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RESEARCH ARTICLE

Spawning habitat selection and behavioural repeatability of stocked Walleye (*Sander vitreus*) in Hamilton Harbour

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Abstract

Efforts to re-establish a self-sustaining Walleye (*Sander vitreus*) population in Hamilton Harbour have occurred against a backdrop of extensive habitat degradation and uncertain spawning behaviour. We paired shoreline habitat surveys (2021) with electrofishing spawning surveys (2022–2024) and acoustic telemetry data (2016–2023) to describe the habitat associations and repeatability of spawning behaviour for stocked Walleye within Hamilton Harbour, a degraded embayment of Lake Ontario. Random forest models revealed that spawning occurrence in electro-fished Walleye was most strongly associated with gentle shoreline slopes, high substrate diversity, and the presence of cobble substrates. For telemetry-tracked individuals, presumed spawning was inferred from detections indicating nocturnal, shallow-water (< 2 m) residency at nearshore stations in April, sustained for ≥20 min and accompanied by multiple sequential detections. Walleye displayed no repeatability in total spawning duration ($R = 0.08 \pm 0.11$), marginal repeatability in station-level specialization (degree of spawning focused on a preferred receiver; $R = 0.29 \pm 0.16$), and significant repeatability in station count (number of receivers where presumed spawning occurred; $R = 0.41 \pm 0.12$), station ratio (proportion of encountered receivers used for spawning; $R = 0.32 \pm 0.11$), and spawning depth (average depth during spawning; $R = 0.47 \pm 0.15$). Fish generally concentrated spawning activity at a small subset of nearshore receivers, demonstrating local site fidelity within the embayment across years. Together, these results identify the habitat features selected by stocked Walleye and show that individuals express consistent spatial spawning strategies, which may influence how they encounter and use restored habitat. These findings inform ongoing efforts to support natural Walleye recruitment in Hamilton Harbour.

Keywords Spawning behaviour · Habitat selection · Acoustic telemetry · Behavioural repeatability · Spawning site fidelity

Introduction

Walleye (*Sander vitreus*) support substantial recreational, commercial, and Indigenous fisheries across North America (Barton 2011). In the Laurentian Great Lakes, Walleye have historically used large portions of nearshore waters, such as the western regions of Lake Huron (Hayden et al. 2014) and Lake Erie (Wang et al. 2007), and the eastern half of Lake Ontario (Bowlby and Hoyle 2011). However, Walleye populations declined across the Great Lakes between the 1950s and 1970s due to habitat loss, invasive species establishment, over harvest, and pollution (Schneider and Leach 1977; Johnson et al. 2015), with many potential spawning habitats subsequently fragmented and degraded, further reducing recruitment (Holmes 1988; Roseman et al. 2010). To support Walleye recovery efforts, managers intensified hatchery-based stocking programmes (Regier et al. 1969;

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Kerr and Letendre 1991; Schmalz et al. 2011; Euclide et al. 2024). The release of hatchery-reared fish can be a valuable tool for restoration when combined with habitat rehabilitation and fishery regulations (e.g., Fielder and Baker 2019; Hyatt and Stockwell 2019); however, hatchery fish differ from wild populations in their genetic composition, physiology, and behaviour (Claussen and Philipp 2023). An improved understanding of the spawning behaviour of hatchery-reared Walleye is needed to inform management efforts focused on Walleye restoration in the Laurentian Great Lakes.

