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Ex-situ experimentation to determine if introduced artificial habitat can provide alternative refuge to hazardous anthropogenic structures: success with habitat management

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artificial habitat as alternative refuge

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JN, JB conceived and designed the research; JN, DC performed the experiments, MC, JN analysed the data; JN wrote the manuscript; RW provided funding acquisition, AH provided facilities; JN, JB edited the manuscript. All authors reviewed the manuscript.

Abstract

Highly degraded lowland river ecosystems are of global concern to restoration practitioners. Hazardous anthropogenic structures, such as those used for water level management (i.e., pumping stations), present a mortality risk to fish and associated channelization, dredging and removal of in-channel and riparian vegetation during winter dramatically reduces habitat availability. Paradoxically, fish seeking habitat for predator refuge in these systems can lead to ecological traps, i.e., the undesired occupation of pumping stations. Artificial habitats installed upstream could provide safe alternative refuge, but the effectiveness of this restoration technique is poorly understood. Here, we uniquely quantified habitat occupancy and preference of a ubiquitous European freshwater fish (*Rutilus rutilus*) between an artificial reed bed and pumping station habitat, with access to open water in a tank experiment. Generalised linear mixed models revealed that fish preferred the pumping station when the artificial habitat was absent (baseline) and when it was introduced (pre-exclusion). Habitat management (exclusion from pumping station) was performed, during which artificial habitat occupancy was highest. When the pumping station was reintroduced (post-exclusion), pumping station occupancy probability decreased from 87.5% (pre-exclusion) to 3.7%, whilst artificial habitat occupancy probability increased from 18.4% to 87.9%. Therefore, our results demonstrate a preferential change in habitat occupancy of *Rutilus rutilus* and suggest introducing artificial habitat alone may lead to restoration failures and ecological traps, stressing the need for habitat management to accompany artificial habitat restoration plans which aim to provide a safe alternative refuge for fish which occupy hazardous anthropogenic structures.

Keywords

Artificial habitat, pumping station, habitat preference, habitat restoration, ecological trap, perceptual trap

Implications for practice

- Implementing artificial habitat to restore ecological function in heavily modified freshwaters with hazardous structures could provide a suitable restoration technique where full-scale restoration to a natural state is either costly, challenging or not possible.
- Effective and long-term fish occupation of artificial habitats as a safe alternative to occupying low-quality habitat in hazardous anthropogenic structures (i.e., pumping stations) could require active habitat management (i.e., physical exclusion) to provide settlement stimulus and prevent formation of an ecological trap.
- Restoration managers and ecologists should attempt to quantify wild fish distribution and movement before and after artificial habitat installation to inform management requirements and determine effectiveness, respectively.

Introduction

Lowland rivers are essential ecosystems which support much of the world's freshwater fish diversity (Huckstorf et al. 2008) and are critical for the day-to-day foraging and refuge movements and seasonal spawning migrations of resident fish (Oglecki et al. 2021). Still, lowland rivers are threatened globally by anthropogenic land use activities (Dudgeon et al. 2006), especially flood risk management during winter (Angelopoulos et al. 2008). Flood risk management strategies frequently require river maintenance measures (see review Baczyk et al. 2018) including the installation and operation of hazardous anthropogenic water level management infrastructure (pumping stations hereafter) to regulate flow and water level. The resulting effect of river maintenance measures is that channelisation, dredging and the winter removal of riparian vegetation dramatically reduce the available habitat for resident fish. Habitat degradation is now considered a major cause of global biodiversity loss and restoration of ecological function in freshwater ecosystems is required (Maxwell et al. 2016; Cowan et al. 2021).

The presence of physical habitat is fundamental for anti-predator behaviours used by prey, as shelter allows for inconspicuousness whilst observing approaching predators (Helfman 1981) and structures provided by submerged habitats limit predator access to prey fish (Ellner et al. 2001; Nunes et al. 2019). Indeed, previous studies have shown that the ecological demand for winter refuge habitats in modified freshwaters can lead to resident fish occupying pumping stations for refuge from predators (e.g., cormorant (*Phalacocorax carbo*)) (Norman et al., 2023a; see also Chester & Robson 2013; Sousa et al. 2019). These structures concentrate and confine fish, have poor resources for fish (i.e., space, food, light) and mortality risk is high when pumps operate (Rytwinski et al. 2017; Norman et al. 2023b). Attempts to reduce the risks associated with pumping stations has previously included physical and behavioural deterrents to reduce entrainment into pumps (Turnpenny & O'Keeffe 2005), opening gravity drainage channels to restore passage of migratory fish (Baker et al. 2021) and pump shutdown during diel movements of resident fish (Reckendorfer et al. 2018; Norman et al., 2023c). However, these remediation measures do not address predator-prey interactions or provide attractive alternative habitat to reduce fish occupancy at hazardous structures. Cormorants are protected by the European Community Directive on the Conservation of Wild Birds (EEC/79/409) and therefore lethal methods are undesired for ecological management. Ideally, ecological restoration should aim to re-establish natural processes to alleviate the impacts of aquatic habitat degradation (Cowan et al. 2021). Except, ecological restoration is challenging in modified freshwaters as reintroduction of natural refuge features is prevented by anthropogenic activities, such as winter vegetation removal (Baczyk et al. 2018).

