be incorporated into management of hazardous intakes and associated river infrastructure? The predictions from these research questions are that (i) the temporal periodicities in fish counts will show diurnal/nocturnal preferences due to movement patterns expected between main-river and lateral refuges i.e., fish will immigrate towards the hazardous intake at dawn and emigrate at dusk, albeit with intra- and inter-annual variability (linked to thermal and hydrological conditions); (ii) operation of the hazardous intake will disrupt the temporal dynamics of the fish counts, i.e., fish counts will be reduced after operations; and (iii) the maximal periodicities in the temporal fish counts will inform when to operate the intake and associated river infrastructure i.e., modify timing of floodgate operation.

2. Materials and methods

2.1. Study catchment and site

The Yorkshire Ouse is a lowland main-river in North Yorkshire, England, that drains into the Humber Estuary and has a catchment area of at least 3315 km^2 when combined with its tributaries (namely, the Aire, Don, Wharfe, Ure and Foss). The study site was Foss pumping station ('Foss PS' hereafter) in York (Lat: 53.952714 N, Long: 1.078850 W) (Fig. 1a), which is part of the York Flood Alleviation scheme consisting of Castle Mills Lock, Castle Mills Sluice and the Foss flood defence barrier ('floodgate' hereafter). Castle Mills Lock and Castle Mills bypass sluice work in conjunction to maintain the upstream stretch of the River Foss at 7.6 m above ordnance datum (mAOD). The remaining downstream stretch of the river formulates Foss basin and is maintained by Foss PS and the adjacent floodgate. Foss PS consists of eight 6.5 m^{3}s^{-1} pumps, with a total pumping capacity of 52 m^{3}s^{-1} and a 27 m wide intake weedscreen (bar thickness and spacing of 20 mm and 70 mm, respectively). Foss floodgate is positioned across the River Foss at the confluence with the Yorkshire Ouse. When the Yorkshire Ouse reaches 7.6 mAOD, the PS complex becomes operational in two stages:

(1) The floodgate is lowered into the channel from its normal raised position to prevent the movement of water (and fish) from the Yorkshire Ouse into the Foss basin
(2) The PS operates to move water from Foss basin into the Yorkshire Ouse. Pumps operate until flood water in the Yorkshire Ouse subsides (<7.6 mAOD) and meets the level of Foss basin, at which point the floodgate is raised

2.2. Field methods

2.2.1. Multi-beam sonar

It is difficult to non-invasively gather temporal information on fish that is inclusive of 24-h, multi-seasonal and pluriannual outputs. Here, high-resolution multi-beam sonar (DIDSON, 300m, Sound Metrics, USA. http://www.soundmetrics.com/) addresses this by providing near video-like images of fish in turbid and dark water during the day and night over many months and multiple years. To provide optimal data on the temporal dynamics of lateral fish movements, the DIDSON imaged across the full width of the downstream channel entrance of the River Foss (Fig. 1b). The DIDSON was installed on a 6 m vertical steel pole, at a submerged depth of 3 m (Fig. 1c), and the sonar image was aligned with steel pilings on the adjacent river bank to ensure consistent orientation. When pumps operated, the DIDSON was rotated to image across the

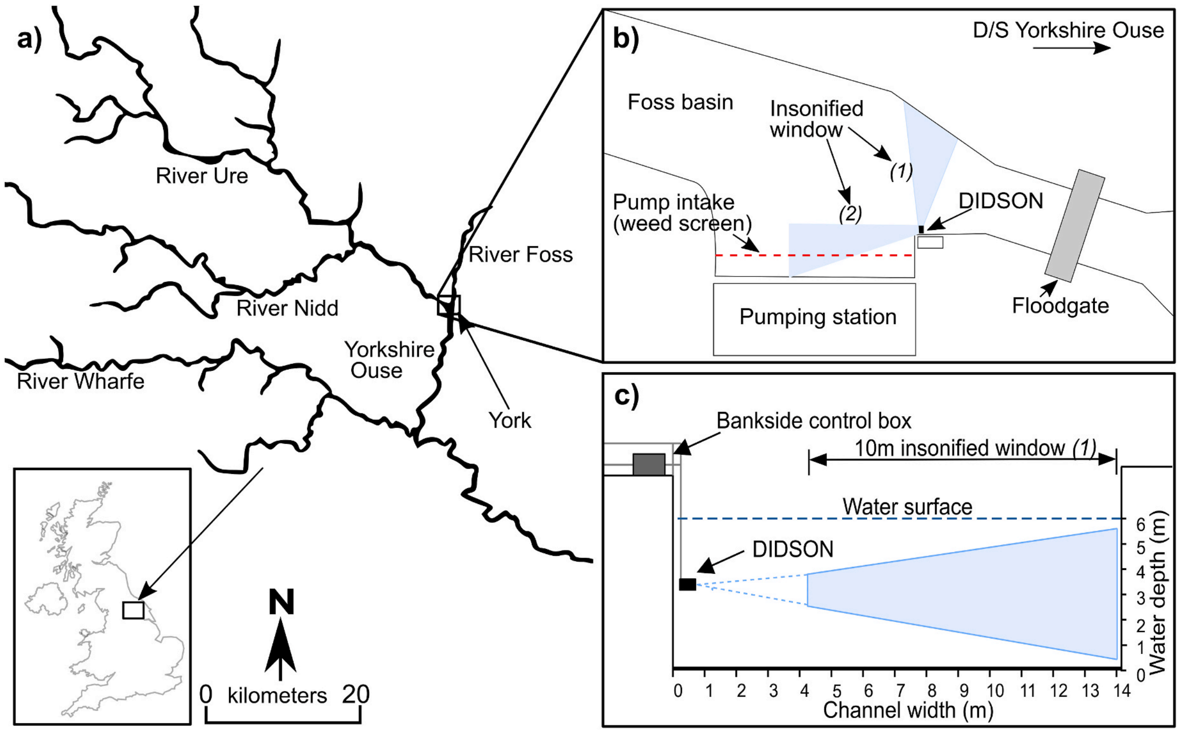

Fig. 1. The location of the Yorkshire Ouse catchment (a), a schematic representation of Foss PS and floodgate, and the DIDSON insonified window across the channel (1) and across the weed screen (2) (b) with a cross-section representation of (1) (c). D/S = downstream. (colour required online, full page width) 33. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

weed screen to confirm fish presence, but the rate of fish entrainment during pump operation were not assessed due to inadequate coverage of the weed screen.

