Journal name

Freshwater Biology

Article type

Research article

Manuscript title

Impact of anthropogenic infrastructure on aquatic and avian predator-prey interactions in a modified lowland river

Running head

Anthropogenic impacts on predator-prey

Author names

Josh Norman[a], Jake Reeds[b], Rosalind M. Wright[c] and Jonathan D. Bolland[a]

Author affiliations

[a] Hull International Fisheries Institute, University of Hull, Hull, UK

[b] Environment Agency, Stepping Stone Walk, Winfrey Avenue, Spalding, Lincolnshire, PE11 1DA, UK

[c] Environment Agency, Rivers House, Threshelfords Business Park, Inworth Rd, Feering, CO5 9SE, UK

Corresponding author

Josh Norman, Hull International Fisheries Institute, University of Hull, Hull, UK. Email: J.Norman2@hull.ac.uk

Keywords

behavioural game; habitat; landscape of fear; non-consumptive effects; pumping station

Abstract

1. The relationship between aquatic and avian predators and prey is a fundamental process that influences the ecological dynamics of freshwater communities; a landscape of fear underpins spatial and temporal habitat use of prey, i.e., non-consumptive predation effects. For example, complex marginal vegetation and other natural in-river refuges are known to be important for prey to manage predation risk and predators must alter their behaviour in response to habitat patches prey occupy. However, it is unclear how prey respond to predators, and vice versa, in heavily modified degraded lowland rivers with a high degree of river maintenance measures; a component critical for flood risk management globally. Such modifications could lead to prey seeking refuge at hazardous anthropogenic infrastructure, but a robust quantification of predator-prey interactions in this context is required to develop this understanding.
2. Using multi-beam sonar (Dual-Frequency Identification Sonar: DIDSON), we non-invasively and simultaneously quantified the temporal rate of predator-prey interactions, the attack behaviour of predators, and the refuge seeking behaviour of prey at a pumping station intake during winter in a heavily modified lowland river.
3. Prey fish experienced temporally dynamic, density-dependant and species-specific predation risks from two dissimilar predators (i.e., aquatic vs avian); pike (*Esox lucius*) and cormorant (*Phalacrocorax carbo*). Generalised Linear Modelling (GLM) revealed that prey refuge use was positively associated with predator attack rate. Non-consumptive effects were evidenced by quantified changes to shoal structure (density, area), shoaling (group aggregation) and schooling (coordinated directional movement), including diurnal migrations to and from the pumping station intake for refuge.
4. Our results show that in the absence of natural refuge habitats the natural landscape of fear shifted and speculate that prey fish were paradoxically dependant on hazardous anthropogenic infrastructure, i.e., a pumping station intake, for refuge from predators in a degraded lowland river.
5. These findings strongly enhance our understanding of the impact of anthropogenic infrastructure on predator-prey interactions by demonstrating how flood risk management, including river maintenance measures, and associated anthropogenic infrastructure can impact the behavioural game played between aquatic and avian predators and their prey.

1 Introduction

River maintenance measures, including the installation and operation of anthropogenic infrastructure, for example water level management structures (here; pumping stations), are required for winter flood risk management in anthroposised water bodies such as lowland freshwater systems (Angelopoulos *et al.,* 2018; Bolland *et al.,* 2019). Globally, lowland rivers provide essential foraging resources and refuge habitats for freshwater communities including aquatic and avian predators and their prey but are becoming increasingly vulnerable to negative impacts from anthropogenic modifications (Oglecki *et al.,* 2021). Previous work in lowland systems has identified negative ecosystem impacts associated with anthropogenic modifications to ecohydrological processes, including increased nutrient run off (Kupiec *et al.,* 2021), water quality pollution (dos ReisOliveira *et al.,* 2019) and creation of unnatural hydrological conditions (Davis *et al.,* 2015). River maintenance measures required for operating anthropogenic structures may also be ecologically inconsiderate; channelisation and dredging homogenise river structure (Harrison *et al.,* 2004), and the seasonal removal of riparian vegetation and natural in-stream features (e.g., fallen trees) can exacerbate winter die-off of habitat (Singh *et al.,* 2021). Thus, river maintenance measures damage the distribution of macrophytes and remove macroinvertebrates (Darr *et al.,* 2014), and can lead to ecological degradation of freshwater communities (Baczyk *et al.,* 2018). Loss of winter refuge habitat is particularly problematic for prey fish species as aquatic and avian piscivorous predators are known to frequently overwinter on lowland rivers (Gardner *et al.,* 2013; Jepsen *et al.,* 2018). Thus, replacing the natural diversity and spatial distribution of aquatic habitats with anthropogenic structures is expected to have a negative impact on the ecological interactions between predators and prey, but this remains poorly understood.

The relationship between piscivorous predators and prey fishes is a fundamental process which influences the ecological dynamics of freshwater communities (Beauchamp *et al.,* 2007). Consumption of prey by predators exerts a strong influence on food-web dynamics by reducing the abundance of prey (Preisser *et al.,* 2007). Species-specific predation (i.e., aquatic or avian predators) factors then directly affect the structure of freshwater communities by altering size, growth and age structure of prey (Beauchamp *et al.,* 2007). For instance, in Martinoli *et al.* (2003) predation by wintering grebes (*Podiceps cristatus*) increased juvenile bleak (*Alburnus alburnus*) mortality and decreased overall fishery stocks. In contrast, Marchowski *et al.* (2022) found no long-term effect of goosander (*Mergus merganser*) predation on a multi-species fishery. Similarly, although others have shown aquatic predators (i.e., pike *Esox Lucius)* can induce population level mortality (e.g., Berg *et al.,* 1997), predator and prey in these systems must coexist within shared habitats and thus sympatric relationships typically moderate top-down predation. However, considering only the consumptive effects of predation neglects to capture non-consumptive interactions (e.g., non-mortal) and the resulting behavioural games of predator and prey (Laundré *et al.,* 2010).

Non-consumptive effects describe alterations to activity, habitat use, foraging and morphology (e.g., growth) of prey resulting from predation (Orrock *et al.,* 2013). For example, Kallo *et al.* (2020) found that whilst cormorant (*Phalacrocorax carbo*) predation pressure increased instantaneous mortality of trout (*Salmo trutta*), growth of surviving trout was also reduced. Fundamentally, prey species must trade benefits to reduce predation risk (Lima & Dill, 1990) and predators must alter their behaviour in response to habitat patches prey occupy (Laroche *et al.,* 2008). Shoaling (group aggregation) is important for predator risk detection, dilution, and confusion (Pitcher, 1998) and shoals may form dynamically in response to diurnal differences in the rate of predator attacks (Becker *et al.,* 2014). Management of predation risk then includes the movement of fish shoals into safer refuge habitats (e.g., boulders, trees, undercut banks, vegetation, and structures: Copp, 1997; Orrock *et al.,* 2013; Conallin *et al.,* 2014). However, long-term refuge use can also be costly to prey fish as resources are concentrated, competition is increased and foraging opportunities are reduced, a phenomenon which strengthens the non-consumptive effects of predation (Donelan *et al.,* 2017). In turn, schooling (coordinated directional movement) occurs when prey fish shoals move between low risk (refuge) and high risk (open water) habitats. For instance, Katz *et al.* (2010) experimentally demonstrated a 63.4% reduction in the time a prey fish (*Carassius auratus*) spent in open water when an avian predator (*Egretta garzetta*) was present and Campanela *et al.* (2019) found crepuscular anti-predator movements of a multi-species prey fish community into refuge in response to multiple aquatic predators. The successful evasion of predators is therefore expected to be dependent on the local distribution and availability of refuge habitat (Heithaus *et al.,* 2009). Notwithstanding, predators must maximise foraging opportunities and therefore periods of density-dependent predation occur when prey leave refuge (Sih, 1984; Holbrook & Schmitt, 2002). Consequently, this behavioural game played by both parties influences the ecological dynamics of freshwater ecosystems by creating a landscape of fear, underpinning spatial and temporal habitat use of prey and the rate of interactions with predators (Laundré *et al.,* 2010; Basille *et al.,* 2015). However, to-date there is a paucity in the ecological information on predator-prey interactions in freshwater systems with anthropogenic modifications, and exactly how predators and prey interact at anthropogenic infrastructure in these settings is unknown.

Interestingly, non-operational pumping stations may inadvertently provide refuge for prey fish behind bar racks (weed screens) that prevent entrainment of debris (Norman *et al.,* 2023a). This structurally complex environment offers protection to prey fish from large aquatic and avian predators which are seldom able to fit through the bar apertures, and once passed the screen, the pump chamber is sheltered and able to hold thousands of fish. Additionally, many of these structures operate infrequently (e.g., once in five years), meaning large aggregations of fish accumulate over time and especially during winter. However, these refuges come with several caveats; when pumps operate they become hazardous to prey fish, with a high likelihood of mortality (Rytwinski *et al.,* 2017) and because they are often situated at terminal points (e.g., confluences), they can concentrate and confine fish (e.g., Smith *et al.,* 2020). The latter exacerbates density-dependant predation (Lannin & Hovel, 2011), and may counterintuitively enhance the non-consumptive effects of predators (e.g., Donelan *et al.,* 2017).

The operation and maintenance of anthropogenic infrastructure in freshwater ecosystems could lead to previously unquantified changes to natural ecological interactions of predatory fish, birds, and their prey. Additionally, knowledge of the temporal distribution of predators and prey in anthroposised water bodies, particularly the rate of their interactions and the behaviour of predator and prey at anthropogenic infrastructure is lacking. To address this knowledge gap, inform conservation of freshwater ecosystems and direct management of anthropogenic infrastructure, the objective of our study was to quantify the behavioural interactions between piscivorous fish and birds and prey fish at a pumping station intake, by measuring the temporal periodicities in the rate of predator-prey interactions, the attack behaviour of predators and the anti-predator response of prey fish during winter using multi-beam sonar. The risk allocation hypothesis predicts that prey will respond strongly to predators which are usually absent (Lima & Bednekoff, 1999; Ferrari *et al.,* 2010), and therefore in this study it was hypothesised that avian predation is more likely to evoke rapid responses (i.e., fleeing) in prey shoals than from aquatic predators which potentially occupy shared habitats. These differences were expected to affect refuge use in the presence of piscivorous birds because of increased tendency of prey fish to flee from unpredictable attacks.

2 Materials and methods

2.1 Study catchment and site

The Welland catchment is in the east Midlands of England and forms a catchment area of at least 1656 km^2 (Figure 1a). At its sources, water flows through pasture-dominated hills before reaching the floodplains in the lower Welland. The major tributaries of the West Glen and East Glen Rivers flow easterly into the Rivers Glen and Welland and a series of drainage channels. The River Welland then flows through Market Harborough, Stamford and Spalding, before becoming tidal and discharging into the sea. Historical catch data suggests common lowland prey fish expected in this catchment include roach (*Rutilus rutilus*), dace (*Leuciscus leuciscus*), perch (*Perca fluviatilis*) and chub (*Leuciscus cephalus*) with localised piscivorous predators including the northern pike and great cormorant (Environment Agency, 2022).