Walleye spawning behaviour in natural populations is well understood throughout their range. Walleye are broadcast spawners that require shallow habitats (Bozek et al. 2011b) with gravel and cobble substrates, where interstitial spaces offer protection for eggs (Kerr et al. 1997; Raabe and Bozek 2012; Crane and Farrell 2013). Recruitment is influenced by abiotic factors such as lake size, spring warming rate, and water level (Nate et al. 2000; Quist et al. 2004; Hansen et al. 2015), as well as biotic factors, including egg predation by invasive Alewife (*Alosa pseudoharengus)* (Rutherford et al. 2016) and White Perch *(Morone americana*) (Roseman et al. 2006; Krabbenhoft et al. 2023). Walleye exhibit diverse spawning strategies, with individuals spawning in either riverine or lake systems relating to riffles, reefs or shoals, depending on local habitat availability and population origin (Jennings et al. 1996). River-spawning Walleye typically seek shallow riffle habitats with gravel and cobble substrates, whereas lake-spawning Walleye use offshore reefs or gravel, cobble, and rubble shoals (Bozek et al. 2011a; Gatch et al. 2021). Male and female Walleye differ in how they interace with spawning habitat. Females spawn, then move off the spawning grounds, whereas males remain at spawning sites longer to maximize reproductive opportunities with multiple females (Bade et al. 2019). While these patterns are well documented, the specific factors influencing spawning site selection at fine spatial scales remain poorly understood (Raabe and Bozek 2012). Evidence from movement studies suggests Walleye migrate in the spring to spawn (Hayden et al. 2018; Matley et al. 2020; Bihun et al. 2025) and often display site fidelity, returning to the same spawning grounds across years (Zhao et al. 2011; Hayden et al. 2018; Chen et al. 2020), though the spawning behaviours of stocked Walleye have been less studied than those of wild-type Walleye.

Spawning site fidelity in Walleye may be related to natal homing (Chen et al. 2020), with presumably a genetic basis (Jennings et al. 1996), or a learned behavioural component. Though past studies suggest that stocked and natural Walleye populations can exhibit similar habitat use (Weber and Weber 2020), critical spawning information may be lost for conspecifics in systems with stocked Walleye and no native population. Introducing individuals into a novel environment creates uncertainty in their individual habitat and spawning decisions, and understanding how stocked Walleye navigate these decisions may inform recovery efforts. Walleye in Lake Ontario have displayed repeatable long-distance spawning migrations (Elliott et al. 2023) and regional spawning fidelity (Hayden et al. 2018; Chen et al. 2020; Zhao et al. 2011). Building on this, evidence of repeatable fine-scale spawning behaviour and site fidelity would indicate that individuals adopt distinct spawning strategies despite interannual variation in environmental conditions. Documenting such repeatability is important because persistent individual behaviours and habitat use can shape population-level dynamics, and similar patterns in other freshwater fishes have been used to inform management actions (Miller et al. 2001; Forsythe et al. 2011). Understanding how stocked Walleye navigate these decisions in degraded environments is critical, as habitat fragmentation and anthropogenic alteration may constrain access to preferred habitat and disrupt cues that guide spawning behaviour.

Hamilton Harbour, a large embayment at the western end of Lake Ontario, historically supported a Walleye population that spawned in the harbour's tributaries (Dymond et al. 1929). Population declines were evident by the late nineteenth century, and by the 1970s, spawning activity had ceased (Whillans 1977). The system has been heavily impacted by decades of anthropogenic degradation and was designated as an Area of Concern (AOC) in 1987 (HH RAP 1992a, b). Efforts to improve conditions in the system have included upgrades to wastewater treatment systems, which have led to reductions in ammonia (City of Hamilton 2023) and the management of contaminated sediments (Graham et al. 2017). More targeted measures to support Walleye population recovery have included opportunistic transfers of adult fish and fingerlings from the Bay of Quinte, Lake Ontario, in the 1990s (Hoyle et al. 2017). These earlier stocking efforts were largely unsuccessful at seeding a sustainable population, as adult Walleye abundance declined between 2006 and 2012 (Hoyle 2015). Subsequently, the Ontario Ministry of Natural Resources (OMNR) established an adult population in the system by stocking summer fingerlings in 2012, 2016, 2018, 2020, and 2022, which were sourced from the Bay of Quinte and reared in hatcheries (Ontario Ministry of Natural Resources and Forestry 2021; Ontario Ministry of Natural Resources (OMNR) 2022; Ontario Ministry of Natural Resources and Forestry 2023; Midwood et al. 2024a). Walleye from both river- and shoal-spawning sources have been stocked in Hamilton Harbour, but there has been no evidence of genetic structuring between source groups (Wilson and Gatt 2001), and eggs collected in 2020 and 2022 were sourced exclusively from Trent River (S. Beech, personal communication). These stocked Walleye have exhibited high growth rates and survival (Brooks et al. 2019); however, there is to

date no evidence of natural recruitment of Walleye within Hamilton Harbour (Croft-White, et al. 2026; Midwood, et al. 2026). An assessment of the barriers to natural recruitment of Walleye within the harbour identified that the bottleneck is likely early life phase survival, with factors such as water quality, sedimentation, wind and wave transport, and predation limiting survival (Midwood, et al. 2026); however, assumptions of suitable spawning habitat remain untested (Midwood et al. 2026).