Directly addressing habitat loss by providing suitable alternative refuge habitats which can be seasonally introduced to reduce homogenisation and predator vulnerability could mitigate the undesired fish occupation of hazardous anthropogenic structures. Indeed, the installation of artificial habitat has received increasing attention as an approach to mitigate ecological degradation (see reviews Cowan et al. 2021; Watchorn et al. 2022). Artificial habitats, which in aquatic ecosystems include pipes and felled trees (Frehse et al. 2021), caged rocks (Mercader et al. 2019) and PVC structures with interstitial spaces (Baumann et al. 2016) have wide application. For example, in Allen et al. (2014), artificial habitats were used to supplement degraded natural habitat and improve angling success in reservoirs. Similar work has shown artificial habitats increased the local abundance and biodiversity of fish in reservoirs (Frehse et al. 2021). Elsewhere, Lemmens et al. (2016) suggested artificial habitat can facilitate the coexistence of lowland prey fish, such as rudd (*Scardinius erythrophthalmus*) and roach (*Rutilus rutilus*), with cormorants, in lakes and ponds which lacked natural predator refuge. Floating artificial raft habitats have also been used to increase local abundance of invertebrates in modified rivers, an important feeding resource for fish (Francis et al. 2008). Accordingly, a pilot study in an artificial drain upstream of a pumping station demonstrated occupancy of artificial habitats when pumps were not operating, but findings were limited by extreme flood-relief pump operations (Norman et al. 2023b). So far, this work has been promising, but the use of artificial habitat as a safe alternative to hazardous structures for resident fish requires further investigation to prevent future restoration failures.

Currently a major problem with habitat restoration programmes is the tendency for artificial habitat installation to lack robust planning (Hale et al. 2017) and accompanying monitoring (Lindenmayer et al. 2017). Thus, their ecological functioning and relative fish occupation are often unknown. Fish use settlement cues (e.g., enclosed space & shade) to select habitats which maximise their fitness (i.e., adaptive habitat selection; Orians & Wittenberger 1991). However, maladaptive habitat selection may occur in anthropised rivers with degraded habitat (Hale & Swearer 2016). Paradoxically then, fish may be attracted to and prefer habitats where their fitness is reduced (i.e., ecological trap; Robertson & Hutto 2006). This is true of pumping stations, which in degraded rivers offer shelter and winter predator refuge and thus have become attractive daytime habitat (Norman et al. 2023a). Previous work has shown habitat restoration can, unfortunately, be a major cause of traps (Robertson et al. 2013). Providing alternative artificial habitat should increase in-channel habitat heterogeneity and provide prey fish with predator refuge that is preferred to the pumping station. However, maladaptive habitat selection can limit perception of available habitat meaning fish may avoid restored habitats and poor habitats counterintuitively become even more attractive (i.e., a perceptual trap; Pattern & Kelly 2010).

Generating a robust understanding of fish habitat preference whilst planning habitat restoration work is required to prevent restoration failures (Hale et al. 2020). A major concern for the provision of artificial habitat for resident fish which occupy hazardous anthropogenic structures is ensuring artificial habitat is attractive. Elsewhere, Lemmens et al. (2016) demonstrated the importance of artificial habitat design, and found sheltered habitats were preferred by roach over unsheltered habitats. A further method to help ensure fish occupy artificial habitat would be to physically exclude fish from the poor habitat, although this must be performed with caution in the real-world as fish not attracted to artificial habitat would be highly vulnerable to predation during the day. Although the use of fish exclusion devices has increased over recent years, for example at the hazardous intakes of hydropower and pumping stations which are screened to prevent entry of protected migratory fish (e.g., European eel (*Anguilla Anguilla)*; Turnpenny & O'Keeffe 2005), such methods are expensive and logistically challenging, and thus are rarely recommended for non-migratory resident fish. Instead, it may be possible to temporarily exclude fish from hazardous intakes (e.g., a net across the entrance) provided artificial habitat occupancy initially increased and persisted once exclusion ceased, especially as this could be more cheaply, easily and quickly implemented in the real-world. Subsequently, in accordance with the framework presented in Hale et al. (2015), direct testing of fish habitat preference both with and without habitat management activities (i.e., physical exclusion) is required to determine if fish will occupy artificial habitat naturally in systems where ecological traps may occur.