This study was performed during winter (October – December) 2017 after river maintenance measures (i.e., weed removal) took place at Bourne Eau pumping station. The pumping station is located at the confluence between the Bourne Eau and the River Glen (Lat: 52.754185 N Long: -0.289369 W) (Figure 1b) and is fronted by a 7m wide intake weed screen designed to prevent entrainment of debris. The Bourne Eau is a short, embanked temperate river (temperature range October – December 2017: 12.5 – 0.8 °C, Environment Agency, 2017) which rises in the town of Bourne and flows to join the River Glen at Tongue End. The Bourne Eau typically drains into the River Glen via gravity through a bypass channel with over spill weir and pointing doors adjacent to Bourne Eau pumping station which operates when the River Glen infrequently floods (Figure 1b).

2.2 Acoustic imaging (DIDSON)

Dual frequency IDentification SONar (DIDSON 300m, Sound Metrics, USA. http://www.soundmetrics.com/) was used to collect data on predator-prey interactions at Bourne Eau pumping station. The high-resolution multi-beam sonar allows for the passive collection of natural information on predator and prey in both light and dark, and without the need for invasive monitoring. Additionally, the DIDSON can provide an accurate measurement (meters (m)) of the insonified window which provides calibration and standardisation fish shoal measurements.

The DIDSON was installed on a bottom-mounted 2m vertical wooden post via a SoundMetreics X2-rotator. The post was driven into the right-hand riverbank and provided a submerged depth of 0.5 m (Figure 1b). Data and power cable was routed inside the compound building to 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°x14° beams, 512 bins) with a window length of 10 m (starting 0.42 m from point of transducer) at 8 frames s^{-1}, receiver gain at default and focus set to auto to account for changes in fish distance from the transducer.

The position of the DIDSON was aligned with the adjacent bank wall and imaging of the weed screen was used to confirm the correct underwater orientation of the sonar. This provided optimal data collection for this study, where imaging predator-prey interactions in front of the weed screen was a priority. Data collection was only interrupted to maintain equipment. Files were time and date stamped (hh:mm:ss – d/m/y) and stored in 10-minute intervals. All software inputs were performed in SoundMetrics software (DIDSON V5.26.24).

2.3 Data processing

This study uses a modified methodology first proposed in Price *et al.* (2013). To identify the temporal periodicities in predator-prey interactions, a 7-day sample period at the start of each month was selected to enable a representation of the full study duration (e.g., 7-days per sample month). Of this, the data were further sub-sampled into four two-hour discrete sample periods over a 24-hour day. These were dawn, daytime, dusk, and night-time. Day- and night-time samples were taken at midday and midnight respectively (11:30 – 13:30, 23:30 – 01:30). The crepuscular sample period was equal to civil twilight ± 1h to best capture fish behaviour around sunrise and sunset when fish were most likely to be active. The recorded files provided by the sonar were processed minute-for-minute by an experienced reviewer using an adjusted playback speed between 5x and 10x. This allowed quick backward and forward navigation and accounted for differences in fish activity.

2.3.1 Predation Related Event (PRE)

Verifying prey consumption in sonar images was difficult, ambiguous, and unreliable and instead predator presence in the sonar window was used to determine if a Predation Related Event (PRE) had occurred, which allowed for discrete predation events to be used as sample points for detailed analysis. Both predator and prey needed to be present in the insonified window for a PRE to be recorded. The duration of a single PRE was recorded from the first point when a predator entered the insonified window until the end point of prey shoal response after a predator left the insonified window. If a predator re-entered the insonified window within 30 s of a PRE ending (i.e., after prey shoal response) this would be considered a single PRE, rather than recording a new PRE which could result in artificially increasing the number of PREs observed. A total of 168 hours of DIDSON footage was analysed in which 147 PREs were identified. Based on initial exploratory observations, eight measures of predators and nine measures of prey were selected to include in the analysis (Table S1).

2.4 Measurements of predators

The species and number of predators present in the PRE was recorded. Only single predator encounters were observed and in all instances it was possible to visually identify predator species and attack status from body shape (e.g., fin shapes in fish and wingspan and/or body length of birds), swimming characteristics and dynamics of predator attack behaviour in sonar images. Two predator species were identified; northern pike (median, InterQuartile Range (IQR): 118, 17.25 cm) and great cormorant (med, IQR: 84, 18.5 cm) (Figure S1). Whilst it was not possible to explicitly confirm species, there were no other known piscivorous fish and birds present during this study. Predator size (±1 cm) was measured within the DIDSON software using the fish measurement tool. To quantify differences between attacked and unattacked prey, the attack status of the predator was recorded including number of attacks and attack duration. Diving behaviour is indicative of foraging in cormorants (White *et al.,* 2008). A predator attack was determined by rapid acceleration of a predator towards a prey shoal. Acceleration and deceleration of both predator and prey was associated with frame-by-frame differences in body shape and measurable change in spatial position of individuals in the insonified window. Attack duration was based on predator trajectory towards prey fish, with attacks being timed from the point of rapid acceleration until deceleration and interaction with prey shoal. As PREs typically met or exceeded one minute in length, the attack rate of predators was defined by the number of attacks per minute during a single PRE.

2.5 Measurements of prey

A prey shoal was defined by an aggregation of pre-sized fish (< 30 cm total length) which included synchronised movements and close inter-individual distances (e.g., one body length apart) within the insonified window. Although species-level identification was not possible due to dense fish targets and a fixed focal window (i.e., the sonar could not be moved to aid in identification), shoals were presumed to be multi-species prey communities based on historical catch records and behavioural response to predators (i.e., refuge association) (Environment Agency, 2022). Prey response to predators was evident by a rapid change in prey trajectory and areal response. The end point of prey response was considered when prey had aggregated and slowed movements relative to previous swimming behaviour prior to predator interaction. To provide a quantification of anti-predator prey responses, sonar images from discrete PREs required preparation. A background subtraction algorithm was applied in DIDSON software to discard static objects (e.g., walls) and speckle noise and image parameters (intensity: 25, threshold 10) were adjusted for image clarity. This process also removed the static weed screen of the pumping station from the image to facilitate frame analysis. To measure prey shoal size, area, density and to detect the areal and density response of prey to predators, two frames for every PRE were prepared for export to JPEG images. These were (1) 1s prior to the PRE (PRE_1) and (2) at the onset of prey reaction to predator (PRE_2) (e.g., when individual aggregations in the prey shoal rapidly change trajectories).

Exported frames were processed in ImageJ (Schneider *et al.,* 2012). DIDSON images were first converted to 8-bit JPEGS and image threshold set to 30/255 to allow for contrast between foreground and background fish shapes. To ensure accurate shoal measurements a fixed length (2 m) was acquired from the DIDSON images and calibrated to 169 ± 1 pixels. Once calibrated, the region of interest was set to the boundary of the prey shoal and measured using the area measurement tool. All fish present in the region of interest were counted using the particle counting tool to provide a measurement of shoal size. Density was then calculated as shoal size divided by area. The difference in areal and density measurements between PRE_1 and PRE_2 was used to determine the extent of prey areal and density response to predators.

2.5.1 Behaviour of prey fish at the weed screen

The extent at which prey switch sides at the weed screen was measured to determine the rate at which prey fish interact with the weed screen structure for refuge during predator interactions. Switching sides was determined by prey schooling and collectively crossing the centre line of the weed screen from left to right, or right to left. For comparison with the attack rate of predators, the weed screen switching rate was defined as the number of switches per minute during a single PRE. To enhance this level of analysis, the behavioural response of prey fish, including the direction of school movement towards and away from the weed screen was measured using seven discrete behavioural identifiers (Table S1).

The behavioural categories were chosen to reduce labour intensive data processing and best represent the clearest observation of different prey behaviours. Prey fish were defined as fleeing if there was an obvious rapid change in shoals trajectory (e.g., the shoal ‘bursts’) away from a predator attack. Conversely, fish were defined as avoiding predators if fish aggregated and avoided the predator by swimming away slowly without rapid acceleration or burst activity. When there was no obvious directionality to prey movements (e.g., when a shoal bursts), behaviour was recorded as (0) no response, (1) flee or (4) avoid. When directional movement (schooling) was observed this was categorised as (2) flee (into weed screen), (3) flee (away from weed screen), (5) avoid (into weed screen), (6) avoid (away from weed screen). Because PREs could include more than one predator interaction (e.g., multiple attacks), changes in prey behaviour were recorded and the duration of each behaviour was measured from the start of the reaction until the end of the reaction. Because of the unbalanced distributions of behavioural responses, it was not possible to determine the relationship between the directional response recorded and the weed screen switch rate.

2.6 Data analysis

The PRE data, including event duration, predator attack rate, prey areal and density response, prey weed screen switching and prey shoal behaviours were not normally distributed (Shapiro-Wilk normality tests: R function ‘shapiro.test‘), so results were summarized as medians + IQR and non-parametric Wilcox rank sum tests (R function ‘wilcox.test’) and Kruskal-Wallis rank sum tests (R function ‘kruskal.test’) were used for comparisons. Post-hoc testing was performed using Dunn’s test (R function ‘dunn.test’ in package ‘dunn.test’) to determine which levels of the independent variables differed from each other across the categorical variables. Proportional differences between species-specific predation factors were compared using a test of equal proportions (R function ‘prop.test’). Correlation testing was performed using Spearman's rank correlation (R function ‘cor.test’). To investigate if PRE duration and attack rate (continuous independent variables) and predator species (discrete independent variables) influenced weed screen switching rate (continuous dependant variable) a pair of Generalized Linear Models

(GLMs) were constructed (R function ‘glm’). A global model containing all terms was considered but multicollinearity across the independent variables caused erroneous coefficient estimates. Species interactions were also considered but increased the Akaike's Information Criterion (AIC) and thus were excluded. Given that the data were nonnormal (right-skewed) and nonnegative, the model was first fitted using Gamma distribution. However, this was dropped in favour of using Gaussian distribution and a log link function, which in this application reduced the AIC and provided more accurate predicted values (compared to fitted values), than a Gamma model. To remove zeros ($n = 5$) and allow the log-linked models to run, 1×10^{-9} was added to the dependant variable weed screen switching rate. All data were analysed using R version 4.0.2 (RCore Team, 2022) in RStudio 1.4.11 (RStudio Team, 2022) and figures were created using R packages ‘ggplot2’, ‘ggpubr’, ‘gridextra’ and ‘cowplot’.