A clearer understanding of how stocked Walleye select spawning habitat within Hamilton Harbour would better inform natural recruitment efforts. To address this need, we combined electrofishing spawning surveys with shoreline habitat data to identify key habitat features associated with spawning. We then utilized acoustic telemetry data to target spawning events and describe derived spawning behaviours (i.e., station count, station count proportion, total residency, and mean spawning), their repeatability, and the extent of individual spawning-site specialization. Our goal was to determine the habitat characteristics and behavioural patterns associated with stocked Walleye spawning to inform management strategies that will support the development of a self-sustaining Walleye population in Hamilton Harbour.

Methods

Hamilton Harbour

Hamilton Harbour is a 21-km^2 embayment located at the western end of Lake Ontario (43.300 N, 79.806 W). The harbour contained productive wetlands and shoals before extensive land development and industrialization in the 1800s and 1900s reduced this habitat to 35 % of historic amounts and created eutrophication and contamination in the remaining habitats (HH RAP 2003; Brooks et al. 2017). Habitat loss and degradation led to declines in fish abundance and species richness, which have recovered little since the system was initially listed as an AOC (Turner et al. 2025b; Midwood et al. 2026). The fish community is largely dominated by eutrophic-tolerant native (e.g., Brown Bullhead [*Ameiurus nebulosus*], Gizzard Shad [*Dorosoma cepedianum*]) and non-native species (e.g., Common Carp [*Cyprinus carpio*], Goldfish [*Carassius auratus*]) (Midwood et al. 2024b). Water below the hypolimnion is routinely hypoxic during the summer, with wind-driven hypoxic incursions toward nearshore environments (Flood et al. 2021). The shoreline of Hamilton Harbour is highly developed and primarily characterized by vertical seawall, rip-rap, cobble, and rubble (Gardner Costa et al. 2020). Substrates are primarily composed of sand and silt, with increasing clay at greater depths (Doolittle et al. 2010). The harbour is exposed to prevailing westerly winds that align with the greatest fetch spanning the basin from west to east (Doolittle et al. 2010).

Data collection

Habitat survey

Habitat surveys were conducted to determine the depth and substrate of available spawning habitat (Supplementary Table 1). Light pollution at these sites was also assessed, given the potential for anthropogenic light at night to deter Walleye spawning, as has been observed in other light-sensitive and nocturnally spawning fishes (Bassi et al. 2022). In 2021, surveys were completed on September 15, 21, and 28 (Fig. 1). For each transect, coordinates were recorded at the 1-m depth position, and habitat was assessed along two or three points between 1 m depth and the shoreline, according to transect length. For each point, the depth was determined using a measuring pole, and the substrate composition within an approximately 1-m^2 area was estimated visually, or by feel (when water clarity was too poor). Substrate categories were based on a modified Wentworth scale presented in (Raabe and Bozek 2012). The Euclidean distance from 1 m depth to the shoreline was measured and converted into slope degrees. Water level was recorded at Burlington station 13150 (2025), which is < 1 km from the nearest habitat site, and was checked at the start of each day, and periodically throughout the surveys. Finally, an index of the categorical level of light pollution was recorded for each transect, where 1 represents low ambient light, and 4 represents the highest observed levels of artificial light pollution (i.e., streetlights immediately above the sampling location; Supplementary Figure 1). Light categories were assigned through visual assessment in the field, based on the relative intensity and proximity of artificial light sources such as streetlights, building illumination, and other infrastructure lighting.