The data and power cables were routed to a bankside weatherproof box containing a sonar command module and a laptop with remote internet connection (Panasonic TF-19). The DIDSON was operated in high frequency mode (1.8 MHz; 96 0.3° × 14° beams, 512 bins) with a window length of 10 m (starting 4 m from point of transducer) at 6 frames s^{-1} (fps), receiver gain at default and focus set to auto to account for changes in fish distance from the transducer (Fig. 1c). Continuous observations were captured to a 4 TB external HDD which was exchanged throughout the study period. Files were time and date stamped (hh:mm:ss – d/m/y) and stored in 10-min intervals. All software inputs were performed in SoundMetrics software (DIDSON V5.26.24).

2.2.2. Field survey effort

Foss PS was surveyed during the winter for three consecutive years between October and February in 2017/18 (deployment duration of 153 days, 12 days of no sonar operation), 2018/19 (173 days, 25 days) to 2019/20 (147 days, 25 days). The sampling period was selected based on the propensity for river-resident fish to use the backwater for flow and predator refuge and increased likelihood of pump operation. Remote connections were made to the laptop on a daily basis to confirm operation. Pump operation could disturb stabilised sediment in Foss basin and thus weekly site visits were performed to check for and remove silt deposits in the sonar housing. Insufficient data were collected in October in year one, and local flooding prevented data collection in February of year three.

2.2.3. In-stream parameters and pump operations

River level data were provided by the Environment Agency using river levels recorded in hourly intervals in the Yorkshire Ouse, downstream of the floodgate at Foss PS (site code: L2404; Lat: 53.952378 N, Long: 1.078385 W) (Fig. S1). The commencement of the study in year one was associated with steady river levels (river level min, max, med, IQR: 5.1, 8.1, 5.7, 0.6 mAOD), but there were three pumping events in response to elevated river levels (November; four days, January; three days, two days) and smaller test operations not represented by local river conditions. Year three was similar (river level min, max, med, IQR: 5.1, 8.5, 6.2, 1.1 mAOD), but pumps were operated frequently in response to stochastic river levels, with a total of five events (September; four days, October; two days, one day, two days, December; one day). Year two was characterised as a dry year and river level was lower (river level min, max, med, IQR: 4.9, 7.9, 4.9, 0.5 mAOD); pumps did not operate throughout the sample range allowing for effective baseline data to be gathered. Thus, years one and three were the most hydrologically comparable, with year two serving as a baseline.

Temperature (°C) data were unavailable in year one, but was recorded in year two and three at hourly intervals using a temperature logger (Tinytag Aquatic 2 tg-4100) attached to the DIDSON mount. A seasonal decline in water temperature was similar in both years two and three (Fig. S1).

2.3. Analysis of sonar footage

2.3.1. Fish counts across the channel during non-operational river levels (question 1)

To provide accurate fish counts, the recorded files were manually reviewed (Hateley and Gregory, 2006) by an experienced reviewer in the DIDSON software. For each sample month, a 14-day period with no pump operation (floodgate raised) was analysed to assess seasonal variation in fish presence. This allowed the number of consecutive days imaged to be maximised and data loss due to sonar failure to be minimised. Fish counts were taken hourly (individuals·1 frame·h^{-1}, 5 min past the hour ± 5 s^{-1}) from a 2 m^2 field at the centre of the insonified window (presented as individuals·2 m^2 h^{-1}). Automated counting was determined to be unsuitable due to a combination of a large insonified window range (Han et al., 2009), dense fish targets vulnerable to pseudoreplication and a concern with identification of non-fish targets, particularly leaf-litter and other floating detritus (Ebner et al., 2009; Doehring et al., 2011). Small (<30 cm) shoaling fish species are challenging to identify in sonar images (Egg et al., 2018) and thus sonar assessments of multi-species communities may be supplemented by historic catch records (Hughes and Hightower, 2015). Previous fish surveys in the Yorkshire Ouse catchment suggest the fish community is comprised of river-resident eurytopic and rheophillic species, such as roach (*Rutilus rutilus*), common bream (*Abramis brama*), dace (*Leuciscus leuciscus*), perch (*Perca fluviatilis*), chub (*Squalius cephalus*) and bleak (*Alburnus alburnus*) (Lucas et al., 1998; Bolland et al., 2015; Environment Agency, 2022).

Playback speed was adjusted between 5x and 10x by the reviewer to remove non-fish targets. Background subtraction was enabled if floating debris reduced resolution of fish targets. Fish were measured using the DIDSON measurement tool when perpendicular to the sonar beam and grouped into six size classes, 0–10 cm, 11–20 cm, 21–30 cm, 31,40 cm, 41–50 cm and >50 cm total length.

2.3.2. Fish counts before and after pump operation (question 2)

Fish counts were compared before (Pre-PO) and after (Post-PO) two independent pump operations in year three (Operation one: 11/10/19, 36h duration; Operation two: 26/10/19; 56h duration) to determine the effect of pump operation on diel fish counts. To include comparable day and night counts, the sub-sampled fish counts were taken from a fixed 24-h period (24 samples on the hour; 00:00–23:00) and then summed to provide a total daily count. During this period the floodgate was not lowered and the hydrological conditions were comparable (falling; see Fig. 5b).

2.3.3. Crepuscular floodgate operation testing (question 3)

In year three, a five day trial (13–January 17, 2020) was constructed where the floodgate was strategically lowered 1-h ahead of dawn for 2 h (07:30–9:30) to determine whether it prevented fish immigration into Foss basin and thus could be applied prior to pump operation to protect fish in the future. The floodgate trial ran independent of pump operations, but local hydrological conditions were similar, i.e., the downstream river level was rising. Fish counts were sub-sampled at 1 frame·15minute^{-1}, and also incorporated 30-min pre- and post-floodgate closure to ascertain whether fish were deterred by the floodgate entering the water. The median dawn counts were then used for statistical comparison between two other five day periods of normal operation (floodgate raised); (1) immediately after the floodgate trial (20–January 24, 2020), and (2) a period with comparable magnitude and duration of rising and falling river levels to control for hydrological effects on fish movements (09–February 13, 2018).

2.4. Statistical analysis

The effect of diel phase on hourly fish counts was examined by creating four categories (photoperiod); dawn and dusk (equal to civil twilight ± 1h (i.e., three sample points)), day and night. Similarly, river level was divided into four categories (lvl_stage); rising water level (an increase of ≥0.5 m in 12h), falling water level (a decrease of ≥0.5 m in 12h), steady (reference) water level (≤6.5 m, neither rising or falling), and steady (elevated) water level (>6.5 m, neither rising or falling).