Studying fish behaviour and artificial habitat installations in the natural environment is preferred, but robust measurement of habitat occupancy and the effect of habitat management were not possible in a previous study, and studying an operational pumping station also had a confounding impact on findings (Norman et al. 2023b). Accordingly, pilot tank-based experiments which represent real-world scenarios (i.e., introducing artificial habitat) are required to test fish habitat preferences and likelihood of artificial habitat success in a controlled environment and in the absence of predators, prior to further full-scale restoration to provide safe alternative fish refuge in the real-world. Using roach, a cyprinid ubiquitous to rivers and lakes in Europe, and simulated habitat designs, the objective of this study was to quantify habitat preference between pumping station and artificial habitats (with access to open water). Fish habitat occupancy was measured in four experimental scenarios that replicated sequential management interventions in the real-world to determine habitat preference; pumping station only (baseline), pumping station and introduced artificial habitat (pre-exclusion), artificial habitat only (pumping station exclusion), and artificial habitat and reintroduced pumping station (post-exclusion). Roach are nocturnal (Fu et al. 2015); maximal movement activity occurs during the crepuscular period (Heermann & Borcherding 2006), structured habitat is occupied during the day and feeding happens at night (Metcalfe et al. 1999*)*. Thus, the main hypothesis (H_1) of this study were evaluated in consideration of daytime pumping station and artificial habitat use, which were (i) in the absence of artificial habitat, habitat occupancy will be higher in the pumping station compared to open water, (ii) when artificial habitat is introduced without pumping station exclusion (pre-exclusion), habitat occupancy will be highest in the pumping station, demonstrating habitat preference, (iii) when excluded from the pumping station, habitat occupancy will be increase in the artificial habitat, and (iv) when the pumping station is reintroduced (post-exclusion), habitat occupancy will be highest in the artificial habitat, demonstrating a preferential shift towards occupying the artificial habitat compared to the pre-exclusion phase. Additionally, (v) in accordance with Orpwood et al. (2010), artificial habitat occupancy will be higher in sheltered than unsheltered treatments. The findings from this study are important to prevent restoration failures by furthering our understanding of fish habitat preference and improve the success of artificial habitat installation in heavily modified freshwaters (i.e., lowland rivers and artificial drains) with hazardous anthropogenic structures.

Materials and methods

Fish collection and housing

A total of 186 (mortality = 14) wild roach (mean fork length ± SD; 116 ± 12 mm) were caught (rod and line) from a lake (Lat: 53.716473N, Long: -0.555654W) with known cormorant predation pressure on 16 and 29 September 2019. Captured roach were transported to the experimental facility (Environment Agency, Calverton Fish Farm, England) in two aerated (O^2 0.1L min^{-1}) transportation tanks (200L) pre-dosed with Virkon (1g), Vidalife (20ml) and Protex (2ml). Upon arrival at the experimental facility, roach were first treated for external parasites in a partially salinated (0.1% salinity) water bath before being transferred to a sheltered holding tank supplied (in parallel) with biologically filtered ground water (temperature = 9.8 ± 0.3 °C). All roach received a 14-day acclimation period (no feeding) with no human interaction to allow recovery from capture and transportation.

Experimental design

The experimental trials were conducted in six ~780L gravity drained (0.1L s^{-1} inflow and 4% gradient) opaque fiberglass tanks (2800 $_x$ 600 $_x$ 440mm, length $_x$ width $_x$ height), which were again supplied (in parallel) with biologically filtered ground water and were divided into three compartments using opaque Perspex dividers (Figure 1a). Two compartments at each end of the tank (600 x 600mm) were simulated habitats and the centre compartment (1600 x 600mm) was open water, and thus simulated a lowland river where fish could swim between a pumping station and adjacent artificial habitat. The bottom of the tanks was covered with self-adhesive white film to provide maximum contrast between fish shapes and the background in video images. Photoperiod was controlled with a 25W 100cm LED unit (NiCrew N13274B) above each tank with a 30-minute transition during the crepuscular period (8:16h L:D; 06:30 – 15:30).

Simulated habitat designs

To determine roach habitat preference, three habitat designs were simulated, i.e., a pumping station, a reed bed (unsheltered; treatment A) and a sheltered reed bed (treatment

B). In the real-world, pumping stations are effectively concrete boxes with the pump intake protected by steel bar screens (weed screens). Thus, to simulate a pumping station, the habitat compartment was covered and a Perspex panel with 20mm bars and 50mm apertures was placed at the entrance to the compartment to simulate a weed screen (Figure 1b, right). This could be exchanged with an opaque Perspex screen to prevent access during habitat management. The simulated reed bed (artificial habitat) was constructed using a light-gauge steel mesh (50mm aperture) secured to a plywood board (600 x 600mm) and approximately 100 cable ties (10 x 400mm) hung vertically from the mesh. For treatment A (unsheltered), a large aperture (500x500mm) was cut in the plywood board (Figure 1b, left), which conversely provided the cover in treatment B (sheltered). The artificial habitat was mounted on top of the experimental tank and the simulated reed bed (i.e., cable ties) extended throughout the entire water column. During baseline measurements, an opaque Perspex screen was fitted at the entrance to the habitat compartment to prevent access.

Video system

Six infra-red IP cameras (Hikvision 5MP IP POE H265 30m IR 2.8mm D150H) were mounted above the experimental tanks and the field of view (FOV) covered of all three habitats (Figure 1b). The cameras were networked to a desktop computer with a dedicated graphics adapter (Windows 10) using an 8-way PoE switch (YaunLey YS082G-P). To provide maximum contrast with the experimental tank and consistency between day and night recordings, the cameras were always operated in infra-red and greyscale. A freeware video client (iSpy v7.2.1.0) provided continuous recording of all cameras to a 4tb external HDD at 1280x720p, 12 frames s^{-1} (fps) using an MPEG-4 codec. This allowed for unencrypted access to video files post-experiment. Files were time and date stamped (hh:mm:ss – d/m/y) and stored in 10-minute intervals. The raw video files did not require any processing prior to examining habitat occupancy.