Electrofishing survey

Walleye spawning locations were surveyed via boat electrofishing. Boat-accessible shorelines with suitable depths (i.e., ~1.5 m) were sampled between April and May each year (2022–2024; Supplementary Table 2) using an electrofishing vessel manufactured by Outlaw-Eagle, using a Smith-Root Apex boat electrofishing unit (Seattle, USA) powered by a Honda 7000 generator (Tokyo, Japan). Electrofishing settings were initially set below the estimated threshold for fish response in the system (approximately 3000 Watts at 140v, 10% duty, 120 Hz DC) and adjusted upward as needed by the operator. Specific tuning of the settings was dictated by fish shockability (increased intensity to improve catchability) and recovery time (lowered settings if Walleye were

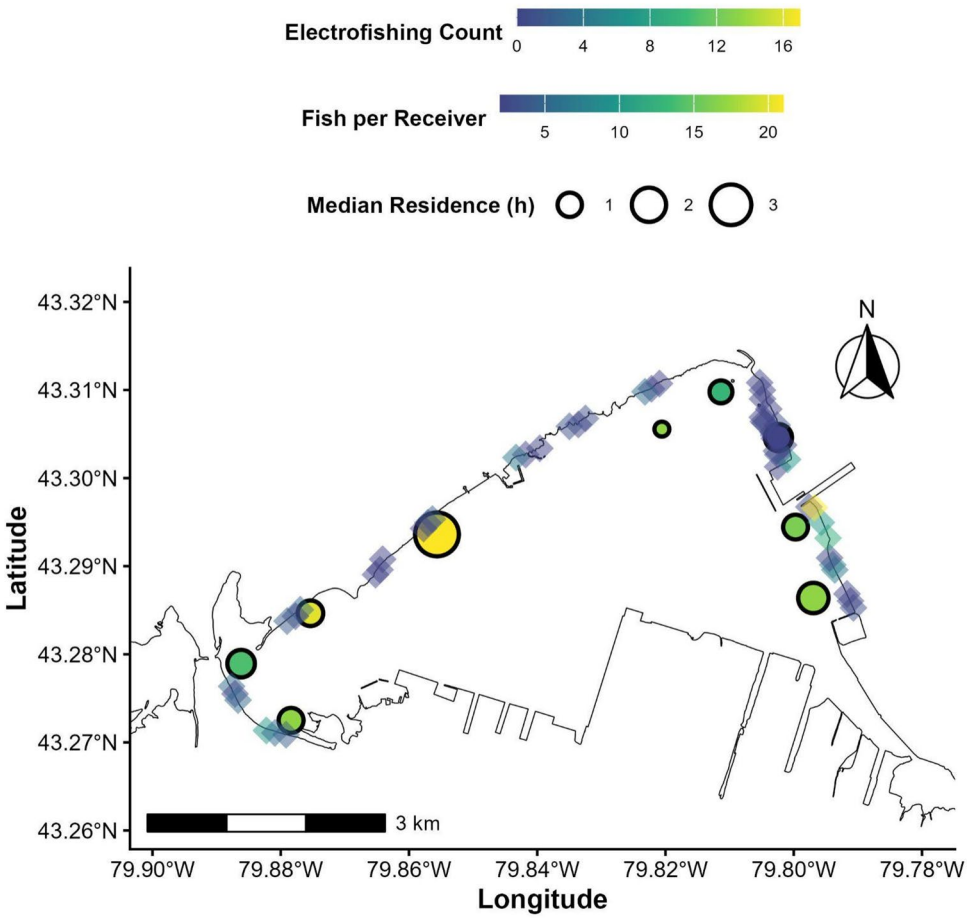


Fig. 1 The location of acoustic telemetry receivers (circles) and Walleye spawning habitat survey sites (diamonds) in Hamilton Harbour, Lake Ontario. Receiver circles are coloured according to the count of Walleye detected spawning at each receiver, while larger circle size indicates higher average spawning duration (h). Shoreline habitat data are scaled with colour denoting higher culumative electrofishing counts (caught + observed). Habitat surveys were conducted in September 2021, and electrofishing surveys were conducted annually in April from 2022 to 2024. Telemetry data were gathered for the month of April across 2016–2023

taking > 10–15 s to recover in the live well). Settings were variable depending on water chemistry and substrate composition but typically fell between 3200 and 4000 W. All surveys were conducted at night from 30 min after sunset to approximately 0200 local time. Favourable winds were required, with onshore winds ≤ 10 kph. Water temperature was regularly monitored beginning the first week of April, and survey timing was coordinated to ensure water temperatures had reached 6 °C, an anticipated lower threshold for Walleye spawning (Scott and Crossman 1973).