The fish count data were analysed using R version 4.1.2 (R Core Team R, 2021) in R Studio 2022.02.3 (RStudio Team R., 2022). All statistical figures presented in the results were created using R packages 'ggplot2', 'ggpubr', 'gridextra' and 'cowplot'. The fish count data were not normally distributed (Shapiro-Wilk normality tests (R function 'shapiro.test')) and non-parametric testing was used throughout, with descriptive values presented as medians (IQR). For statistical comparison between variables, a combination of Wilcoxon (R function 'wilcox.test') and Kruskal-Wallis rank sum tests (R function 'kruskal.test') was used (summary statistics generated with R package 'Rstatix'). Post-hoc testing was performed using Dunn's test (R function 'dunn.test' in package 'dunn.test'). Correlation testing was performed using Spearman's rank correlation (R function 'cor.test').

2.4.1. Modelling

The spread of variance in temporal fish count data were unbalanced across the grouping factors hour, lvl_stage, photoperiod, year and month and had a large proportion of zeros (20%). Multicollinearity of the predictor variables was checked by analysis of pairwise scatterplots and the Variance Inflation Factor (VIF ≥3) (R function 'vif' in package 'car') and all variables met rejection criteria (max VIF = 2.7). The variance between sample years was a concern due to the confounding effect of unpredictable pump operations. Therefore, a model with annual grouping factors was rejected to avoid overparameterisation and excess model complexity (Bates et al., 2015). Instead, the data were modelled using two approaches; (1) a Generalized Additive Model (GAM) to determine the non-linear effect of diel cycle (hour) and (2) a Generalized Linear Mixed Model (GLMM) to estimate the linear effects of environmental factors on the temporal fish count data within each study year.

The GAM was constructed using R function 'gam' in package 'mgcv', with the smoothing factor hour and subject specific deviation of month (formula = total ~ s(hour, by = month)). Model fit was checked by analysis of the k-index and the deviance explained by the GAM was calculated as 1 – (residual deviance/null deviance). The GLMMs for each study year were specified using the dependant variable fish count and the independent variables river temperature, river level, lvl_stage and photoperiod (fixed effects) (R function glmmTMB in package 'glmmTMB'). Sample month was included as a random effect to account for non-independence present in the response variable (using glmer optimizer 'bobyqa'). The maximal global model was favoured over a stepwise elimination to avoid overestimating the effect size of significant predictors, and Akaike Information Criterion (AIC) was used to assess model performance between Poisson and negative-binomial families (Schmettow, 2021). Overdispersion and zero inflation tests were used to assess the fit of each model (using R function 'testDispersion' and 'testZeroInflation' in package 'DHARMa') (Linden and Mantyniemi, 2011). Model assumptions were verified by plotting residuals versus fitted values in accordance to Zuur and Ieno (2016).

3. Results

3.1. Temporal dynamics of fish during non-operational river levels (question 1)

Hourly fish counts showed significant inter-annual differences ($\chi^2{}_2 = 88.517$, $p = <0.001$). The total (hourly) fish count was highest in year two (total, med, min, max, IQR = 7892, 3, 0, 20, 6 individuals·2 m^2 h^{-1}) and lowest in year three (total, med, min, max, IQR = 4238, 2, 0, 22, 3 individuals·2 m^2 h^{-1}). Year one was most similar to year three (total, med, min, max, IQR = 5500, 3, 0, 19, 5 individuals·2 m^{-2}) (Table S1). Furthermore, the intra-annual (hourly) fish counts were significantly different in all years when grouped by month ($\chi^2{}_5 = 845.71$, $p = <0.001$), and a post-hoc Dunn's test revealed no two months had similar fish counts, except February, which was not significantly different to January (all years combined) ($Z = 0.59$, $p = 0.277$).

Examining the fit of the GAM smoothed lines (hour smoothed by month) revealed a highly contrasting inter-annual relationship in the temporally dynamic fish count data (Fig. 2). Overall, the maximal daytime fish count (med, IQR: 4, 7 individuals·2 m^2 h^{-1}) was significantly higher than night-time (med, IQR: 2, 3 individuals·2 m^2 h^{-1}) ($W = 3407$, $p = <0.001$) (Fig. 3a). Accordingly, a spearman's rho correlation (r_s) was used to determine if daytime fish counts followed daylight hours, of which there was a positive correlation in year one ($r_s = 0.61$, $p = <0.001$), but not year two ($r_s = -0.79$, $p = <0.001$), or three ($r_s = -0.42$, $p = 0.0011$).