3 Results

3.1 Temporal dynamics and predator behaviour

Pike were the most frequent predator observed, making up 81% of PREs. There was a positive linear trend in the count of pike PREs between October and December 2017 (Figure 2.1). There was no clear trend in cormorant PREs, which were highest in October and December but lowest in November (Figure 2.2). The duration of pike PREs was significantly longer (med, IQR: 85, 125 s^{-1}) than cormorant PREs (med, IQR: 39, 51 s^{-1}) (Wilcox rank-sum: W = 847, p = <0.001), and showed a positive linear trend between October and December where increased PRE duration was associated with night-time pike presence (Figure 2.1c). Differences in pike PRE duration were then attributable to sample period (Kruskal-wallis: $\chi^2{}_2$ = 14.16 p = <0.001) and attack dynamics (W = 1946, p = 0.04) as pike events were shorter when foraging at dawn and dusk, and longest during night-time with no observed attacks (Dunn's test: Z = -3.6, p = <0.001). Conversely, cormorant PRE duration was longest at dusk (51 s^{-1}), but overall, there was no significant effect of sample period ($\chi^2{}_2$ = 0.59 p = 0.74).

A total of 98 behaviours defined as attacks were captured throughout the duration of the study; 32% of pike PREs featured predator attacks (48 attacks in 120 PREs), from which the attack rate was highest during the crepuscular periods (med, IQR: 1.6, 0 $\text{attack}\cdot\text{min}^{-1}$) with no daytime and night-time foraging observed ($\chi^2{}_2$ = 13.66 p = 0.003; Table 1). In contrast, 100% of cormorant PREs featured attacks (50 attacks in 27 PREs), for which the attack rate (med, IQR: 3.3, 1.7 $\text{attack}\cdot\text{min}^{-1}$) was significantly higher than pike (W = 2916, p = <0.001). Cormorants, like pike, followed a crepuscular foraging dynamic, except foraging was maximised at dusk, and daytime, but no night-time foraging was observed (Table 1). The attack rate of both predator species was maintained throughout the duration of the study (Spearmans rank: pike r_s = -0.35, p = 0.15; cormorant: r_s = 0.06, p = 0.76), although the increase in pike PREs without attacks would suggest that foraging was reduced from October to December.

Shoal density was significantly higher in cormorant PREs (W = 1672, p = 0.012). Density-dependant predation was evidenced in pike PREs where pike attacked shoals that were denser than unattacked shoals (W = 548, P = <0.001). It was not possible to measure time until attack in cormorant PREs as their diving behaviour resulted in recording of instantaneous attack from the point of entry into the insonified window. Similarly, there was little variation in time until attack in pike PREs (med, IQR, 0, 28 s^{-1}), except in instances where pike attacked after a period of 'sit and wait' (max = 294 s^{-1}) (Table 1). However, the duration of attacks by cormorants (med, IQR: 3, 2 s^{-1}) was significantly longer than pike (med, IQR: 2, 2 s^{-1}) (W = 1599, p = 0.007).

3.2 Prey fish behaviour

3.2.1 Shoal size, areal and density response of prey

Overall, prey fish aggregated and used shoaling as their primary anti-predator response. From the frames used for analysis, an estimated 33000 prey fish were counted (using a particle counting tool; ImageJ). There was no significant difference in shoal size between sample months ($\chi^2{}_2$ = 4.46 p = 0.1). Although, prey shoal size exhibited a strong diel trend where individual counts were lowest at day and night and highest during the crepuscular period (dawn and dusk), which coincided with the maximal predator activity ($\chi^2{}_2$ = 46.69, p = <0.001).

Concerning the measurable areal response of prey fish to predator interactions, prey responded to pike attacks by rapidly forming a tighter shoal (med, IQR Δ area = -2.82, 2.64 m^2) with a significantly smaller response recorded for unattacked shoals (med, IQR Δ area = -0.63, 2.28 m^2) (W = 1403, p = <0.001; Figure 3a). Similarly, pike attacks resulted in shoals becoming denser (med, IQR Δ density = 2.4, 13.6) although this was not significantly different to unattacked shoals (med, IQR Δ density = 1.00, 7.12) (W = 792, p = 0.30; Figure 3b). Likewise, although not statistically different, the areal response to cormorant attacks was smaller than to pike (med, IQR Δ area = -1.94, 2.79 m^2) (W = 510, p = 0.16; Figure 3a). The density response was particularly interesting as prey shoals lost individuals when attacked by cormorants (med, IQR Δ density = -

2.3, 19.2), which was significantly different to the density response of prey when attacked by pike (W = 290, p = 0.04; Figure 3b).

3.2.2 Directional schooling behaviour and refuge use

In the presence of predators, observations of uni-directional prey fish movements from the river into the pumping station through the weed screen and vice versa (weed screen switching) confirmed the importance of this structure and provided a basis for inferential prey refuge use. Weed screen switching rate was significantly different between attacked and unattacked (med, IQR: 0.8, 2.87 switches·min^{-1}) shoals in pike PREs (W = 290 p = 0.004; Figure 3c), but there was no species-specific difference when attacked by either cormorants (med, IQR: 3.3, 3.4 switches·min^{-1}) or pike (med, IQR: 3.3, 3.8 switches·min^{-1}) (W = 277, p = 0.77; Figure 3c). Additionally, weed screen switching rate was positively associated with the attack rate of both predator species (Table 2, Figure 4a) and PRE duration in which cormorants were predicted to evoke a stronger weed screen switching response over event time when compared to pike (Table 2, Figure 4b). Thus, although prey fish that experienced a higher attack rate by both predator species were predicted to disperse more frequently into the pumping station as refuge, overall refuge use was predicted to be higher under cormorant predation when considering event duration.

Prey shoal behaviour at the weed screen was further described by movement in response to predator interactions; a total of 223 of which were observed with 48% fleeing and 52% avoiding (Table 3; Figure 5). The difference between response duration and response category was significant ($\chi^2{}_6$ = 116.75, p = <0.001) where flee responses were shorter (med, IQR: 12, 18.5s^{-1}) in duration than avoid responses (med, IQR: 91, 114s^{-1}) (Z = 6.40, p = <0.001) (Table 3). Prey fish mainly responded to cormorant attacks by fleeing towards the weed screen (56%) (17% flee away, 25% flee, 2% no response) (test of equal proportions: $\chi^2{}_2$ = 17.48, p = <0.001; Figure 5b). Conversely, prey fish fled away from the weed screen when attacked by pike (45%) (33% flee away, 22% flee) ($\chi^2{}_2 = 6.67$, p = 0.03; Figure 5a). Unattacked shoals did not flee, and their movements were described as avoiding (63%) with limited directionality towards (7%) or away from the weed screen (14%) (16% no response) ($\chi^2{}_2 = 125.4$, p = <0.001).

4 Discussion

This study has shown that predators exerted temporally dynamic and species-specific (aquatic and avian) predation risks on a multi-species freshwater fish community that was negatively impacted by anthropogenic infrastructure in a heavily modified lowland river. Non-consumptive predation effects were evidenced by quantified changes to shoal structure (density, area) and both shoaling (group aggregation) and schooling (coordinated directional movement), including diurnal migrations and use of an anthropogenic structure (pumping station intake) as prey refuge. Indeed, our results suggest that heavily modified freshwater ecosystems impact predator-prey dynamics by concentrating predator and prey resources and creating an unnatural landscape of fear. Although the use of refuge habitat to manage predation is well established in the literature (Berryman & Hawkins, 2006), these findings provide the first quantified evidence for the use of a hazardous anthropogenic infrastructure as prey refuge in modified rivers (but see Chester & Robson, 2013; Norman *et al.,* 2023a). In turn, this study proposes important considerations for how anthropogenic activities (i.e., flood risk management and river maintenance measures) in freshwater ecosystems can influence the behavioural interactions between piscivorous birds and fish and their prey.

Three winter months were chosen for the study period as this was after river maintenance measures (seasonal macrophyte removal) were performed. Correspondingly, the study area was associated with heavily degraded riverbanks and depleted instream habitat, which created a high risk to prey from predators. The results show no temporal (monthly) relationship in the rate of PREs (with attacks) for aquatic or avian predators, although there was a positive linear trend in the number of pike PREs (without attack) during winter. Measuring avian predation on fish is challenging and potential bird encounters (i.e., did not enter water) were not recorded, whereas aquatic predator presence was. Additionally, decreasing water temperature promotes more sessile behaviours in pike (Kobler *et al.,* 2008) and can reduce frequency and speed of attacks

(Ohlund *et al.,* 2015), which would explain why pike PREs increased throughout winter, but the number of attacks did not. Why cormorant PREs were reduced in November is unclear; the prey fish were still numerous and pike predation was not reduced. Amongst the possible reasons then include deterrence from agricultural practices (Lemmens *et al.,* 2016), turbidity conditions (Dodrill *et al.,* 2016) and movement to alternative foraging sites (Gremillet & Wilson, 1999).

Piscivorous birds rely on sight to hunt and require good visibility to locate prey fish (Becker *et al.,* 2014), so it was not surprising that cormorant predation in this study included daytime hunting. However, whilst overall pike presence was diurnal, there was no evidence for daytime foraging by pike, as seen elsewhere (Jacobsen & Perrow, 1998). The daytime foraging differences possibly result from contrasting avian (pursuit-dive) and aquatic (sit and wait) hunting strategies of cormorant and pike. Maximal activity and interactions of both predators and prey fish occurred during the transitional (crepuscular) period; similar to what has been described elsewhere for cormorants (Russell *et al.,* 2003; White *et al.,* 2008), pike (Kobler *et al.,* 2008) and prey fish (Helfman, 1986; Campanella *et al.,* 2019). During this low-light period, the twilight hypothesis would suggest that predators may have a visual advantage over prey because the ability for prey to detect predators is lowered (Pitcher & Turner, 1986). Thus, the crepuscular period made for a favourable hunting time at the structure studied here.

The temporal recurrence of this diel pattern suggests that prey fish in this modified freshwater ecosystem experience long periods of predation risk. According to the landscape of fear hypothesis (Laundré *et al.,* 2010), it is likely that prey have learnt to assess this temporal predation risk (Bosiger *et al.,* 2012) and diel activity of prey fish in this study was timed to avoid maximal predator activity (e.g., Ory *et al.,* 2014). Accordingly, prey fish shoal size at the pumping station intake varied within the diel period, ranging from small (<30 individuals) dispersed and infrequent shoals at night, to medium (≤ 200 individuals) shoals during the daytime and large (> 300 individuals) dense shoals during the crepuscular period. The reduced fish counts during the day certainly suggests daytime cormorant predation has a major influence on prey activity (Bosiger & McCormick, 2014). In brief, we speculate that predictable predation risk stimulated prey to seek refuge at the pumping station intake during the day, which was associated with recurring diel movement of prey towards reduced-risk refuge at dawn, and movement towards high-risk foraging sites at dusk, as has been previously proposed at a flood-relief pumping station elsewhere (Norman *et al.,* 2023a). Therefore, diurnal movement behaviour was carefully timed to facilitate trade-offs between foraging out of refuge and predator evasion (Fu *et al.,* 2015), with prey presumably foraging nocturnally (Metcalfe *et al.,* 1999). Elsewhere, this has been reported for lowland fish including brown trout (*Salmo trutta*) (Conallin *et al.,* 2014), but observations in multi-species communities like that studied here, are scarce. Overall, these findings demonstrate how isolated anthropogenic infrastructure could impact freshwater ecosystem structure by modifying the landscape of fear and concentrating interactions between predators and their prey (see Sand *et al.,* 2021).