Electrofishing spawning surveys systematically covered the entire north, east, and west shorelines within the target depth range rather than fixed-length transects. The south shore was not sampled as it is constructed from sheet piling and hardened vertical walls, at greater depths (Gardner Costa et al. 2020). Previous investigations on the south shore during the Walleye spawning window found few locations of suitable substrate, and no Walleye were detected proximate to these locations. When Walleye were encountered, netters captured as many individuals as possible, with multiple fish captured within a single boat length (approximately 6 m) considered an aggregation (1.7 ± 1.0 fish, mean ± SD; Supplementary Figure 2) and marked with a single GPS point. A live-well divider was used to maintain separation among aggregations. Any Walleye that were observed in the water but not netted (21%; Walleye were easily identifiable by the white tip on the lower lobe of the caudal fin) were recorded separately and included in the aggregation data. The fork length (mm), wet mass (g), sex (female, male, or unknown), and external gonad condition (green, ripe, or spent) were recorded for each individual captured. Fish were processed and released several hundred metres back along the transect to prevent recapture within the same pass. To associate Walleye with habitat conditions, the dataset was trimmed to include only regions within a 25-m buffer around habitat survey locations (Supplementary Figure 3).

Walleye telemetry tagging

Presumed Walleye spawning behaviours were tracked with an acoustic telemetry array that has been deployed throughout Hamilton Harbour with ongoing tracking since 2015 (see Brooks et al. 2019 for details), and data were processed as per Larocque et al. (2024a, b). Individuals (n=45) were captured and tagged as per Brooks et al. (2019), but briefly, Walleye were captured in trap nets set as part of the

OMNRF's NSCIN survey (Lester et al., 1996) or with boat electrofishing. Walleye were measured at the time of tagging (fork length = 523 ± 71 mm; mass = 2023 ± 793 g; mean ± SD; Supplementary Table 3; Supplementary Table 4, Supplementary Figure 4), but fish sex was not identified. Upon capture, Walleye were placed in holding tanks filled with ambient lake water to await surgical procedures. Fish were immobilized for surgery using either a Portable Electroanesthesia System (PES; Trushenski et al., 2012, Rous et al., 2015) or Smith-Root electrofishing gloves (Vandergoot et al., 2011). Individuals were placed in a padded trough, and ambient lake water was pumped into their mouths to keep their gills wet. Transmitters fitted with pressure sensors to determine depth (Innovasea V13P-1x-069k-1-0034m, 13 mm diameter, dry mass 11 g, battery life 1386 days, vertical accuracy 1.7 m, vertical precision 0.15 m) were inserted into the body cavity through a 2–3-cm mid-ventral incision. Incisions were closed with two or three interrupted sutures (3-0 polydioxanone-II violet monofilament, 24 mm; Ethicon, USA). Fish were released within 100 m of their capture location. Fish handling and surgical procedures were approved by a Canadian Council on Animal Care protocol administered by Carleton University and Fisheries and Oceans Canada (AUP OPA-ACC-2079, AUP OPA-ACC-2179).

Data processing and analysis

All data processing and statistical analyses were conducted in R version 4.3.0 (R Core Team 2023) via RStudio (RStudio Team 2020), with data processing and plotting performed using the {tidyverse} (Wickham et al. 2019) and {ggmap} (Kahle and Wickham 2013) packages.