Further interpretation revealed the daytime fish counts were typi-

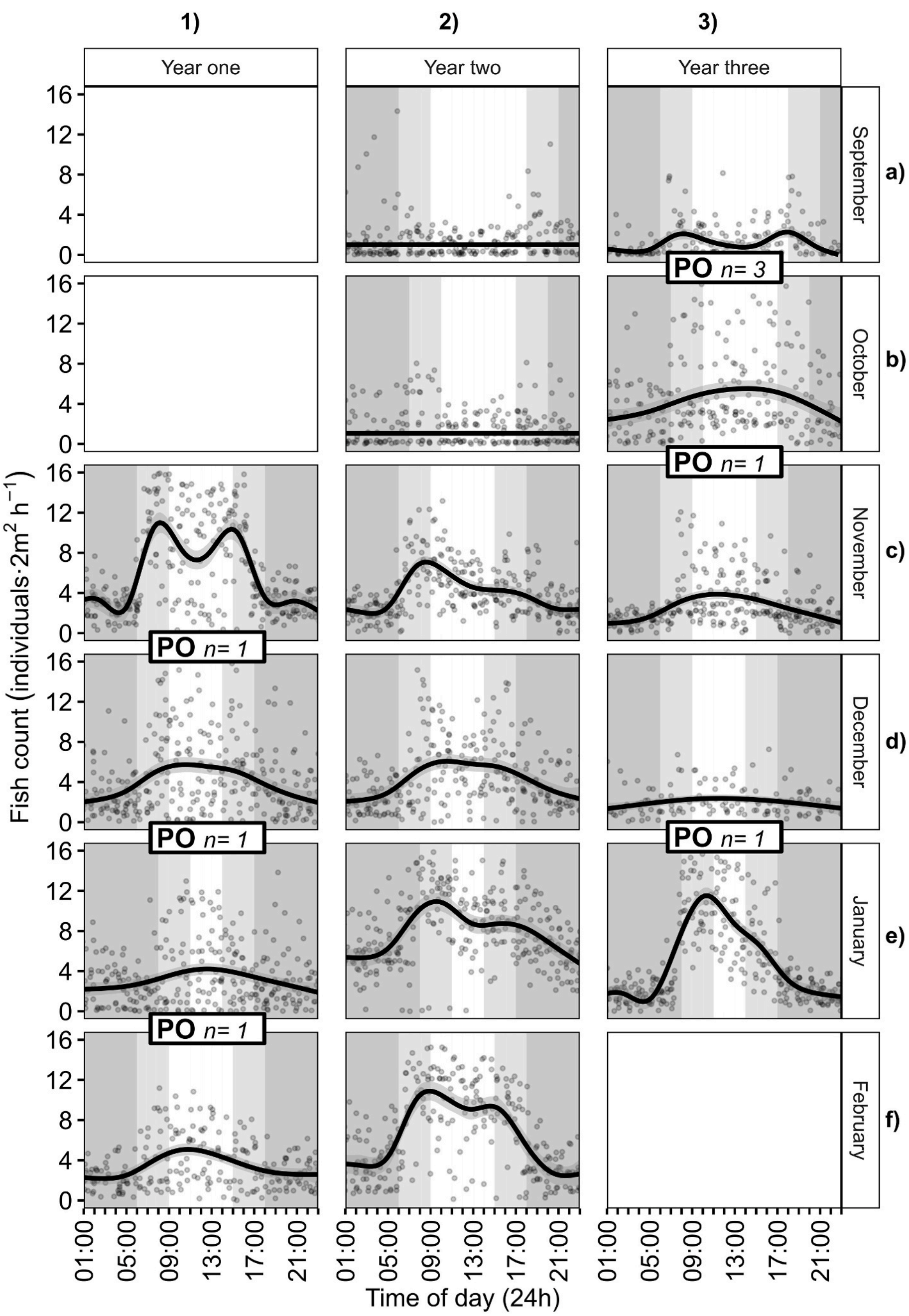

Fig. 2. Temporal dynamics of fish counts at Foss PS between November 2017 and January 2020 given by hourly sample point (insonified window). Plotted smoothed lines fitted by GAM with 95% confidence intervals (shaded envelope surrounding smoothed line). Grey dots are jittered points to reduce over-plotting. The photo period is represented by shaded bars in the plot area (light grey for crepuscular period). PO = pump operation between sample months (n = number of operations). (one and a half page width) 34.

cally maximised around the crepuscular period, peaking within 1h of sunrise (adjusted for season) and decreasing throughout the day before peaking a second time within 1h of sunset (Fig. 2). Thus, when testing for crepuscular fish activity, fish counts were significantly different between all photo periods ($\chi^2{}_3 = 321$, $p = <0.001$) (Fig. 3a), but fish counts were not significantly different between dawn (N = 3199, med, IQR: 4, 8 individuals·2 m^2 h^{-1}) and dusk (N = 2991, med, IQR: 4, 6 individuals·2 m^2 h^{-1}) ($Z = -0.59$, $p = 0.277$). Both photoperiods had significantly higher fish counts than during the day (Dawn: $Z = -2.45$, $p = 0.008$, dusk: $Z = -3.13$, $p = 0.0013$) and night (Dawn: $Z = 12.27$, $p = <0.001$, dusk: $Z = 13.04$, $p = <0.001$), confirming the importance of the crepuscular period.

The intra-annual differences in fish counts were further interoperated by including the frequency of pump operation. For example, fish counts in November of year one were clearly modulated by the crepuscular period (Fig. 2.1c), but the slope of GAM fitted line flattens throughout subsequent sample months as sequential pump operation takes place. Year two, in which pumps did not operate, was in direct contrast to year one where the strength of the crepuscular relationship increased throughout monthly samples. The stochastic pump operation in year three was in turn associated with an inconsistent crepuscular relationship between months.

3.1.1. *GLMM selection*

The GLMMs using Poisson distribution (family = Poisson) were overdispersed (dispersion >1.2) which was improved (Δ AIC ≥400) by using a negative-binomial model (family = nbinom2) (Table S2). After zero inflation tests indicated excess zeros in the simulated values (ratioObsSim >1), adding a zero-inflation parameter (ziformula = ~1) to the negative-binomial GLMMs further improved the models. These zero-inflated GLMMs with negative-binomial distributions resulted in the lowest AIC values. In year three an increase in AIC by 2 was accepted