Recordings of singular predators throughout this study suggest that predator activity, rather than predator abundance, influenced the diel behavioural pattern of prey. The results here show that cormorants were very active hunters with at least 50 attacks recorded in 125 hours of DIDSON footage (dawn, day, dusk), although this was not comparable to other studies due to methodological disparities. Despite having over 4x as many PREs as cormorants, there was 48 attacks by pike during the same period, which was like pike attack rates recorded elsewhere (Turesson & Bronmark, 2004). Accordingly, when hunting, the attack rate of cormorants was twice that of pike. This is in line with previous suggestions that cormorants have a high attack rate, in part because of limited underwater vision and a tendency for multiple short-distance pursuits once underwater (White *et al.,* 2007).

On the other hand, pike in this constrained lowland setting were frequently observed to 'sit and wait', especially at night where they selected nocturnal resting sites close to the pumping station. This was followed by morning periods of active pursuit and attack on nocturnal prey fish returning from the upstream river, which was exemplified by maximal foraging at dawn. Conversely, cormorant foraging was maximised at dusk; probably because they were able to exploit high densities of prey leaving shelter in contrasting light. Indeed, the results show that the response of birds to prey behaviour included density-dependent predation i.e., cormorants selected denser shoals than pike for hunting, similar to other studies (e.g., Lemmens *et al.,* 2016). Given, pike consistently attacked denser shoals than those where attacks did not occur, contrasting previous findings which found prey density was less important for determining when pike attacks occur (Turesson & Bronmark, 2004). These findings reflect the behavioural game between predator and prey (e.g., Laroche *et al.,* 2008).

The extent of prey shoal response to both predator presence and attacks included changes to area and density, which followed typical descriptions of shoal structure (Pitcher, 1986; but see Romenskyy *et al.,* 2020), and was accompanied by directional movement behaviours associated with refuge use. In encounters where pike did not attack, the primary anti-predator response was avoidance and shoal contraction, which was associated with small reduction to shoal area and marginal increases in density, but no apparent refuge use. The fact that prey were able to avoid pike without fleeing proposes some level of active risk assessment, and that pike presence may not be a threat alone (Ferrari *et al.,* 2010). Increased shoal density as an anti-predator strategy agrees with findings form others (e.g., Meuthen *et al.,* 2016), and the tendency for shoal density to increase when pike were present suggests a sit-and-wait strategy could invoke significant non-consumptive effects over time (Preisser *et al.,* 2007).

This study found significant differences in the way prey responded to dissimilar predator strategies. The initial shoal response to attacks by both predators was a ‘burst’ i.e., expansion from the point where the predator entered the shoal, followed by contraction. Prey shoals then responded to attacks from pike by fleeing and rapidly forming a smaller and denser shoal.

Conversely, when attacked by cormorants, the areal response was reduced and the density response suggested shoals lost fish i.e., cormorant attacks had a more immediate negative impact on shoal structure. Multiple successive attacks (i.e., a high attack rate) by cormorants was probably a combination of both predator behaviour (i.e., maximising number of attacks with limited dive duration) and prey behaviour (i.e., exploiting dense aggregations of prey) (e.g., Rieucau *et al.,* 2015). Faster prey aggregation during pike predation suggests that prey were able to respond more predictably to cues from aquatic predators, whereas they were unable to prepare a robust shoal response to cormorants without information on distance or trajectory (Hemmi & Pfeil, 2010). This pattern closely follows the risk allocation hypothesis (Lima & Bednekoff, 1999) i.e., prey responded strongly to predators that were usually absent (Supekar & Gramapurohit, 2020) and agreed with this studies hypothesis that avian predators will evoke stronger responses in prey.

Other studies have shown that structurally complex habitats reduce predation risk for prey (e.g., Ory *et al.,* 2014). Here, the weed screen used to protect the pumping station intake structure appeared to function as a refuge habitat and quantifying the weed screen switching rate provided evidence for species-specific predator-mediated habitat use (Mittelbach, 1986). During periods of high predator activity, the prey shoals increased the number of transitions between open water and refuge, i.e., inside the pumping station, behind the weed screen. When attacked by pike, prey fish fled but directional movement towards and away from the refuge was unbiased. But, when attacked by cormorants, prey fish primarily fled into refuge. Hence, prey fish were probably only protected from cormorants during the day when they could hide in the pumping station. Although there was no significant difference in refuge use when attacked by pike or cormorants, the high proportion of flee response into refuge in cormorant events, but not pike events, combined with increased refuge use under cormorant predation, but not pike predation, suggests the pumping station intake was most important as a refuge from cormorant predation.

The reduced refuge use during pike predation may suggest prey are more habituated to this predator due to their persistence in shared space (Ferrari *et al.,* 2010). In turn, when prey occupy the transitionary zone between refuge and open water, it allows them to swim into cover when fleeing from predators (Fu *et al.,* 2015). Likewise, anti-predator behaviours of prey in this study depended on the attack behaviour of predators and suggest prey may not always use structured habitat for protection (Martin *et al.,* 2010). Shoaling thus appears to be more appropriate for managing pike predation but may be ineffective for cormorant predation. These findings add real-world, non-experimental evidence to previous suggestions that enclosed and sheltered habitats are more important to protect prey from cormorants than pike (Lemmens *et al.,* 2016). Given, understanding this problem is confounded, in part, by the potential for multiple predator effects (Griffin *et al.,* 2013). In this study pike were more likely to concentrate and confine fish, resulting in evasive behaviour of prey and denser shoals, which may increase encounters with cormorants. On the other hand, unpredictable attacks by cormorants could overwhelm and distract prey, potentially increasing the success of ambush predators. Evidently, the behaviours of all parties can facilitate each other's hunting success if the response of prey to one predator increases the risk to the other predator (Ford & Swearer, 2013; Palacios *et al.,* 2018).

4.1 Conclusions and implications

Anthropogenic modifications are recognised as a major threat to freshwater biodiversity in lowland rivers (Dudgeon *et al.,* 2006). Similarly, anthropogenic infrastructure associated with river maintenance measures and flood risk management degrades freshwater ecosystems by removing essential habitats for predatory fish and birds and their prey. The findings in this paper highlight a previously unconsidered impact of anthropogenic infrastructure on predator and prey ecology in freshwater ecosystem by direct observation of predator-prey interactions. The majority of studies which have aimed to determine the non-consumptive effects of predation on the ecological dynamics of predator and prey have relied on studying isolated effects i.e., activity

(Orrrock *et al.,* 2013) and foraging (Catano *et al.,* 2015), but this study is amongst the first to simultaneously quantify the behavioural games of predator and prey in an aquatic setting. Multi-beam sonar has proved to be an effective tool for generating this understanding by quantifying unprovoked behaviours and interactions of predators and prey in a real-world setting. The outcomes of this study highlight the need for managers implementing flood risk management practices and river maintenance measures to include ecological considerations for the response of freshwater communities.

These findings argue that the impact of anthropogenic practices which modify freshwater ecosystems is underappreciated. Suitable winter habitats are lacking in modified lowland rivers, and fish in these ecosystems have increasingly fewer places to evade predators. Whilst fish in healthy ecosystems move between refuges to avoid predators, prey fish in the modified lowland setting studied here were likely confined to living with predators in hazardous habitats. Indeed, a scarcity of upstream habitat availability and tendency for dispersed prey populations to form large shoals over winter combine to speculate that prey fish in this study were paradoxically dependant on hazardous anthropogenic structure for refuge, and aquatic and avian predators have learnt to exploit this, similar to that proposed by Smith *et al.* (2020). This refuge provided the greatest level of protection for prey, but it is likely that resource quality is low i.e., access to food, space, and light (Donelan *et al.,* 2017), which could counterintuitively exert stronger non-consumptive effects of predators (Orrock *et al.,* 2013), potentially imposing individual (growth, foraging) and population level (reproduction) fitness costs. Additionally, the specific implication for the structure in this study is that fish may be exposed to hazardous water management strategies, i.e., pump start-up for flood protection purposes, which could remove thousands of fish from the upstream catchment (Norman *et al.,* 2023b).

Simultaneous observation and quantification of predators and prey, as presented here, is rare due to the methodological and financial challenges of studying such interactions in the wild using passive methods (see Becker *et al.,* 2014; Campanella *et al.,* 2019; Smith *et al.,* 2020). Given, the overall predation rates presented in this paper should be considered minimum estimates; the real-world predation rate is presumably higher since the PREs were subsampled from four discrete time periods, and data was limited by the width of the sonar field-of-view. Despite this, the findings from this study provide new evidence for previous suggestions that pumping stations can function as prey refuge (Norman *et al.,* 2023a & 2023b) and propose universal ecological considerations for understanding predator-prey interactions and the landscape of fear which are expected to transfer to similar anthropogenic lowland rivers with river maintenance measures. Anthropogenic lowland systems vary in their construct which could impact the behavioural games between aquatic and avian predators and their prey. The river studied here was isolated, void of winter habitat with no other anthropogenic structures which could hold vast numbers of prey and thus it was unlikely that fish were using habitats outside of the study pumping station. However, other systems will differ in the number of anthropogenic structures and thus future research should aim to empirically demonstrate the phenomena observed here by gathering control data across multiple structures. Moreover, the multi-species nature of the freshwater community studied here means concluding species-level impacts is not yet possible. Development of pluriannual monitoring programs which are supplemented by species-specific investigations is therefore recommended to determine the long-term impact of anthropogenic infrastructure on predator-prey relationships.

With continuous anthropogenic growth the resulting pressures on ecological processes in lowland catchments are expected to increase. The future of freshwater rehabilitation for ecosystem enhancement and protection of prey should diverge from past practices which focus on physical modifications (e.g., restoring floodplains), and instead consider modifying river maintenance measures so that ecological interactions can occur more naturally. Primarily, decreasing the length of maintained river stretches could provide prey with increased refuge habitat (Baczyk *et al.,* 2018), in turn reducing episodes of density-dependent predation and balancing the landscape of fear (Laundré *et al.,* 2010). Alternatively, providing artificial refuge in the form of enclosed cages with overhead cover appears to be a promising option for protecting prey from avian predators in modified freshwater ecosystems, even with multiple predators (Lemmens *et al.,* 2016). Ultimately, this study is the first to establish the temporal rate of interactions between aquatic and avian predators, a prey fish community and anthropogenic infrastructure in a heavily modified lowland setting, which strongly enhances our understanding of the impact of anthropogenic infrastructure on predator-prey ecology.