Survey data processing and exploration

The shoreline habitat and electrofishing datasets were combined following data filtering and removal. Substrate diversity at each survey point was quantified using Simpson's diversity index ($D = 1 - \Sigma pi^2$), which represents the probability that two randomly selected substrate units belong to different types, calculated using the {vegan} package (Oksanen et al. 2026). Shoreline habitat data were processed to reduce co-occurrence amongst substrate types (Supplementary Figure 5). Armourstone, which was highly correlated ($R > 0.65$) with substrate diversity and slope, as well as rare substrate categories (fines, silt) that occurred in < 5% of the sites, were removed. The remaining habitat categories had correlations < 0.75 and were retained. The electrofishing dataset was then processed to align with habitat sites. For this, Walleye capture or observation data (i.e., counts) was filtered to include only data found within 25 m of the nearest sample site. When multiple Walleye aggregations occurred within this range, counts were summed for each year and sample site, a radius that balanced spatial precision with sample size (52 of 257 aggregations, 20% of total). To correlate Walleye occurrence with habitat features, pseudo-absences were assigned to shoreline habitat sites where Walleye were not found. Fetch data were modelled for each sample site using the {fetchR} package (Seers 2020). Fetch was calculated as the average of the minimum distance to shore in 16 cardinal directions (starting at 0 and increasing by 22.5 until 337.5°).

Random forest models

Walleye occurrence and abundance were modelled in separate random forest models. Random forest models can fit nonlinear relationships and are relatively insensitive to autocorrelation (Booher and Walters 2021), which has led to their increasing application in assessing habitat preference (Brownscombe et al. 2021; Kim et al. 2021; Bzonek et al. 2024, p. 202; Larocque et al. 2024a). Each model included year, slope (°), light index, fetch (m), substrate [cobble (%), gravel (%), sand (%), rubble (%)], and substrate diversity) as predictors against the electrofishing Walleye data. The occurrence and abundance datasets were split into training and test sets in a 70:30 ratio. The random forest models were trained using {randomForest} (Liaw and Wiener 2002) where they were fit with 1000 trees, and the default *mtry* setting was defined as the square root of the number of predictors, where *mtry* represents the number of predictors randomly selected as candidates at each node split. Model performance for Walleye occurrence was evaluated using sensitivity, specificity, and balanced accuracy, metrics used to measure, respectively, the ability to correctly predict Walleye occurrences, the ability to correctly predict Walleye absences, and the ability to predict both. Model performance for Walleye abundance was evaluated using mean error, root-mean-square error, and R^2, which describe prediction bias, accuracy, and explained variance, respectively.

Predictor importance was assessed following the protocol described by Brownscombe et al. (2022). The relative importance of each predictor variable was evaluated using a pseudo-R^2 (pR^2) metric, calculated by comparing the mean squared error (MSE) of fitted trees that included the variable of interest to those that excluded it. The percent increase of MSE (%IncMSE) was scaled from 0 to 1 and multiplied by the total model accuracy (occurrence model) or R^2 (abundance model) in test data (Fig. 2). Partial dependencies—representing the relationship between the predictor and the response with other predictors held constant at their mean—were calculated with the {pdp} package (Greenwell 2017).

Spatial autocorrelation in the habitat selection models was assessed following the methods presented in (Larocque et al. 2024b). Briefly, Moran's I was calculated using with the {spatialRF} package (Benito 2021) at predetermined lag