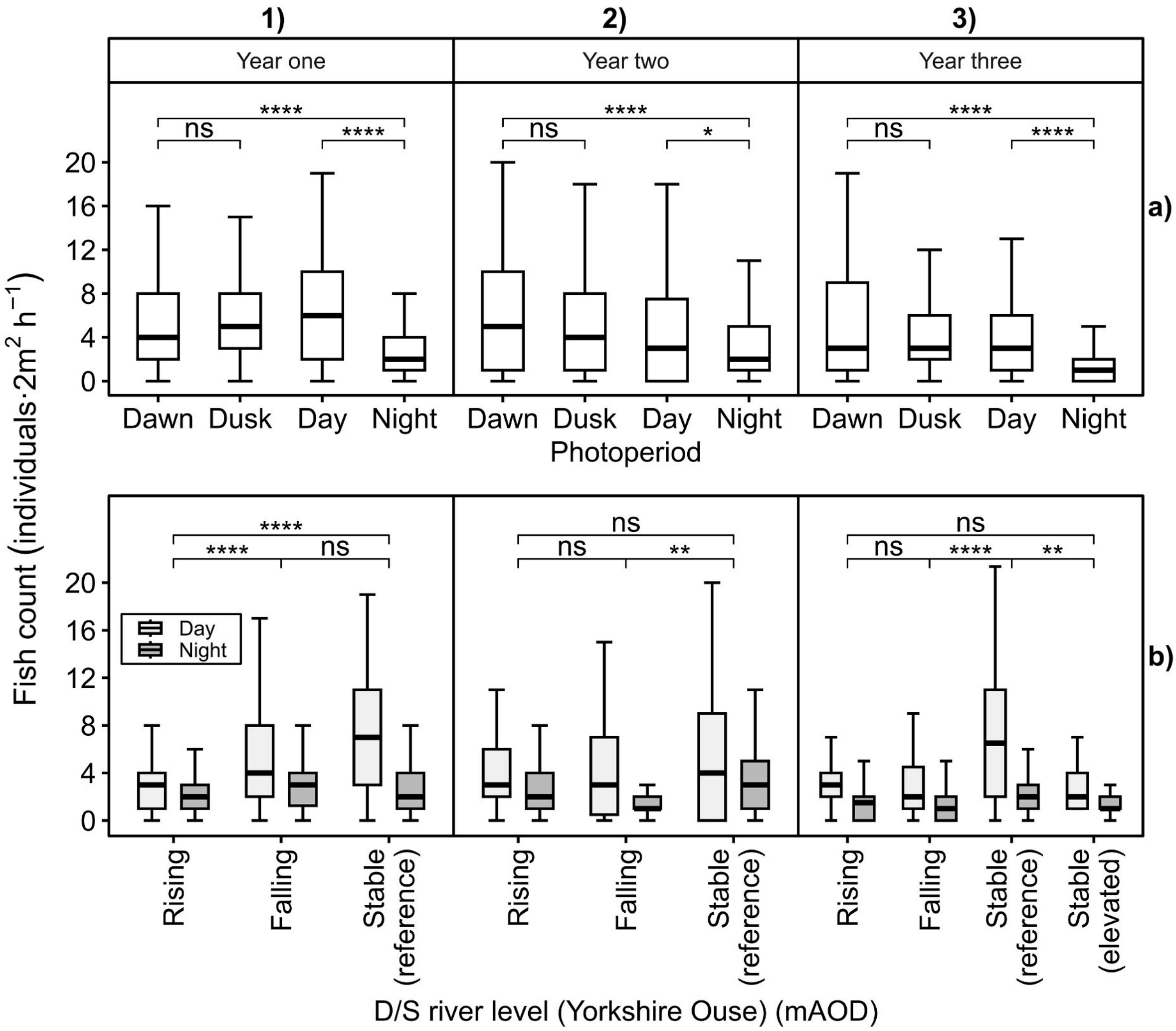

Fig. 3. Fish count at Foss PS in categories a) photoperiod and b) lvl_stage within day and night light periods. Lines represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance between categories indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001). D/S = downstream. (full page width) 35.

to maintain the variance modelling between the three GLMMs. Accordingly, the final three zero-inflated GLMMs with negative-binomial distributions were selected to analyse the effects of environmental variables on the temporal fish count data and model validation indicated no problems (Table S3).

3.1.2. Key correlates influencing temporal fish count

The decision to create independent annual models was supported by the differences in among-month variation between the three study years. In year one, falling and stable (reference) river levels were positively correlated with fish counts, but only falling levels were significant. However, the stable (reference) levels were more important as a predictor of fish count during the day (Fig. 3.1b). The same relationship was observed in year two, except the stable (reference) level was also significant when compared to the intercept of rising levels ($p = 0.001$). In year three, there was no significant relationship with lvl_stage, however the stable (reference) levels showed the same diel relationship as year two and the stable (elevated) levels were also negatively correlated (Fig. 3.3b). Overall then, the hourly fish counts had a significant negative relationship with river level ($p = <0.001$; Fig. 4a). Additionally, there was a negative correlation between fish count and river temperature, which was significant in year two ($p = <0.001$), but not year three ($p = 0.105$; Fig. 4b).

3.1.3. Population size structure

Length-frequency analysis showed that the size distribution of imaged fish had limited temporal fluctuation in size classification. Distribution of fish counts in the three most common size classes (0–10, 11–20, 21–30 cm) suggested the fish count data represents a diverse multi-species community of differing ages. At least 81% of imaged fish were classified as 11–20 cm, which likely represents a younger overall mean population age (Fig. S2). The only exception to this pattern was a recording of fish >50 cm, primarily during the night.

3.2. Temporal dynamics of fish during operational levels (question 2)

Total daily fish counts 24 h before (Pre-PO; total, med, IQR: 323, 6, 8 individuals·2 m^2 h^{-1}) and after (Post-PO; total, med, IQR: 55, 1, 2 individuals·2 m^2 h^{-1}) two independent pump operations (October 2019) were significantly different ($W = 2007$, $p = <0.001$). Fish counts reduced by 85% ($W = 478.5$, $p = <0.001$) and 82% ($W = 547$, $p = <0.001$) after the two pump operations (Fig. 5a).

3.3. Dawn floodgate operation testing (question 3)

The fish counts during dawn when the floodgate was lowered (med, IQR: 1, 2 individuals·2 m^2 15minute^{-1}) were significantly lower than the following 5-day period of normal operation (med, IQR: 8, 8

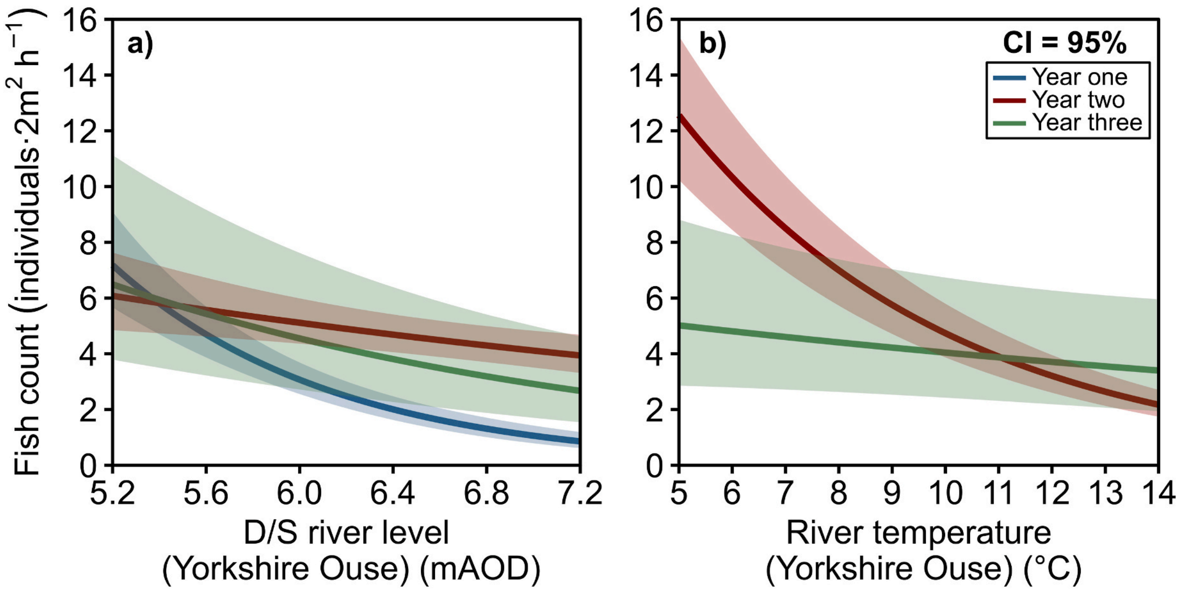

Fig. 4. The effect of environmental factors on fish counts at Foss PS between November 2017 and January 2020. Negative binomial lines fitted by the GLMMs (Table S3) chosen in the model selection process (Table S2). 95% confidence intervals represented by shaded envelope surrounding smoothed line (upper and lower bounds). D/S = downstream. (colour required in print, one and a half page width) 36. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