Experimental process

Baseline pumping station occupancy, habitat preference during artificial habitat introduction, artificial habitat occupancy during exclusion, and habitat preference post-exclusion were examined during 12-day experimental trials. Each treatment (A, B) received 12 replicates forming 24 discrete trials. The position of the simulated pumping station (left-hand, right-hand), and the tank number to receive each treatment (one to six) was alternated to control for tank effects. Prior to starting a trial, a dose of Protex (5ml) was added to the holding tank to minimise handling-induced stress. After 1h exposure, 72 roach were selected at random from the holding tank; 12 roach (e.g., one fish group) were added to the open water compartment of each experimental tank. This group size was deemed sufficient for roach to aggregate and shoal; previous experimental work on roach habitat occupancy found no significant difference at densities of 10, 50 or 100 (Orpwood et al. 2010). Roach were left to acclimate overnight before observations began the next day. To best represent a real-world scenario, this longitudinal study had four interventions (Figure 2), each with a 3-day observation period to control for temporal dependency.

All interventions were performed 1h post-dawn (i.e., 08:00) to allow for fish to first select daytime habitat. Fish were also fed (cubes of frozen blood worm) to minimise human interaction effects. Trial fish were returned to a second holding tank when each trial was completed to ensure they would not be selected as groups in the subsequent trial. Therefore, each fish group was randomised per trial, and all individual fish were studied no more than twice, in accordance with NC3Rs (2022).

Experimental interventions

This study had a longitudinal within-subject design which enabled habitat preference to be measured under sequential interventions (i.e., modifications to habitat availability) and changes in habitat preference to be measured individually (i.e., per trial/fish group). In accordance to Figure 2, the experiment was performed as follows.

- Baseline. Fish were initially exposed to a baseline measurement with pumping station habitat and access to open water. Artificial habitat was inaccessible (opaque Perspex screen installed at entrance).
- Intervention one (I1: pre-exclusion). To determine habitat preference between the artificial and pumping station habitats, artificial habitat was introduced (opaque Perspex screen removed), and thus fish could occupy artificial and pumping station habitats with access to open water.
- Intervention two (I2: exclusion). Fish were excluded from the pumping station (simulated weed screen removed and opaque Perspex screen installed) to determine if habitat management increased occupancy of the artificial habitat, and thus fish could occupy artificial habitat with access to open water.
- Intervention three (I3: post-exclusion). The pumping station was reintroduced (opaque Perspex screen removed and simulated weed screen reinstalled) to determine whether habitat preference had changed (compared to I1) and the effectiveness of habitat management on artificial habitat occupancy. Fish could occupy artificial and pumping station habitats with access to open water.

Data analysis

Video observations

Habitat occupancy and preference was analysed using data collected from a total of 6,912 hours of video footage; a multi-video streaming client (IVSDesktopPlayer 1.0.0.4) was used to playback six 10-minute video files at once. Over each 12-day trial, fish counts were taken every hour (number of individuals occupying each habitat compartment) which was chosen to provide (1) a suitable sample frequency that captures habitat preference, (2) an accurate representation of diel activity and (3) an appropriate cost-benefit sub-sample frequency vs gain in accuracy. The effect of diel phase was examined by creating day and night categories.

Statistical analysis

During the video analysis, 20,827 hourly fish counts were made (i.e., a count of 0 – 12 h^{-1} for each habitat and open water (Table S1). Generalized Linear Mixed Effect Models (GLMMs) were used to account for repeated measures (trial), temporal dependency (hour, day), tank effects (tank), and to investigate habitat occupancy and preference under baseline, habitat introduction and habitat exclusion conditions. Individual GLMMs (R function 'glmmTMB' in package 'glmmTMB') were built to estimate habitat occupancy in the three response categories (pumping station *n = 5,214*, open water *n = 6,943*, artificial habitat *n = 5,214*). For these count data we used a binomial distribution with a (success, failure) structure where the number of observed fish per hour in a habitat represented successes, and applied a logit link to predict success probability. We defined the model structure a priori, including experimental sequence (levels = baseline, I1, I2, I3) and an interaction with light (levels = day, night), and treatment (levels = unsheltered (A), sheltered (B)) as fixed effects. The baseline and I2 categories were not included in the artificial habitat and pumping station models, respectively, as these were inherently not measured according to the experimental design. Repeated measures on fish groups, temporal dependency and tank effects were treated by including the nested random effects of trial, day, and hour and the separate effect of tank, which all had variances higher than zero and improved the models Akaike's Information Criterion (AIC) and goodness of fit (Table S2).

Model assessment was performed on the final models by examining the predicted versus residual diagnostic plots according to Zurr.*et al.* (2007) (R function 'simulateResiduals' in package 'DHARma'). Marginal population-level effects (means ± 99% CI) were calculated using R function 'ggaverage' in package 'ggeffects'. All data were analysed using R version 4.3.1 (Team R, 2023a) in Rstudio 2023.06.0 (Team R, 2023b) and statistical figures were created using R packages 'ggplot2' and 'ggpubr'.

Results

The raw data included a total of 30,120, and 29,004, and 23,924 fish counted in the artificial habitat, pumping station and open water, respectively, across the 24 12-day trials. We found that habitat occupancy was highest during the day, and lowest at night in the pumping station (*GLMM: -5.547 ± 0.276, p = < 0.001*) and artificial habitats (*GLMM: -0.802 ± 0.138, p = < 0.001*); the opposite was found for open water (*GLMM: 4.308 ± 0.181, p = < 0.001)* (Figure 3, Table S3). Nocturnal open water dispersal i.e., fish occupying structured habitat during the day and dispersing in open water at night occurred throughout the study but was reduced when we introduced artificial habitat (Figure 3b). No significant day-to-day variations in this relationship were observed within each experimental sequence, i.e., daytime occupancy was similar 24h vs 72h post-intervention.