Acknowledgements

This study was financially supported by the Environment Agency. The funder was involved with study design and data collection, but had no role in the data analysis, interpretation, and decision to submit for publication. We thank the anonymous reviewers, whose comments improved the quality of the manuscript.

Conflict of interest statement

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.

Author contributions

Conceptualisation: JN, JR, RW & JB. Developing methods: JR, RW & JN. Conducting the research: JR & JN. Data analysis, Data interpretation, Preparation figures & tables: JN. Writing: JN, JR, RW & JB

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.7728490

5 References

Angelopoulos, N. V., Harvey, J. P., Bolland, J. D., Nunn, A. D., Noble, R. A. A., Smith, M. A., Taylor, M. J., Masters, J. E. G., Moxon, J. & Cowx, I. G. (2018) Overcoming the dichotomy of implementing societal flood risk management while conserving instream fish habitat - A long-term study from a highly modified urban river. *J Environ Manage*, 224, 69-76.

Baczyk, A., Wagner, M., Okruszko, T. & Grygoruk, M. (2018) Influence of technical maintenance measures on ecological status of agricultural lowland rivers - Systematic review and implications for river management. *Sci Total Environ*, 627, 189-199.

Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J. P. & Courtois, R. (2015) Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96(10), 2622-31.

Beauchamp, D. A., Wahl, D. H. & Johnson, B. M. (2007) Predator–Prey Interactions, *Analysis and interpretation of inland fisheries data*.

Becker, A. & Suthers, I. M. (2014) Predator driven diel variation in abundance and behaviour of fish in deep and shallow habitats of an estuary. *Estuarine, Coastal and Shelf Science*, 144, 82-88.

Berryman, A. A. & Hawkins, B. A. (2006) The refuge as an integrating concept in ecology and evolution. *Oikos*, 115(1), 192-196.

Bolland, J. D., Murphy, L. A., Stanford, R. J., Angelopoulos, N. V., Baker, N. J., Wright, R. M., Reeds, J. D. & Cowx, I. G. (2019) Direct and indirect impacts of pumping station operation on downstream migration of critically endangered European eel. *Fisheries Management and Ecology*, 26(1), 76-85.

Bosiger, Y. J., Lonnstedt, O. M., McCormick, M. I. & Ferrari, M. C. (2012) Learning temporal patterns of risk in a predator-diverse environment. *PLoS One*, 7(4), e34535.

Bosiger, Y. J. & McCormick, M. I. (2014) Temporal links in daily activity patterns between coral reef predators and their prey. *PLoS One*, 9(10), e111723.

Campanella, F., Auster, P. J., Taylor, J. C. & Munoz, R. C. (2019) Dynamics of predator-prey habitat use and behavioral interactions over diel periods at sub-tropical reefs. *PLoS One*, 14(2), e0211886.

Catano, L. B., Rojas, M. C., Malossi, R. J., Peters, J. R., Heithaus, M. R., Fourqurean, J. W. & Burkepile, D. E. (2016) Reefscapes of fear: predation risk and reef hetero-geneity interact to shape herbivore foraging behaviour. *J Anim Ecol*, 85(1), 146-56.

Chester, E. T. & Robson, B. J. (2013) Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. *Biological Conservation*, 166, 64-75.

Conallin, J., Boegh, E., Olsen, M., Pedersen, S., Dunbar, M. J. & Jensen, J. K. (2014) Daytime habitat selection for juvenile parr brown trout (Salmo trutta) in small lowland streams. *Knowledge and Management of Aquatic Ecosystems*(413).

Copp, G. H. (1997) Importance of marinas and off-channel water bodies as refuges for young fishes in a regulated lowland river. *Regulated Rivers-Research & Management*, 13(3), 303-307.

Darr, N. A., Pandit, A. K. & Ganai, B. A. (2014) Factors affecting the distribution patterns of aquatic macrophytes. *Limnological Review*.

Davis, J., O'Grady, A. P., Dale, A., Arthington, A. H., Gell, P. A., Driver, P. D., Bond, N., Casanova, M., Finlayson, M., Watts, R. J., Capon, S. J., Nagelkerken, I., Tingley, R., Fry, B., Page, T. J. & Specht, A. (2015) When trends intersect: The challenge of protecting freshwater ecosystems under multiple land use and hydrological intensification scenarios. *Science of the Total Environment*, 534, 65-78.

Dodrill, M. J., Yard, M. D. & Pine, W. E. (2016) Assessing Predation Risks for Small Fish in a Large River Ecosystem between Contrasting Habitats and Turbidity Conditions. *The American Midland Naturalist*, 175(2), 206-221.

Donelan, S. C., Grabowski, J. H. & Trussell, G. C. (2017) Refuge quality impacts the strength of nonconsumptive effects on prey. *Ecology*, 98(2), 403-411.

Dos Reis Oliveira, P. C., van der Geest, H. G., Kraak, M. H. S. & Verdonschot, P. F. M. (2019) Land use affects lowland stream ecosystems through dissolved oxygen regimes. *Sci Rep*, 9(1), 19685.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z., Knowler, D. J., Leveque, C., Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L. & Sullivan, C. A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol Rev Camb Philos Soc*, 81(2), 163-82.

Environment Agency. (2017) *Water Quality Archive - Bourne Eau Bourne Eau Pumping Station.* Available online: https://environment.data.gov.uk/water-quality/view/sampling-point/AN-BEAU010P?_all=true

Environment Agency. (2022) *EA Ecology & Fish Data Explorer.* Available online: https://environment.data.gov.uk/ecology/explorer/

Ferrari, M. C. O., Elvidge, C. K., Jackson, C. D., Chivers, D. P. & Brown, G. E. (2010) The responses of prey fish to temporal variation in predation risk: sensory habituation or risk assessment? *Behavioral Ecology*, 21(3), 532-536.

Ford, J. R. & Swearer, S. E. (2013) Shoaling behaviour enhances risk of predation from multiple predator guilds in a marine fish. *Oecologia*, 172(2), 387-97.

Fu, C., Fu, S.-J., Cao, Z.-D. & Yuan, X.-Z. (2015) Habitat-specific anti-predator behavior variation among pale chub (Zacco platypus) along a river. *Marine and Freshwater Behaviour and Physiology*, 48(4), 267-278.

Gardner, C. J., Deeming, D. C. & Eady, P. E. (2013) Seasonal movements with shifts in lateral and longitudinal habitat use by common bream,Abramis brama, in a heavily modified lowland river. *Fisheries Management and Ecology*, 20(4), 315-325.

Gremillet, D. & Wilson, R. P. (1999) A life in the fast lane: energetics and foraging strategies of the great cormorant. *Behavioral Ecology*, 10(5), 516-524.

Griffin, J. N., Byrnes, J. E. & Cardinale, B. J. (2013) Effects of predator richness on prey suppression: a meta-analysis. *Ecology*, 94(10), 2180-7.

Harrison, S. S. C., Pretty, J. L., Shepherd, D., Hildrew, A. G., Smith, C. & Hey, R. D. (2004) The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology*, 41(6), 1140-1154.

Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J. & Dill, L. M. (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. *J Anim Ecol*, 78(3), 556-62.

Helfman, G. S. (1986) Fish Behaviour by Day, Night and Twilight, *The Behaviour of Teleost Fishes*, 366 - 387.

Hemmi, J. M. & Pfeil, A. (2010) A multi-stage anti-predator response increases information on predation risk. *J Exp Biol*, 213(Pt 9), 1484-9.

Holbrook, S. J. & Schmitt, R. J. (2002) Competition for Shelter Space Causes Density-Dependent Predation Mortality in Damselfishes. *Ecology*, 83(10), 2855-2868.

Jacobsen, L. & Perrow, M. R. (1998) Predation risk from piscivorous fish influencing the diel use of macrophytes by planktivorous fish in experimental ponds. *Ecology of Freshwater Fish*, 7(2), 78-86.

Jepsen, N., Ravn, H. D. & Pedersen, S. (2018) Change of foraging behavior of cormorants and the effect on river fish. *Hydrobiologia*, 820(1), 189-199.

Källo, K., Baktoft, H., Jepsen, N. & Aarestrup, K. (2020) Great cormorant (Phalacrocorax carbo sinensis) predation on juvenile down-migrating trout (Salmo trutta) in a lowland stream. *ICES Journal of Marine Science*, 77(2), 721-729.

Katz, M. W., Abramsky, Z., Kolter, B., Altstein, O. & Rosenzweig, M. L. (2010) Playing the waiting game: predator and prey in a test environment. *Evolutionary Ecology Research*, 12, 793 - 801.

Kobler, A., Klefoth, T., Wolter, C., Fredrich, F. & Arlinghaus, R. (2008) Contrasting pike (Esox lucius L.) movement and habitat choice between summer and winter in a small lake. *Hydrobiologia*, 601, 17-27.

Kupiec, J. M., Staniszewski, R. & Jusik, S. (2021) Assessment of the impact of land use in an agricultural catchment area on water quality of lowland rivers. *PeerJ*, 9, e10564.

Lannin, R. & Hovel, K. (2011) Variable prey density modifies the effects of seagrass habitat structure on predator−prey interactions. *Marine Ecology Progress Series*, 442, 59-70.

Laroche, R. K., Kock, A. A., Dill, L. M. & Oosthuizen, W. H. (2008) Running the gauntlet: a predator–prey game between sharks and two age classes of seals. *Animal Behaviour*, 76(6), 1901-1917.

Laundre, J. W., Hernandez, L. & Ripple, W. J. (2010) The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal*, 3(3), 1-7.

Lemmens, P., De Meester, L. & Declerck, S. A. J. (2016) Can underwater refuges protect fish populations against cormorant predation? Evidence from a large-scale multiple pond experiment. *Fisheries Management and Ecology*, 23, 89-98.

Lima, S. L. & Bednekoff, P. A. (1999) Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *Am Nat*, 153(6), 649-659.

Lima, S. L. & Dill, L. M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*.

Marchowski, D., Flis, A., Gwiazda, R., Kavetska, K. M. & Wysocki, D. (2022) The dominant species of piscivorous bird does not adversely affect fishery in the lagoons of the southern Baltic Sea. *The European Zoological Journal*, 89(1), 304-316.

Martin, C. W., Fodrie, F. J., Heck, K. L., Jr. & Mattila, J. (2010) Differential habitat use and antipredator response of juvenile roach (Rutilus rutilus) to olfactory and visual cues from multiple predators. *Oecologia*, 162(4), 893-902.