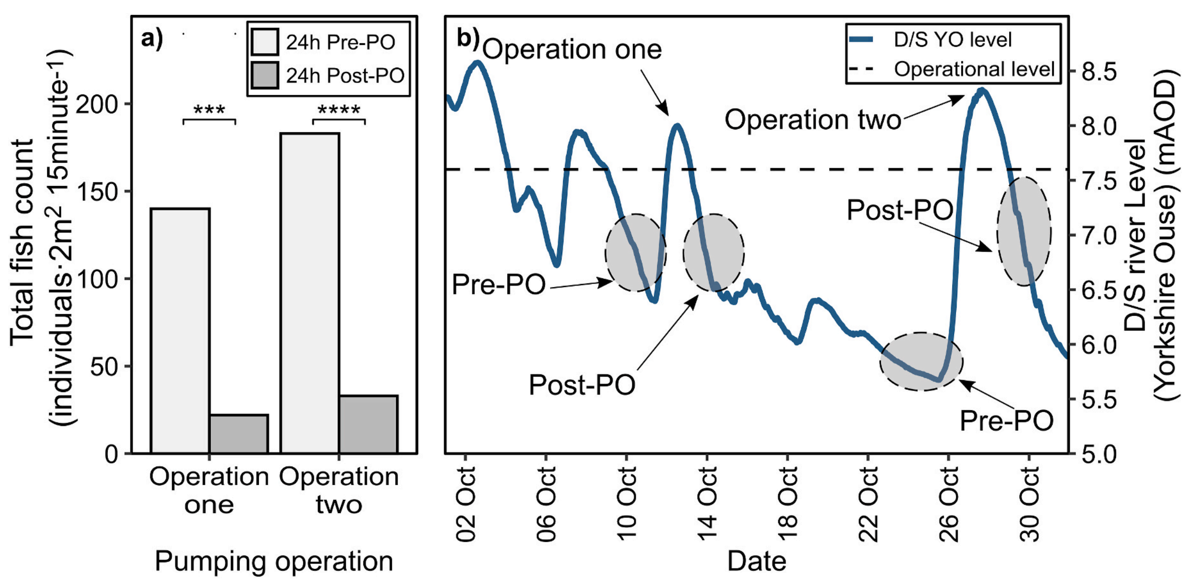

Fig. 5. a) Total daily fish count at Foss PS observed in a fixed 24h period (00:00–00:00) before (24h Pre-PO) and after (24h Post-PO) pump operation and b) annotated hydrograph for October 2019 showing the sonar sample periods (grey circles) during operations one (11/10/19: 36h pumping) and two (26/10/19: 56h pumping). Significance indicted by Wilcoxon rank sum (ns = not significant, * = P ≤ 0.05, ** = P ≤ 0.01, *** = P ≤ 0.001, ***** = P ≤ 0.0001. D/S = downstream. (colour required online full page width) 37. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

individuals·2 m^{-2}) ($W = 546$, $p = <0.001$) (Fig. 6.1a & 6.2a). The same effect was seen when compared to a hydrologically comparable period in 2018 (med, IQR: 7, 7 individuals·2 m^2 15minute^{-1}) ($W = 3664$, $p = <0.001$) (Figs. 6.1a and 6.3a), which was similar to the 5-day period of normal operation in 2020 ($W = 1693$, $p = 0.06$), but the crepuscular periodicities were stronger in the post floodgate trial comparison (Fig. 6.2b).

4. Discussion

Knowledge on the impacts of hazardous intake operation on temporal (seasonal and diurnal) movements of river-resident lowland fish communities remains underdeveloped. Such knowledge needs to be integrated into operational management to protect fish. This pluri-annual study quantified the temporal dynamics and non-spawning movements (Lucas, 2000) of a lowland fish community at an off-channel pumping station in autumn and winter; a period not often considered for conservation and management of river-resident fish. Direct observation of fish movements was achieved using an underwater multi-beam sonar, which allowed for the passive quantification of temporal dynamics of fish movements, without the need for invasive or destructive techniques. This revealed seasonal and inter-annual

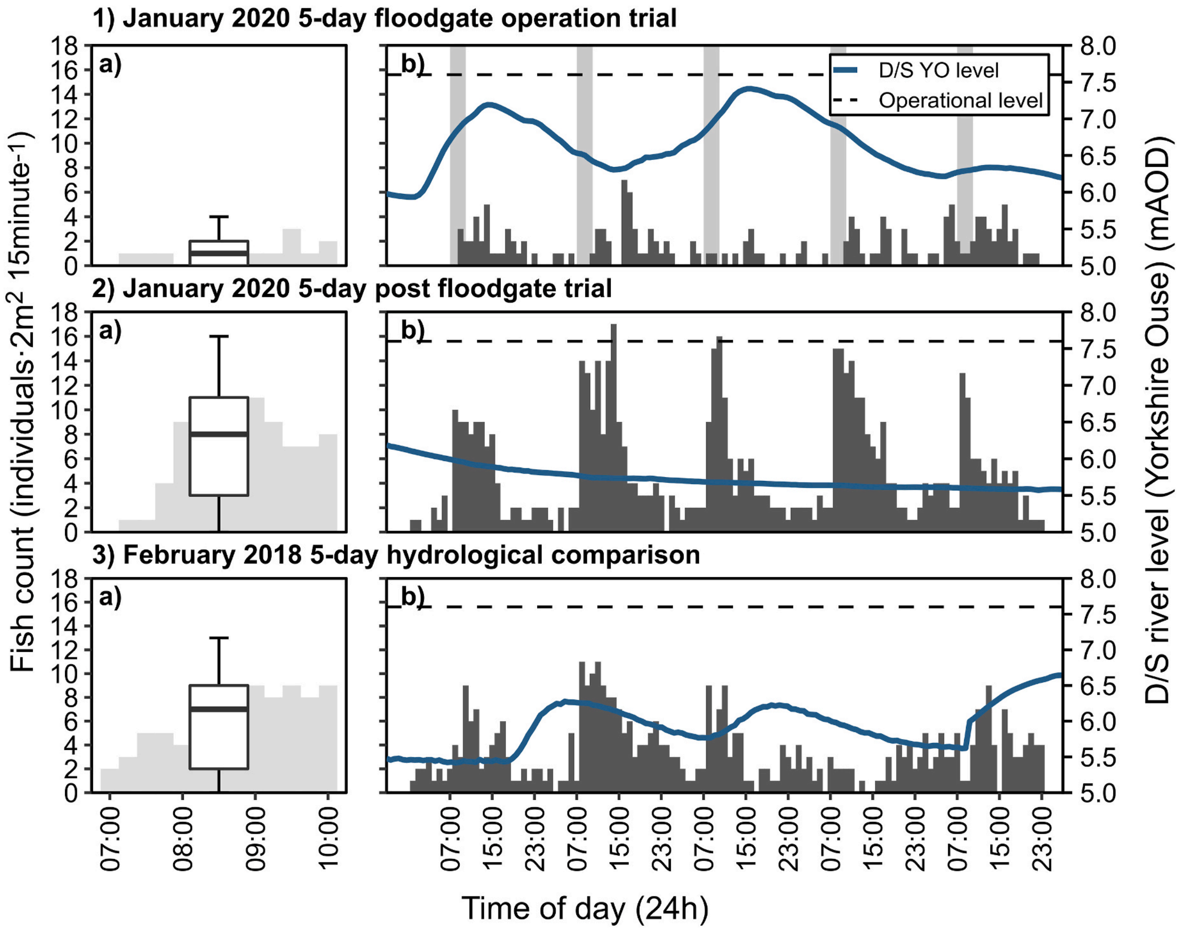

Fig. 6. The floodgate testing process given as a) boxplot (lines represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier) and histogram of fish counts measured during the dawn photo period and b) histogram of the observed fish counts with secondary axis overlaying hydrograph of downstream river level. Facet 1 visualises the floodgate testing process, with the period the floodgate was lowered represented by vertical grey shading (07:30–09:30). Facet 2 provides comparison in the period immediately following the trial, and facet 3 provides comparison with a hydrologically comparable period. D/S = downstream. (colour required online, full page width) 38. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