Habitat availability (i.e., experimental sequence) significantly influenced habitat occupancy across the three habitats; pumping station (*GLMM: Δ log-likelihood = 720, df = 4, p = < 0.001*), artificial habitat (*GLMM: Δ log-likelihood = 849, df = 4, p = < 0.001*) and open water (*GLMM: Δ log-likelihood = 595, df = 6, p = < 0.001*). Following our GLMM analysis, we found significant support for our alternative hypotheses (H_1), which suggests that the data were consistent with hypotheses (i) through (iv). In the absence of artificial habitat, fish occupied the pumping station during the day (*GLMM probability:* 86.5 ± 4.9 %, *p = < 0.001*; Figure 3a, Table S3). When we introduced the artificial habitat without pumping station exclusion (I1), daytime artificial habitat occupancy (*GLMM probability:* 18.4 ± 6.9%, *p = < 0.001*), was significantly lower than pumping station occupancy (*GLMM probability:* 87.5 ± 3.8 % *p = < 0.001*) and therefore fish preferred the latter (Figure 3, Table S3). Artificial habitat occupancy significantly increased when we excluded fish form the pumping station (I2) (*GLMM probability:* 83.1 ± 6.1% *p = < 0.001*) (Figure 3c, Table S3). When we reintroduced the pumping station after exclusion (I3), pumping station occupancy significantly reduced (*GLMM probability:* 3.7 ± 4.1 %, *p = < 0.001*), whereas artificial habitat occupancy significantly increased (*GLMM probability:* 87.9 ± 5.6 %, *p = < 0.001*), demonstrating a preferential shift in fish behaviour towards occupying the artificial habitat, compared to pre-exclusion (Figure 3, Figure 4a, Table S3).

We found no significant support for our final hypothesis (v), as GLMMs indicated no preference for sheltered over unsheltered artificial habitats across the three habitat models; pumping station (*GLMM: 0.784* ± *2.371, p = 0.740*), artificial habitat (*GLMM: -0.576* ± *0.762, p = 0.450*) and open water (*GLMM: 0.238* ± *0.912, p = 0.793*) (Figure 4b; Table S3).

Discussion

The variation in fish habitat occupancy and preference during this experiment emphasises the necessity of rigorous assessment and experimental testing to understand and predict how fish will respond to the introduction of artificial habitat, with and without habitat management practices, in the real-world. We quantified habitat occupancy and habitat preference of roach in four experimental scenarios that replicate sequential management interventions intended to provide alternative refuge for fish that occupy hazardous anthropogenic structures (e.g., pumping stations), and thereby prevent restoration failures. By doing so, our study significantly moves forward our understanding of fish habitat preference, given the challenges of studying at operational pumping stations (Norman et al. 2023b). Roach occupied a pumping station during baseline measurements and preferred this habitat once artificial habitat was introduced (pre-exclusion). Artificial habitat occupancy was then highest during habitat management (exclusion from pumping station). After habitat management (post-exclusion), access to the pumping station was reestablished but occupancy decreased, whereas artificial habitat occupancy increased. Therefore, our findings demonstrate a preferential change in habitat occupancy before and after habitat management and can contribute to habitat restoration plans for degraded freshwaters where fish occupy existing hazardous structures.

During the baseline period, fish exhibited high daytime occupancy in the pumping station habitat and nocturnal aggregation in open water, supporting our hypothesis (i) and consistent with previous observations of roach in experimental settings (Orpwood et al. 2010), and at real-world pumping stations (Norman et al. 2023a; 2023b; 2023c). Although we did not study predation, these behaviours align with known anti-predator strategies, and potentially reflect past avian predation threats as per the ‘ghost of predation past’ hypothesis (Gliwicz & Jachner 1992; Sheriff et al. 2010; Bosiger et al. 2012). That said, nocturnal behaviour was not uniform across fish groups, suggesting inter-individual differences (e.g., Martin et al. 2014;

Camacho & Hendry 2020) and possibly reflecting an ideal free distribution (Fretwell & Lucas 1970), but this was not quantified here.

Introducing artificial habitat without sufficient fish stimulus may lead to restoration failures if fish fail to perceive alternative habitat as higher quality (Pattern & Kelly, 2010). Low daytime artificial habitat occupancy during intervention one supported our hypothesis (ii) but contrasted previous research showing high habitat occupancy rates in a similar introduction context (Lemmens et al. 2016). Indeed, this discrepancy could indicate maladaptive habitat selection, or a 'perceptual trap' where fish avoided the restored habitat if it appeared unattractive (Pattern & Kelly, 2010; Ferrari et al. 2017). Varying fish behaviour, and thus habitat occupancy, could also suggest an 'equal-preference trap', where fish showed no preference for either habitat, speculatively influenced by mixed numbers of neophobic and neophillic individuals (Robertson & Hutto 2006; Cote et al. 2010). Therefore, fish boldness assessments could be incorporated into future experiments, provided fish can be identified during observations (White et al. 2013). Further studies are needed to determine if this effect directly transfers to a real-world setting, but our results suggest that the introduction of artificial habitat without providing stimulus cues will not prevent fish occupying hazardous infrastructure.