Martinoli, A., Gagliardi, A., Preatoni, D. G., Di Martino, S., Wauters, L. A. & Tosi, G. (2003) The Extent of Great Crested Grebe Predation on Bleak in Lake Como, Italy. *Waterbirds: The International Journal of Waterbird Biology*, 26(2), 201 - 208.

Metcalfe, N. B., Fraser, N. H. C. & Burns, M. D. (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology*, 68(2), 371-381.

Meuthen, D., Baldauf, S. A., Bakker, T. C. & Thunken, T. (2016) Predator-induced neophobia in juvenile cichlids. *Oecologia*, 181(4), 947-58.

Mittelbach, G. (1986) Predator-Mediated Habitat Use - Some Consequences for Species Interactions. *Environmental Biology of Fishes*, 16(1-3), 159-169.

Norman, J., Wright, R. M., Don, A. & Bolland, J. D. (2023a) Understanding the temporal dynamics of a lowland river fish community at a hazardous intake and floodgate to inform safe operation. *J Environ Manage*, 336, 117716.

Norman, J., Reeds, J., Wright, R.M. & Bolland, J.D. (2023b) The impact of extreme flood-relief pump operations on resident fish in an artificial drain and the potential for artificial habitat introduction. *Fisheries Management and Ecology*, 12636.

Oględzki, P., Ostrowski, P. S. & Utratna-Żukowska, M. (2021) Natural and Geomorphological Response of the Small Lowland River Valley for Anthropogenic Transformation. *Resources*, 10(10).

Ohlund, G., Hedstrom, P., Norman, S., Hein, C. L. & Englund, G. (2015) Temperature dependence of predation depends on the relative performance of predators and prey. *Proc Biol Sci*, 282(1799), 20142254.

Orrock, J. L., Preisser, E. L., Grabowski, J. H. & Trussell, G. C. (2013) The cost of safety: refuges increase the impact of predation risk in aquatic systems. *Ecology*, 94(3), 573-9.

Ory, N. C., Dudgeon, D., Duprey, N. & Thiel, M. (2014) Effects of predation on diel activity and habitat use of the coral-reef shrimp Cinetorhynchus hendersoni (Rhynchocinetidae). *Coral Reefs*, 33(3), 639-650.

Palacios, M. M., Malerba, M. E. & McCormick, M. I. (2018) Multiple predator effects on juvenile prey survival. *Oecologia*, 188(2), 417-427.

Pitcher, T. J. (1998) Shoaling and Schooling in Fishes.

Pitcher, T. J. & Turner, J. R. (1986) Danger at Dawn - Experimental Support for the Twilight Hypothesis in Shoaling Minnows. *Journal of Fish Biology*, 29, 59-70.

Preisser, E. L., Orrock, J. L. & Schmitz, O. J. (2007) Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, 88(11), 2744-51.

Price, V. E., Auster, P. J. & Kracker, L. (2013) Use of High-Resolution DIDSON Sonar to Quantify Attributes of Predation at Ecologically Relevant Space and Time Scales. *Marine Technology Society Journal*, 47(1), 33-46.

Rieucau, G., Boswell, K. M., Kimball, M. E., Diaz, G. & Allen, D. M. (2015) Tidal and diel variations in abundance and schooling behavior of estuarine fish within an intertidal salt marsh pool. *Hydrobiologia*, 753(1), 149-162.

Romenskyy, M., Herbert-Read, J. E., Ioannou, C. C., Szorkovszky, A., Ward, A. J. W. & Sumpter, D. J. T. (2020) Quantifying the structure and dynamics of fish shoals under predation threat in three dimensions. *Behavioral Ecology*, 31(2), 311-321.

Russell, I. (2003) The potential for using fish refuges to reduce damage to inland fisheries by Cormorants, Phalacrocorax carbo, in Cowx, I. G. (ed), *Interactions Between Fish and Birds: Implications for Management*, 259–277.

Rytwinski, T., Algera, D. A., Taylor, J. J., Smokorowski, K. E., Bennett, J. R., Harrison, P. M. & Cooke, S. J. (2017) What are the consequences of fish entrainment and impingement associated with hydroelectric dams on fish productivity? A systematic review protocol. *Environmental Evidence*, 6(8), 1-9.

Sand, H., Jamieson, M., Andren, H., Wikenros, C., Cromsigt, J. & Mansson, J. (2021) Behavioral effects of wolf presence on moose habitat selection: testing the landscape of fear hypothesis in an anthropogenic landscape. *Oecologia*, 197(1), 101-116.

Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods*, 9(7), 671-5.

Sih, A. (1984) Optimal Behavior and Density-Dependent Predation. *The American Naturalist*, 123(3), 314 - 326.

Singh, R., Tiwari, A. K. & Singh, G. S. (2021) Managing riparian zones for river health improvement: an integrated approach. *Landscape and Ecological Engineering*, 17(2), 195-223.

Smith, C. D., Plumb, J. M., Adams, N. S. & Wyatt, G. J. (2020) Predator and prey events at the entrance of a surface-oriented fish collector at North Fork Dam, Oregon. *Fisheries Management and Ecology*, 28(2), 172-182.

Supekar, S. C. & Gramapurohit, N. P. (2020) Does temporal variation in predation risk affect antipredator responses of larval Indian Skipper Frogs (Euphlyctis cyanophlyctis)? *Canadian Journal of Zoology*, 98(3), 202-209.

RStudio Team. (2022) *RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA.* Available online: http://www.rstudio.com/

RCore Team (2022) *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.* Available online: https://www.R-project.org

Turesson, H. & Bronmark, C. (2004) Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density. *Journal of Fish Biology*, 65(2), 363-375.

Van Den Berg, H., Ankasah, D., Muhammad, A., Rusli, R., Widayanto, H. A., Wirasto, H. B. & Yully, I. (1997) Evaluating the Role of Predation in Population Fluctuations of the Soybean Aphid Aphis glycines in Farmer's Fields in Indonesia. *Journal of Applied Ecology*, 34(4), 971 - 984.

White, C. R., Butler, P. J., GrÉMillet, D. & Martin, G. R. (2008) Behavioural strategies of cormorants (Phalacrocoracidae) foraging under challenging light conditions. *Ibis*, 150, 231-239.

White, C. R., Day, N., Butler, P. J. & Martin, G. R. (2007) Vision and foraging in cormorants: more like herons than hawks? *PLoS One*, 2(7), e639.

Tables

Table 1 Attack dynamics of Northern Pike (*Esox lucius*) and Cormorant (*Phalacrocorax carbo*) observed in multi-beam sonar video. Attack metrics gathered according to Table S1.

	Predator species									
	Northern Pike *(Esox lucius)*					Cormorant *(Phalacrocorax carbo)*				
	Sample period									
	Dawn	Day	Dusk	Night	All	Dawn	Day	Dusk	Night	All
Attack (n)										
Total	18	12	18	0	48	16	6	28	0	50
Attack duration (s^{-1})										
Median	3	4	1	0	2	3	3	3	0	3
Min	0	4	1	0	0	1	0	1	0	0
Max	15	4	3	0	15	8	6	13	0	13
IQR	3	0	1	0	2	3	0.5	3	0	2
Time until attack (s^{-1})										
Median	1	0	27	0	0	0	0	0	0	0
Min	0	0	0	0	0	0	0	0	0	0
Max	243	0	294	0	294	198	0	0	0	198
IQR	21.5	0	41	0	28	0	0	0	0	0
Attack rate (attack min^{-1}) †										
Median	1.6	1.6	1.6	0	1.6	1.6	2.5	3.3	0	3.3
Min	1.6	1.6	1.6	0	0	1.6	1.6	1.6	0	1.6
Max	5	1.6	5	0	5	5	8.3	8.3	0	8.3
IQR	1.7	2.1	2.1	0	2.1	0.7	1.1	1.1	0	1.7
Predator Size (mm)										
Median	118	124	112	121	118	98	85	79	0	84
Min	58	73	75	102	58	72	69	65	0	5
Max	132	153	140	131	153	110	109	120	0	120
IQR	20	29	21	14	18	17	12	12.5	0	8.5

† attack rate calculated without inclusion of unattacked shoals

Table 2 Results of the fitted Generalized Linear Models (GLM) for attack rate and Predation Related Event duration. GLM constructed with *glm* package in R 4.1.2.

Attack rate (switch_rate ~ attack_rate+sp_pred)					PRE duration (switch_rate ~ pre_dur+sp_pred)				
	Est.	**Std. Error**	**Z**	**Pr(>|z|)**		**Est.**	**Std. Error**	**Z**	**Pr(>|z|)**
(Intercept)	0.5551	0.2150	2.5819	0.013	*(Intercept)*	1.0975	0.1849	5.9333	<0.001
attack_rate	0.2432	0.0329	7.3849	<0.001	*pre_dur*	0.0084	0.0020	4.1069	<0.001
sp_predE lucius	0.0938	0.2122	0.4419	0.660	*sp_predE lucius*	-0.5627	0.2512	-2.2401	0.030

Table 3 Number of behavioural responses by prey shoals to predator interactions with Northern Pike (*Esox lucius*) and Cormorant (*Phalacrocorax carbo*) across all predation related events observed.

	Shoal behaviour						
	No response	Flee	Flee (into weed screen)	Flee (away from weed screen)	Avoid	Avoid (into weed screen)	Avoid (away from weed screen)
				Sample period (n)			
Total	25	20	43	30	79	9	17
Dawn	3	10	13	20	45	4	5
Day	7	2	10	2	5	2	4
Dusk	8	8	19	8	24	3	8
Night	7	0	1	0	5	0	0
				Behaviour duration (s^{-1})			
Median	0	11	12	15	90	66	75
Min	0	0	3	2	11	8	15
Max	312	34	66	51	478	181	229
IQR	0	18.5	10	114	72	64	69

Figure captions

Figure 1 (a) The location of the study catchment (bottom left) and the lower Welland catchment. A schematic representation of the study site showing the position of Bourne Eau pumping station, adjacent lock gates, and the insonified window (b).

Figure 2 The overall number of PREs observed using DIDSON between October and December 2017 for 1) *Esox Lucius* and 2) *Phalacrocorax carbo* PREs. Counts are secondarily facetted by month (a - c) and the observed PRE count is given by sample period (coloured bars) and whether a predator attack was recorded during the PRE.

Figure 3 The response of prey fish to predator interactions given by a) prey areal response b) prey density response and c) the weed screen switching rate. Plots represent measured prey responses to the *first* interaction in a PRE and does not include repeat attack behaviours. Error bars represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance indicted by Wilcoxon rank sum (ns = not significant, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, ***** = $P \leq 0.0001$).

Figure 4 The predicted effect of a) attack rate of predators and b) PRE duration on the weed screen switching rate of prey fish. Guassian (link = log) lines plotted by a minimal GLM *((a) switch_rate ~ pre_dur+sp_pred; (b): switch_rate ~ attack_rate+sp_pred).* 95% confidence intervals represented by shaded envelope surrounding smoothed line. Jittered points represent observed values.