variations in diel movements, which were strongest during a 'baseline' year with no pump operation. Two years of 'impact' data revealed pump operations severely disrupted the regular ecological functions (e.g., diel lateral movement between main-river and off-channel area) of the local fish community. Modification of floodgate operations, which is seldom considered for the protection of river-resident fish, appeared to be a promising management option for preventing immigration of fish into a hazardous intake area.

4.1. Seasonal and diurnal temporal dynamics of fish

The diel light cycle is a fundamental factor when considering the phenomena of fish moving between differential day and night habitats (e.g., Janáč and Jurajda, 2013). Here, fish abundance was highest during daylight and lowest at night which was in agreement with prediction (i). However, fish exhibited strong temporal periodicities in abundance, which included both day- and night-active fishes as well as diel and seasonal variability. These findings are probably a consequence of studying a multi-species fish community that have inter- and intra-species differences in diurnal and nocturnal behaviours. Indeed, Nunn et al. (2010) demonstrated that diel movement patterns of lowland fish between a small tributary and the main River Avon was species specific. In Nowak et al. (2019), dace (*Leuciscus leuciscus*), bleak (*Alburnus alburnus*) and roach (*Rutilus rutilus*) showed shifts from nocturnal to diurnal behaviour associated with seasonal movements between a small stream and a main-river. Accordingly, the temporal results presented in this study possibly include an undetected diel changeover in fish assemblage. This was also supported by the tendency for more >50 cm fish to be recorded during the night than the day in this study. Any considerable assemblage changeover could then conceivably include species-specific differences in periods of movement and rest (Shukla et al., 2021), and the resulting temporal dynamics would help explain why the fish counts in this study did not always closely align with light periods.

Lateral movements of fish from main-river channels into backwater habitats are particularly important for flow refuge (Hohausova et al., 2003; Lyon et al., 2010), and thus movement is not exclusively mediated by prevailing light levels. During this study, it was not possible to disentangle whether sonar imaged fish were present due to the backwater, or whether infrastructure at the PS (sub-aquatic concrete structures, weedscreen and sump chamber) provided cover and refuge from main-river stressors (i.e., flow and predation). Given, maximum fish abundance and activity occurred during the crepuscular light periods, which supported predictions (i) and has also been found for lowland fish movements elsewhere (Barry et al., 2020). Roach, for example, may move laterally throughout the diel period, but maximal movement occurs at dawn and dusk (Hohausova et al., 2003; Heermann and Borcherding, 2006). Similarly, Conallin et al. (2011) reported frequent bi-directional movements of fish between a main-river body and perennially connected off-channel habitat, and Bolland et al. (2008) observed lowland fish moving towards a marina at dawn and away at dusk. Therefore, the crepuscular movement patterns found here were likely caused by fish moving towards and away from Foss Basin at dawn and dusk, respectively. Undoubtedly, these findings have important considerations for the operational timing of river structures that can interact with lateral fish movements, especially those associated with emigration and immigration of fish between water bodies (see Section 4.1.5).

4.2. Ecological considerations for temporal dynamics of fish

In year two (no pump operation; baseline year), the GLMM revealed a negative correlation between river temperature and daily fish counts, i.e., the importance of Foss Basin as refuge (during low flow) increased throughout the winter. This finding is in agreement with Allouche et al. (1999), whom suggested low-flow backwaters offer relief from temperature costs (e.g., decreased metabolism, feeding, and swimming performance). That said, diel variations in fish aggregations in Foss Basin were also likely influenced by unquantified ecologically conflicting trade-offs (e.g., Roff and Fairbairn, 2007). One explanation for these movements is a discrete diel shift between foraging phases and predation evasion, particularly from piscivorous birds that feed during the day (Mulder et al., 2019). Notably, in the UK, cormorants (*Phalacrocorax carbo*) migrate inland to forage during the winter (Jepsen et al., 2018), resulting in a seasonal increase in predation pressure that corresponded with the progressively elevated crepuscular periodicities in fish counts observed in year two. Elsewhere, the dispersal of river fish towards isolated winter refuge habitats has also been attributed to evasion of piscivorous winter predators (Nunn et al., 2010; Thurow, 2016). Anthropogenic structures, like the hazardous intake studied here, can also provide refuge for prey fish (e.g., Russell et al., 2008) as vegetation in the main-river dies off during winter. Furthermore, avian predators are deterred by the associated human activity (Lemmens et al., 2016). Accordingly, the stochastic diel fish count data here may have been influenced by temporally variable predator-prey interactions (Brodersen et al., 2008).

Year one and three were characterised by rising river levels and intermittent pump operations, which resulted in periods of contrasting river level criteria to year two. Movements of lowland fish are intrinsically linked with large-scale river hydrology (Poff, 1997), and lateral movement into floodplains (Tripp et al., 2016; Koster et al., 2021), backwaters (Hohausova et al., 2003; Coulter et al., 2017) and off-channel areas (Lyon et al., 2010; Pusey et al., 2020) is common during elevated river levels and floods, particularly over winter. Such movements are considered be a behavioural adaptation to avoid adverse environmental conditions in main-river bodies. Hence, it was perhaps surprising to see that the temporal fish count data here was negatively correlated with river level in the GLMM; overall fish counts were highest during stable (reference) levels, and lowest during rising and stable (elevated) river levels (all years). A common conclusion from other studies which have assessed lateral movements of fish into off-channel habitats during non-flood periods (e.g., Conallin et al., 2011; Cheshire et al., 2016; Magoulick et al., 2021), is that intermittence in the availability of these habitats provides stimulus for lateral (seasonal) movements of fish. However, the prevalence of increased lateral fish movements into Foss basin during stable river levels suggests that hydrological stability was important for this lowland fish community. The potential reasons for reduced fish counts in Foss Basin during rising river levels could be that elevated levels in the Yorkshire Ouse and differing water velocities at the River Foss confluence mean fish either avoided this area during flood (Togaki et al., 2022), sought flow refuge in the main-river (Bolland et al., 2015), or did not exclusively use lateral movements as a strategy to manage harsh ecological conditions. The increase in fish counts during falling levels possibly then represents the gradual repopulation of the backwater once high flows subsided (Lucas and Baras, 2001).