Excluding fish from the pumping station (i.e., habitat management) was critical for influencing artificial habitat preference, aligning with our hypothesis (iii) and suggesting exclusion which enhances fish settlement cues of artificial habitat will be important for future restoration management plans (Hale et al. 2018; Hale et al. 2020). Accordingly, we found strong evidence for our hypothesis (iv); when we reintroduced the pumping station (post-exclusion), fish showed a preferential switch from occupying the pumping station (pre-exclusion) to artificial habitat. After exclusion, the change in preference towards artificial habitat could be attributed to their reed bed-like complexity and small interstitial spaces, known to affect habitat occupancy and prey detectability (Ferrari et al. 2017), and similar to findings in other studies using structured refuges (Santos et al. 2008; Frehse et al. 2021). Some fish showed a preference for the pumping station, potentially preferring more open structures (Baumann et al. 2016). Indeed, although habitat management practices should change habitat selection behaviours of wild fish, phenotypically variable behaviours of fish underpin the need for realistic expectations in habitat restoration success, and even effective management by restoration ecologists is unlikely to attract all fish in real world (Hale et al. 2020).

We found no significant difference in daytime habitat occupancy between sheltered and unsheltered artificial habitat, challenging our hypothesis (v) and contrasting the findings of Orpwood et al. (2010), who proposed unsheltered habitats were lower quality than sheltered habitats for roach. Despite this, we observed behavioural tendencies where roach in unsheltered treatments spent more time in open water and made more frequent visits to the pumping station during the day. These behaviours could align with the adaptive habitat selection hypothesis (Orians & Wittenberger 1991) if roach perceived the threat of predation in open water as less costly than poor quality habitat. However, the absence of a clear preference for sheltered habitats in our study suggest that artificial habitat quality may not be solely determined by the presence of shelter. Further research is therefore needed to understand how factors affecting habitat preference will influence the success of habitat restoration.

Despite limitations in providing empirical controls for each intervention in this longitudinal study, we observed increased daytime occupancy in the complex artificial habitat and decreased occupancy in the pumping station, highlighting the necessity for detailed planning in habitat restoration (i.e., Hale et al. 2017). Our observations challenges the Field of Dreams hypothesis ‘if you build it, they will come’ (Hilderbrand et al. 2005), as roach only partially occupied artificial habitat when it was first introduced. Contrary, our findings suggest that effective habitat management significantly enhanced artificial habitat attractiveness and thus challenge the Field of Dreams hypothesis by suggesting ‘if you build it, they might come’ (e.g., Walsh & Breen 2001; Bond & Lake 2003; Sudduth et al. 2011). Fundamentally, the increased attractiveness of artificial habitat provided by habitat management prevented the creation of a perceptual and ecological entrapment, which could reinforce occupancy of poor habitats (Robertson et al. 2013). Hence, this study proposes that artificial habitats correctly built and installed with associated habitat management activities will provide an attractive and suitable alternative for fish that occupy hazardous anthropogenic structures.

Lessons learnt during previous artificial habitat installations suggest scaling up this experiment to a real-world setting will be challenging (Norman et al. 2023b). Artificial habitat structures must align with fish's spatial usage patterns to be effective (Hale et al. 2019). Implementing a physical barrier will be necessary to disperse fish towards artificial habitat, similar to how flood gate operations were modified in a previous study (Norman et al. 2023c). Long-term monitoring will then be required to adapt management to fish habitat occupancy and preference, potentially leading to periodic exclusion from hazardous anthropogenic structures to promote consistent occupancy of artificial habitats.

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. The authors have no conflict of interest to declare. The authors would like to thank the wider Environment Agency Calverton fish farm team – Richard Pitman, Ian Cook, James Rabjohns, Neil Lincoln and Nick Gill for capture, transport, housing facilities and care of fish. We also thank Hull and District angling club for providing the fish. Additional thanks go to Michael Lee and Paul Coulson, and staff and students at HIFI for their assistance, in particular Liam Carter, Oliver Evans and Steven Storey.