Figure 5 Count of observed prey behavioural responses resulting from interactions with a) *Esox lucius* and b) *Phalacrocorax carbo* given by attack status. Plot represents all behavioural responses recorded during a PRE.

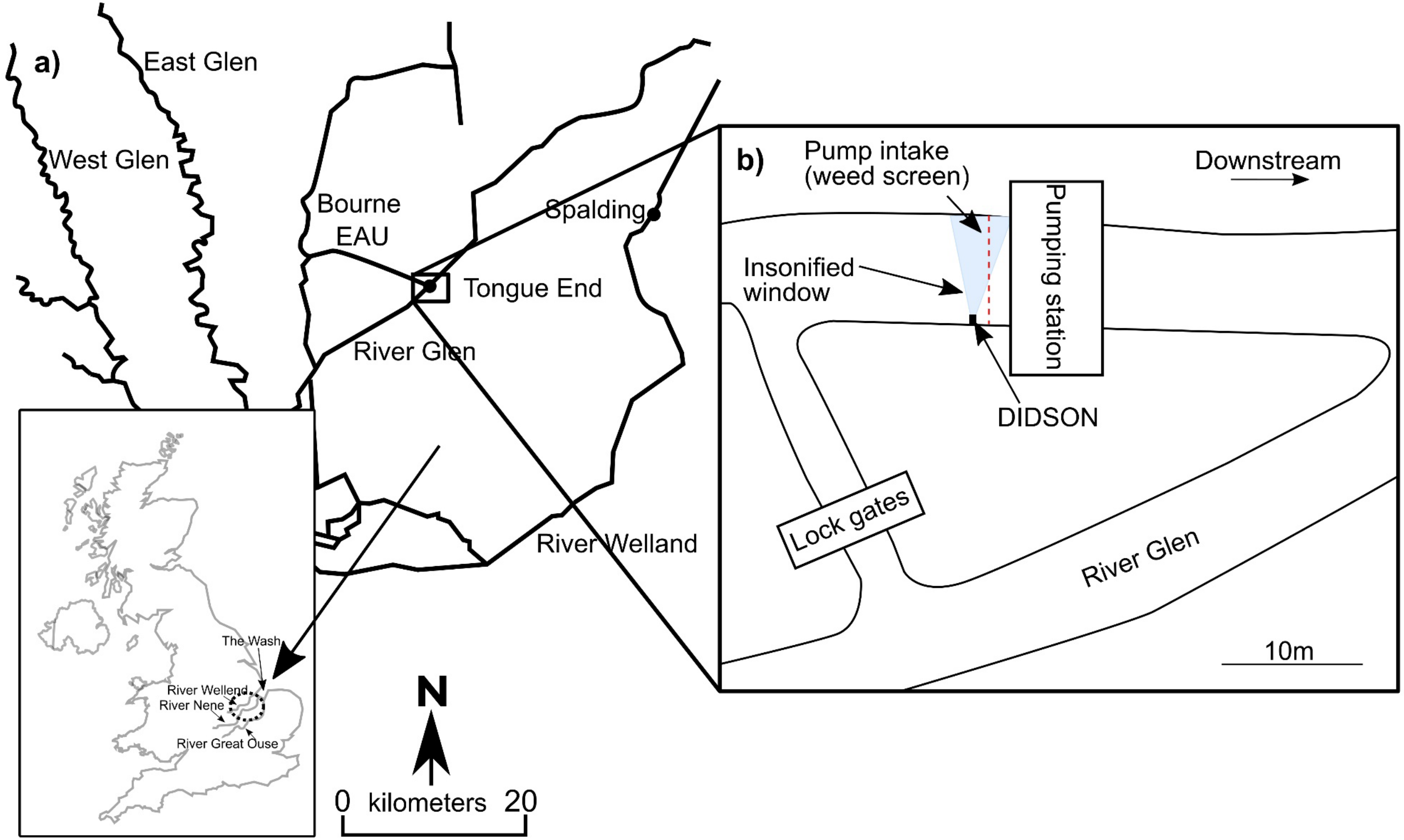

Figure 1 (a) The location of the study catchment (bottom left) and the lower Welland catchment. A schematic representation of the study site showing the position of Bourne Eau pumping station, adjacent lock gates, and the insonified window (b).

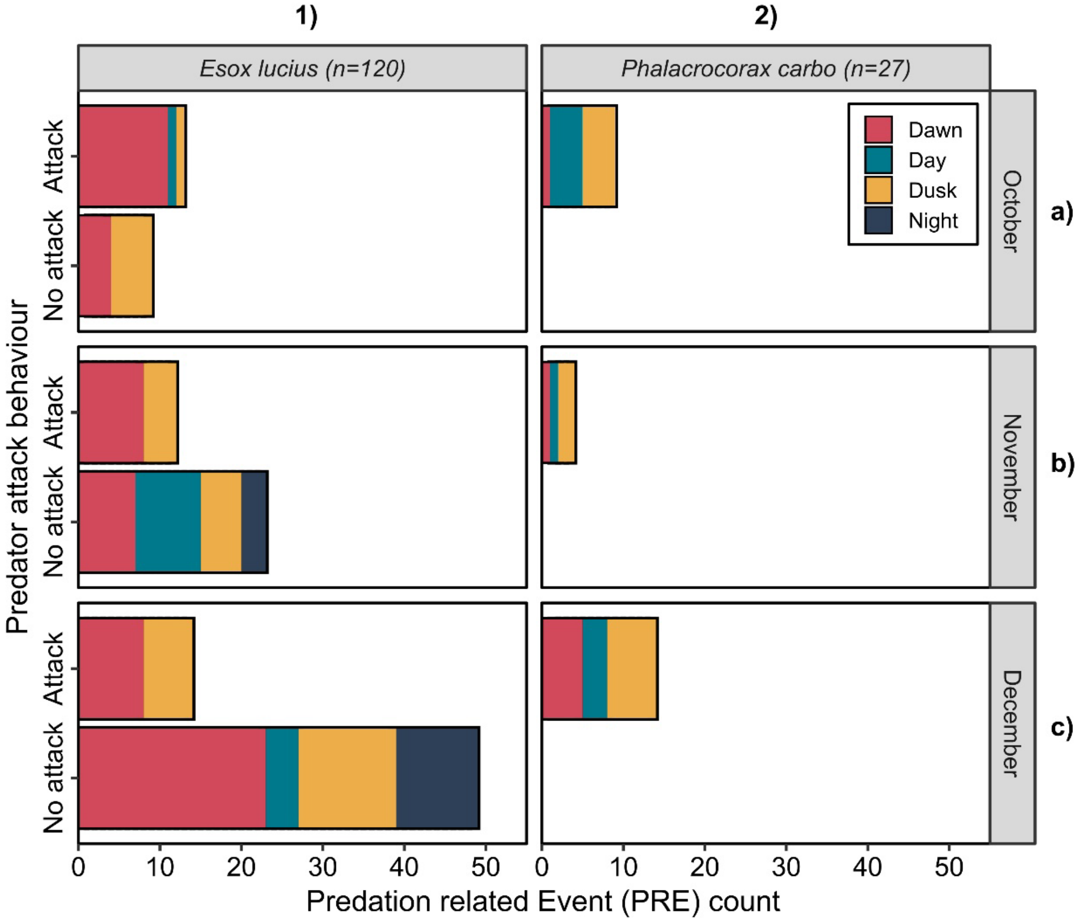

Figure 2 The overall number of PREs observed using DIDSON between October and December 2017 for 1) Esox Lucius and 2) Phalacrocorax carbo PREs. Counts are secondarily facetted by month (a - c) and the observed PRE count is given by sample period (coloured bars) and whether a predator attack was recorded during the PRE.

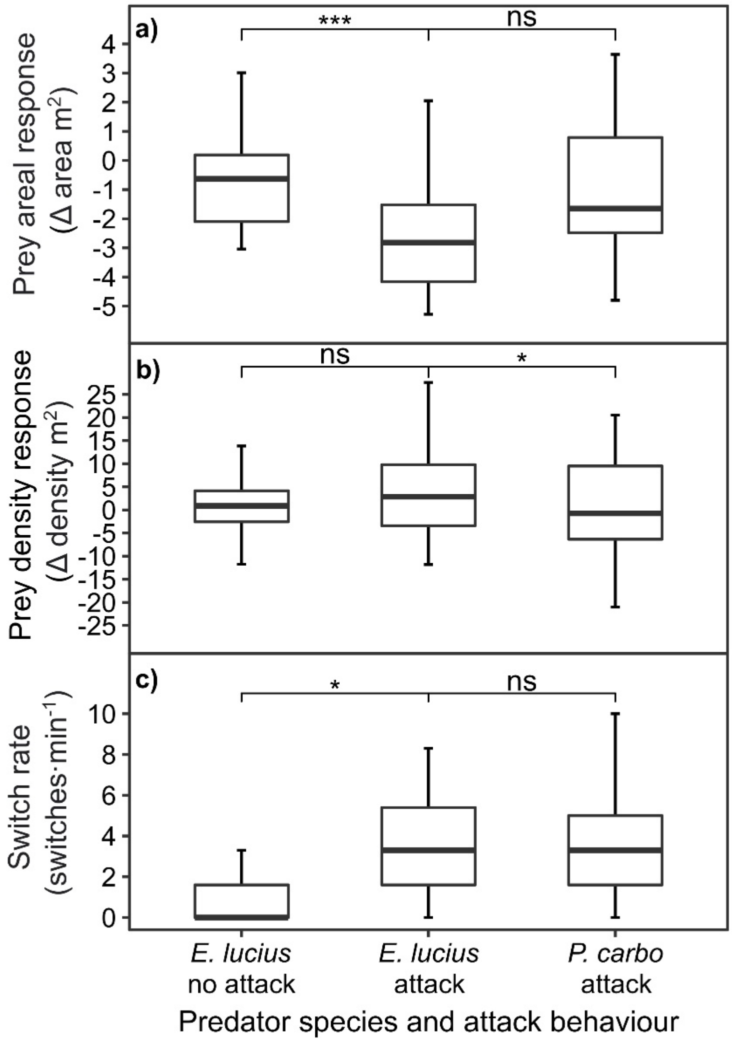

Figure 3 The response of prey fish to predator interactions given by a) prey areal response b) prey density response and c) the weed screen switching rate. Plots represent measured prey responses to the first interaction in a PRE and does not include repeat attack behaviours. Error bars represent quartile 1 to the smallest non-outlier and quartile 3 to the largest non-outlier. Significance indicted by Wilcoxon rank sum (ns = not significant, * = $P \le 0.05$, ** = $P \le 0.01$, *** = $P \le 0.001$).