4.3. Impact of pump operations

When Foss PS operated three independent conditions changed, all with potentially negative implications for fish in Foss Basin; the lateral connection to the main-river was blocked by the floodgate, hydrological conditions in the basin changed (Franklin and Hodges, 2015) and fish in the basin were at risk of entrainment (Martins et al., 2014). It was beyond the scope of this investigation to gather direct evidence of the scale and impact of entrainment (e.g., netting the outfall during pump operation). Nonetheless, in support of prediction (ii), the total daily fish count reduced by 85% following two independent pump operations. Furthermore, the confounding difference in the seasonally progressive crepuscular fish counts between a year with no pump operation (year two) and two years with intermittent operation (year one and three) suggests that these operations disrupted the regular ecological behaviour of this fish community. Indeed, the temporal dynamics in year one were not related to temperature, and the GLMM correlation in year three was insignificant. Ultimately, these results have provided new evidence that hazardous intake operation potentially endangers river-resident fish populations and can severely impair ecological function.

4.4. Impact of floodgate operations (independent of pump operation)

Normal floodgate operation at Foss PS is in direct contrast to floodgates which form a perennial barrier, from which studies on these structures typically recommend more frequent opening to improve fish passage (Doehring et al., 2011; Wright et al., 2015). That said, given that closing floodgates prevents passage of fish, optimising their operation could provide a quick and cheap non-engineered solution for reducing lateral movements of fish into hazardous areas. Using fish movement knowledge gathered in year one and two (e.g., lateral, crepuscular movement), floodgate operation was modified in year three to assess whether immigration of fish from the main river into the backwater was prevented. As predicted (iii), lowering the floodgate ahead of dawn significantly reduced immigration of fish into Foss Basin, independent of hydrological conditions. Coupled with the finding that fish returned to their normal movement pattern immediately after the trial period, the modified floodgate operation could be advantageous for fish protection if implemented at dawn ahead of pump operation.

4.5. Directions for future research

Development of modified floodgate operations to reduce entrainment of fish (e.g., Perry et al., 2015) requires further investigation and studies at different hazardous intakes are recommended to compliment this work. In particular, monitoring downstream of the floodgate would have provided an enhanced understanding of whether fish approached the basin when the floodgate was lowered. It is important to iterate that even though fish counts were lowest during rising river levels, extrapolating these numbers suggests the potential for thousands of fish to be occupying the backwater during pump operation. Understanding the requirement for the protection of fish residing in Foss basin after the floodgate was lowered for pump operation was beyond the scope of this study. In this case, one option would be to install artificial habitat for flow refuge without interrupting flow conveyance and elevating flood risk. Thus, future studies should aim to quantify both natural flow velocities (no operation) and those generated by pump operation, possibly informed by Computational Fluid Dynamics (e.g., Mulligan et al., 2017).

Considering the prevalence of hazardous intakes (including PSs) on lowland rivers around the world, understanding river-resident fish movement around these structures clearly warrants further investigation. Using DIDSON provides a suitable method for moving away from monitoring singular species and enables the entire fish community to be studied. Given the dynamic findings presented here, perhaps future work, including telemetry investigations, need incorporate multi-species analysis. Additionally, in systems without heavy macrophyte growth, which limited this investigation to winter months, it would be beneficial to perform similar investigations during the summer to fully establish seasonal movements.

4.6. Conclusions and management implications

Although there is a growing body of literature which has proposed operational changes to hazardous intakes based on ecological considerations for diadromous fish (Egg et al., 2017; Bolland et al., 2019; Baker *et al.*,2021), river-resident fish are currently underrepresented in management plans for hazardous intakes globally. During this study, many thousands of river-resident fish across a multi-species community were passively and non-invasively quantified (using multi-beam sonar) during autumn and winter over three years with highly contrasting hydrology, including a year without pump operation. The latter enabled an unprecedented understanding of the ecologically sensitive temporal activity patterns of lateral fish movements between the main-river and backwater, the impact of pump operation to be quantified and the formulation of low-cost non-engineered operational changes for fish protection. Specifically, crepuscular movements into the backwater were predicted by the photoperiod and cool temperatures, and were presumably influenced by trade-offs between feeding and predation costs, but were disrupted by intermittent changes to water level. Prolonged periods of pump in-operation in year two led to large aggregations of fish in the basin which, paradoxically, potentially elevates entrainment risk when pumps do start-up. Collectively, the findings in this paper highlight the positive outcomes that can be gained from having a thorough understanding of the temporal movement of fish in the immediate vicinity of hazardous intakes. Indeed, this knowledge has led to the identification of the following management recommendations:

(1) Overall, fish abundance was highest during daylight and lowest at night, which was in agreement with predictions (i); pumps should not be started during the day to protect the most fish.
(2) Given fish tended to immigrate into Foss Basin at dawn and lowering the floodgate during a trial temporarily interrupted this movement, which was in agreement with predictions (i, iii), the floodgate should be lowered prior to dawn ahead of predicted pump operation due to elevated river levels.

The need to balance these operational changes based on ecological fish considerations, i.e., start pumps at night and lowering the floodgate at dawn, whilst maintaining flood protection, cannot be understated. It is hoped these recommendations can be successfully incorporated into management whilst not increasing societal flood risks if they are carefully timed towards predicted hydrological conditions. Manipulating operations of existing infrastructure will be more cost-effective than retrofitting alternative protection measures (e.g., fine-mesh screening). While the findings from this study should readily transfer to management of similar structures, there may be locally specific ecological and hydrological considerations. Ultimately, human-mediated river use is rarely synchronised with the ecological needs of fish, and compromises between both elements are essential to ensure long-term sustainability of riverine ecosystems. Here, this study has uniquely shown how long-term knowledge of the river-resident fish community at a hazardous intake across a wide range of hydrological conditions led to the development of non-engineered protection strategies.

Credit author statement

Josh Norman: Investigation, Validation, Formal analysis, Software, Data curation, Visualization, Writing - original draft, Writing - review & editing. Rosalind Wright: Funding acquisition, Equipment resources, Writing – review. Andrew Don: Initial conceptualization, Funding acquisition, Writing – review. Jonathan David Bolland: Conceptualization (overall project), Funding acquisition, Methodology, Resources, Supervision, Writing - review & editing.

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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

The datasets generated during and/or analysed during the current study are available at https://doi.org/10.5281/zenodo.7696102

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.117716.

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