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Figures

LIST OF FIGURES

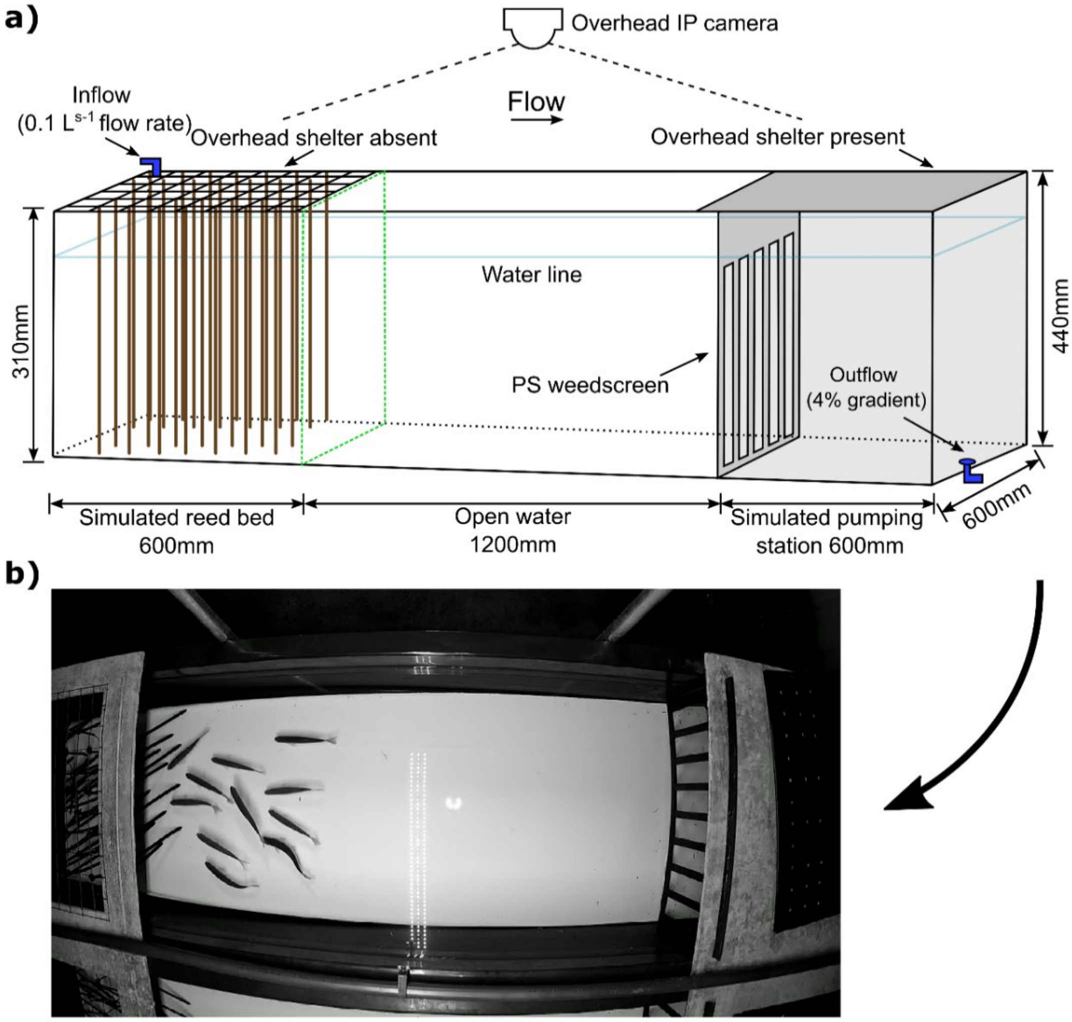

Figure 1 a) a schematic diagram (not to scale) representing the experimental tank used to test roach habitat preference. The diagram represents treatment A. Green dashed line indicates position for opaque Perspex screen installed when preventing access to habitat. Grey shading indicates cover. b) a screen capture from the IP camera showing the overhead view with simulated reed bed (left) and simulated pumping station (right).

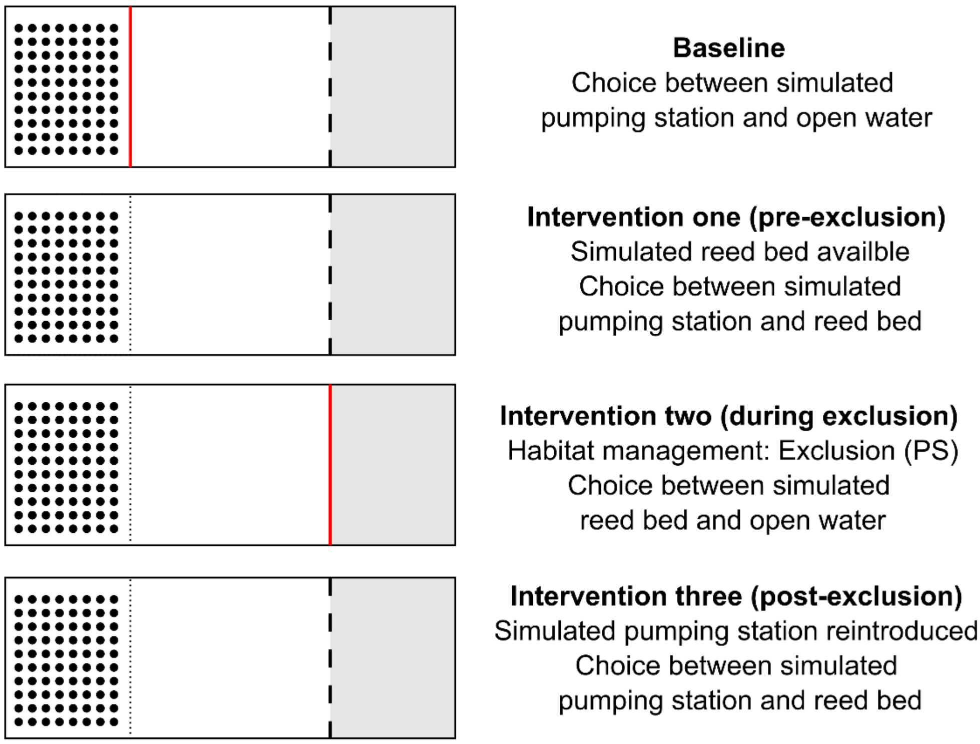

Figure 2 Representation of the iterative experimental design used to test roach habitat preference. Red line indicates opaque Perspex screen installed to prevent habitat access. Dashed line represents weed screen. Dotted line indicates threshold for simulated reed bed compartment.