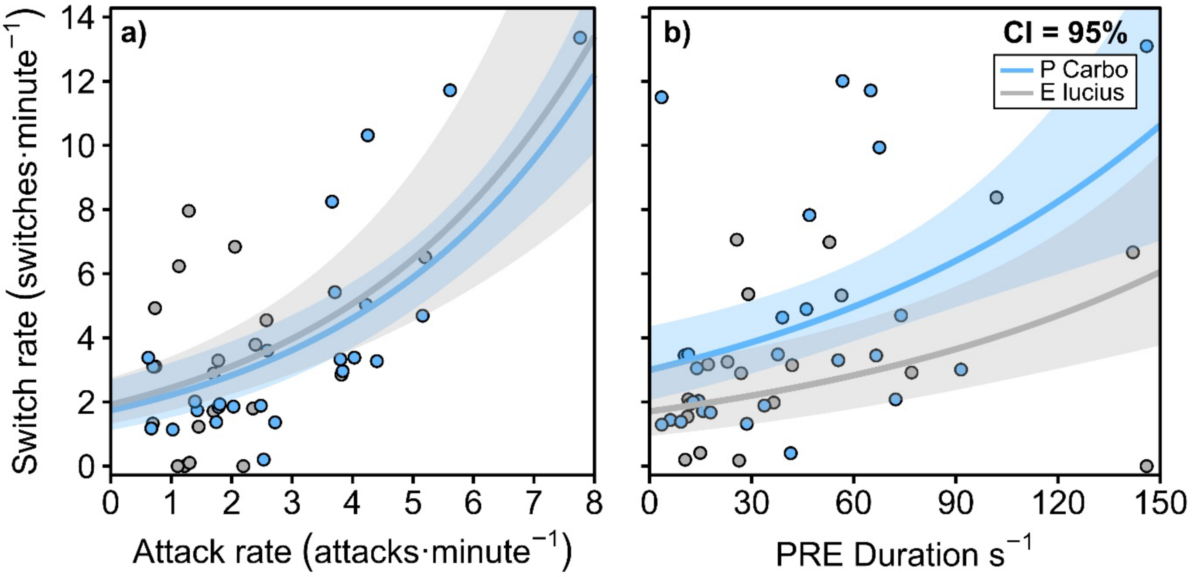

Figure 4 The predicted effect of a) attack rate of predators and b) PRE duration on the weed screen switching rate of prey fish. Guassian (link = log) lines plotted by a minimal GLM ((a) switch_rate ~ pre_dur+sp_pred; (b): switch_rate ~ attack_rate+sp_pred). 95% confidence intervals represented by shaded envelope surrounding smoothed line. Jittered points represent observed values.

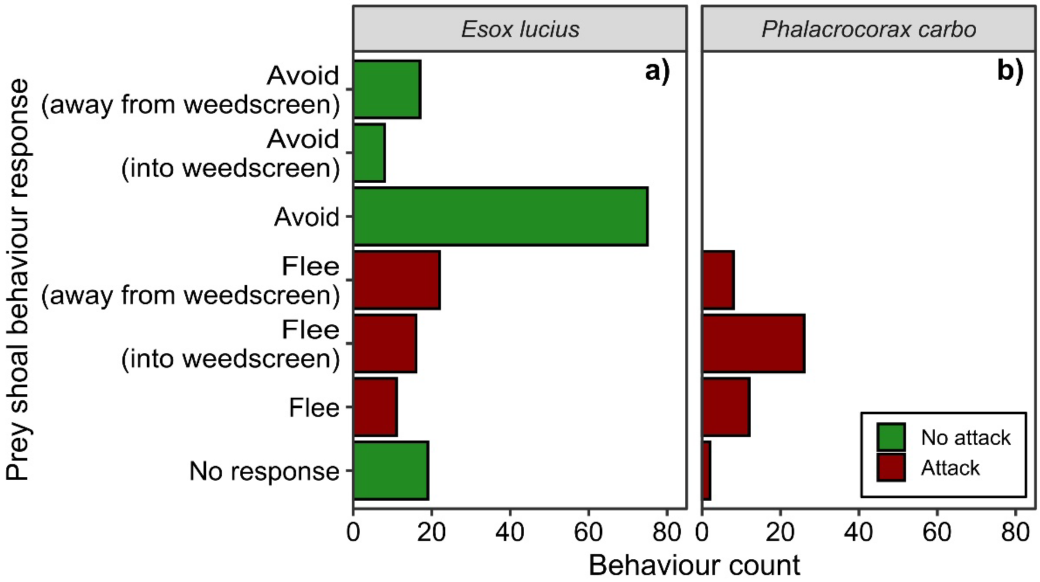

Figure 5 Count of observed prey behavioural responses resulting from interactions with a) Esox lucius and b) Phalacrocorax carbo given by attack status. Plot represents all behavioural responses recorded during a PRE.

Supplementary materials

Table S1 A list of metrics and descriptive terms used to describe predator-prey interactions. PRE = Predation Related Event. Predator presence in the sonar window was used to determine if a Predation Related Event (PRE) had occurred. See section 2.3.1 for further detail.

Term	Description	Data type
Duration of PRE	Duration of a PRE from the point when a predator enters the sonar window until the end point of prey shoal response.	Continuous
Predator metrics taken during a single PRE		
Number of predators present	Number of predators present	Discrete
Predator species	(1) Great Cormorant (*Phalacrocorax carbo*) (2) Northern pike (*Esox lucius*).	Discrete, categorical
Predator size	Length of predator (cm)	Continuous
Predator attack	(0) no attack (1) attack.	Discrete, categorical
Number of attacks	Number of predator attacks	Discrete
Duration of attack	Duration of predator attack	Continuous
Time until attack	Time from when predator enters sonar window until first attack	Continuous
Predator attack rate	Number of attacks per minute (*n attacks·minute*$^{-1}$)	Continuous
Prey shoal metrics taken during a single PRE		
Prey shoal size	Number of prey in a shoal (ImageJ)	Discrete
Prey shoal area	Area in m^2 of a prey shoal (ImageJ)	Continuous
Prey shoal density	Prey shoal size divided by prey shoal area ($n \cdot m^2$)	Continuous
Prey shoal density response	Extent of prey density response to a predator (change in density pre- and post-behavioural reaction)	Continuous
Prey shoal areal response	Extent of prey areal response of a prey shoal to predator (change in area pre- and post-behavioural reaction)	Continuous
Prey shoal behavioural response to predator	(0) no response (1) flee (2) flee (into weed screen) (3) flee (away from weed screen) (4) avoid (5) avoid (into weed screen) (6) avoid (away from weed screen)	Discrete, categorical
Duration of prey shoal behavioural response	Duration of a behavioural response	Continuous
Number of prey shoal behavioural responses	Number of behavioural responses	Discrete
Weed screen switching rate	Number of times prey switch sides at the weed screen (*n switches·minute*$^{-1}$)	Continuous

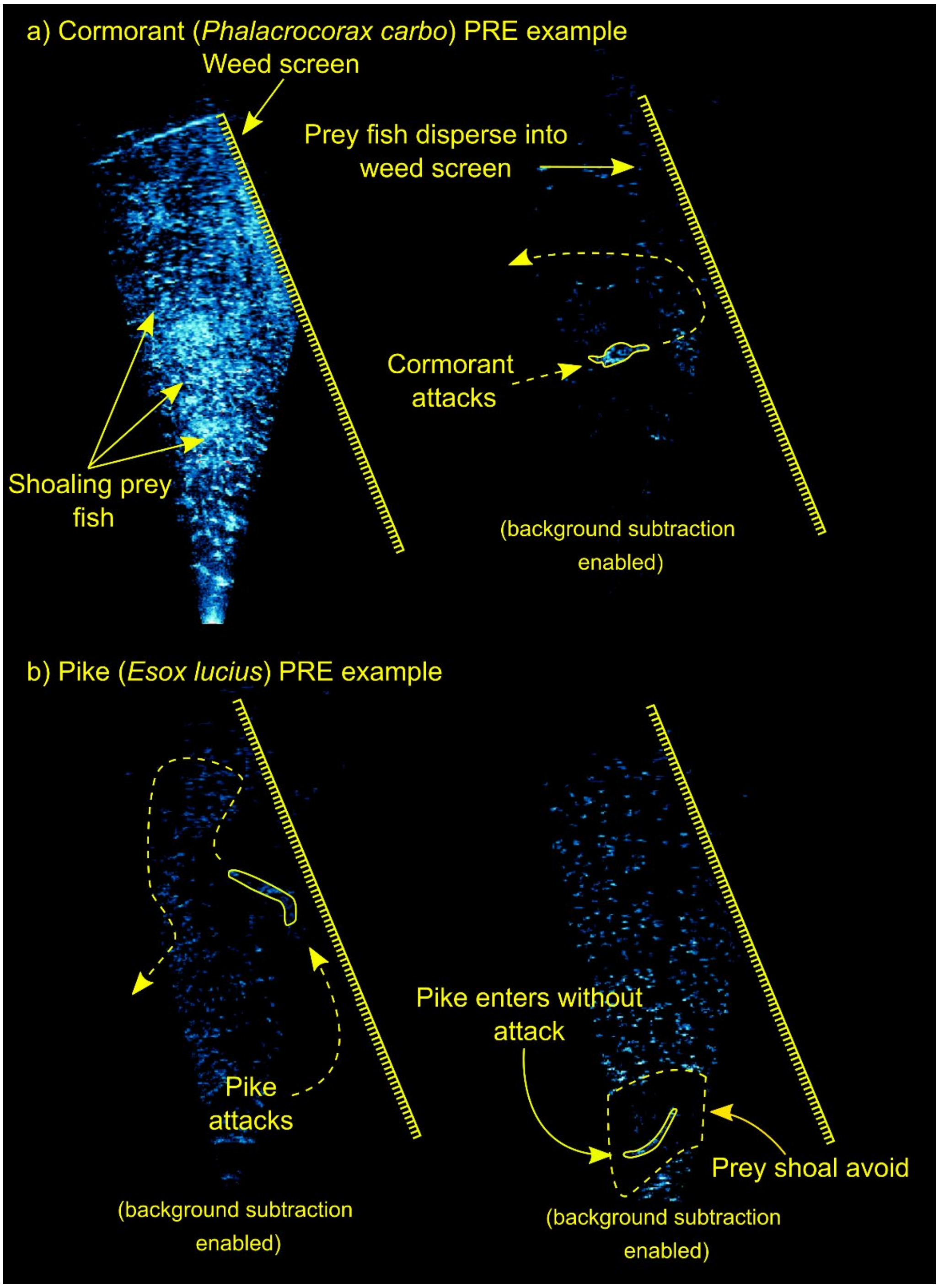

Figure S1 A schematic representation of a) cormorant PRE showing prey shoal and cormorant attack, b) pike PRE showing an attack, and no attack with prey avoidance.