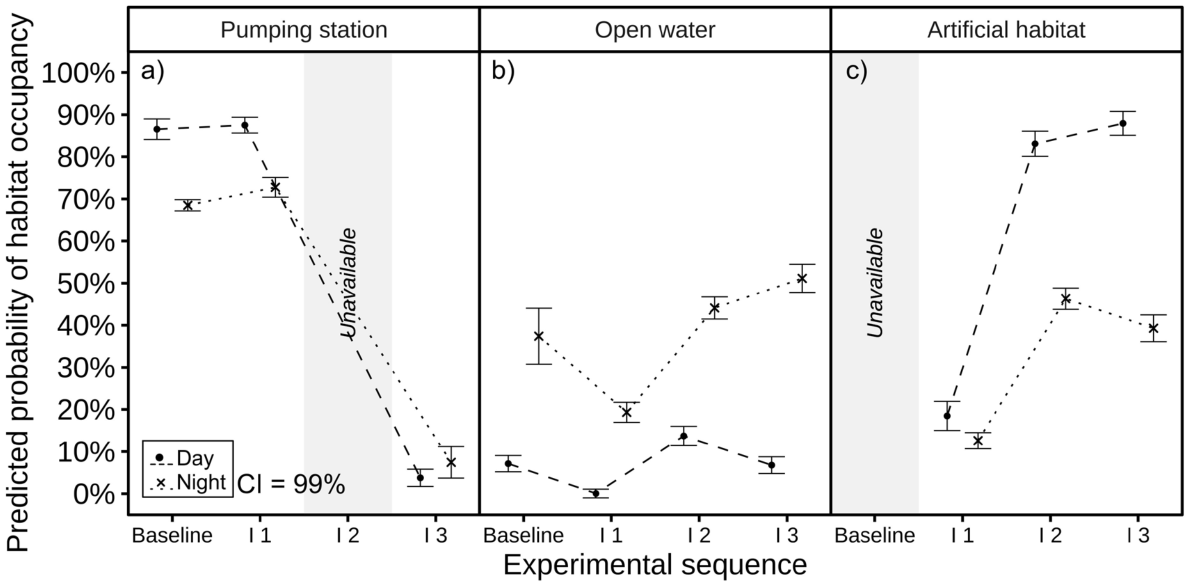

Figure 3 The predicted probability of habitat occupancy across each experimental sequence. Marginal effects fitted by Generalised Linear Mixed Models (logit-linked binomial distributions) for each response variable a) pumping station, b) open water, c) artificial habitat. All models incorporated the random effect of time, day, trial, and tank. Error bars represent 99% confidence intervals. Light grey background shading denoted by 'unavailable' indicates where habitat was not available. Models fitted using glmmTMB and ggeffects in R 4.3.1.

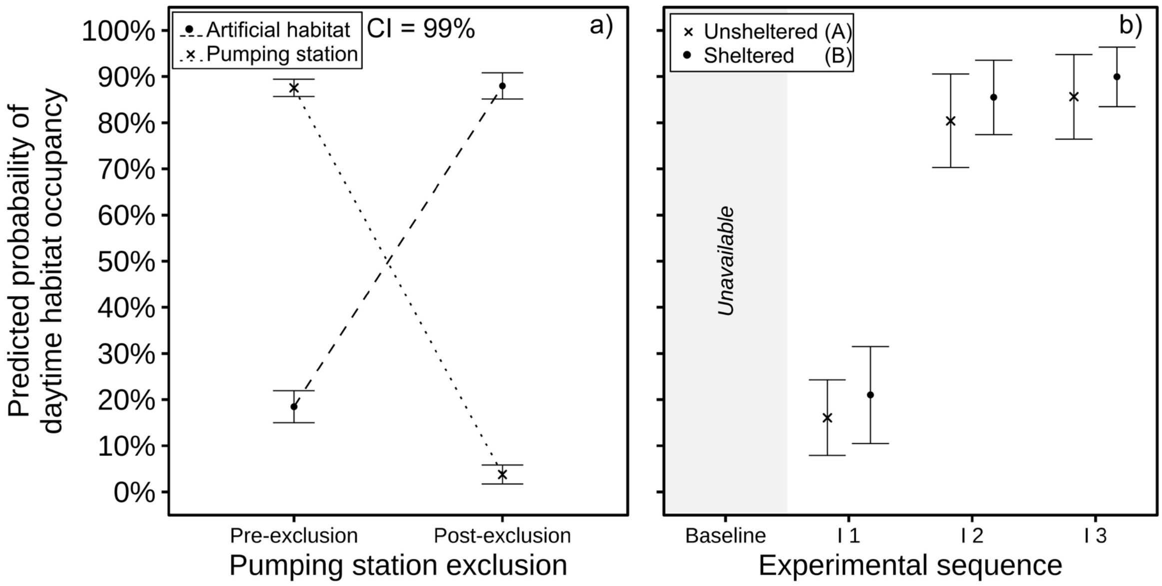

Figure 4 The predicted probability of fish occupying a habitat during daytime determined by a) pumping station exclusion, and b) artificial habitat treatment. Marginal effects fitted by Generalised Linear Mixed Models (logit-linked binomial distributions) incorporating the random effect of time, day, trial, and tank. Error bars represent 99% confidence intervals. Light grey background shading denoted by 'unavailable' indicates where habitat was not available. Models fitted using glmmTMB and ggeffects in R 4.3.1.