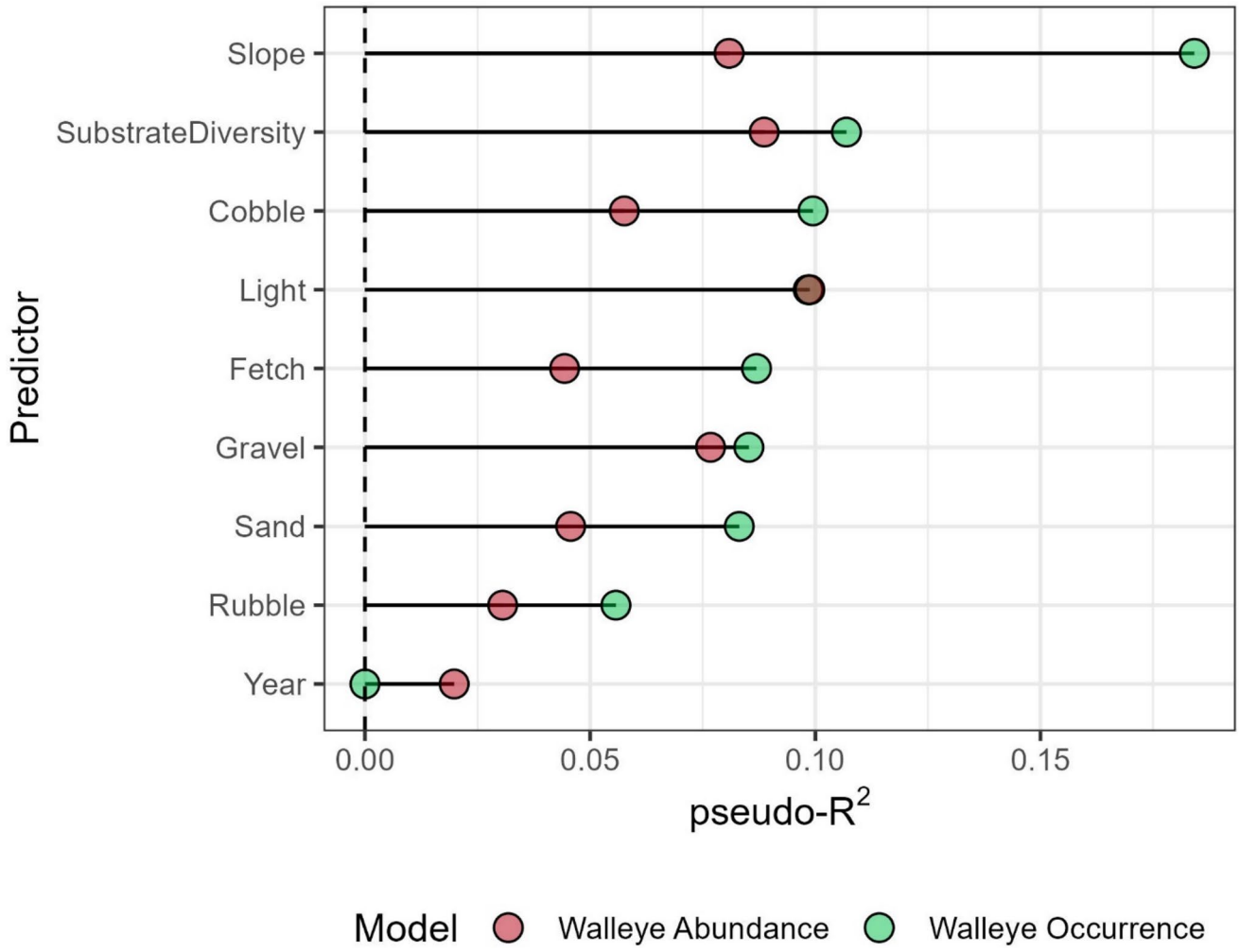


Fig. 2 Relative importance of the predictors used in the Walleye occurrence (green) or abundance (red) random forest models

distances of 0.5, 1.0, 2.0, 4.0, and 6.0 km. All Moran's I estimates were near zero (−0.005 to 0), indicating that residuals from the Walleye occurrence model showed no meaningful spatial autocorrelation.

Telemetry processing

We identified Walleye spawning events from acoustic telemetry data using a multi-stage filtering approach. Our methodology was designed to distinguish presumptive spawning behaviour from general movement patterns by focusing on sustained shallow-water residency during nocturnal hours in April.

First, raw detection data were processed. Erroneous detections were excluded if they met established criteria for false-positive detections [i.e., single occurrences with > 6000 s between successive detections or 30 times the typical 200-s nominal delay of the tags; (Pincock 2012)], were detected on the same receiver earlier than the minimum ping rate of the tags, or were not spatially possible, e.g., in another lake system (Larocque et al. 2024b). Fish were inferred to be dead if they exhibited static depth profiles and residency within a localized area of the array for the remainder of their tag life, possibly involving multiple nearby receivers (Klinard and Matley 2020).

Acoustic telemetry data were used to infer whether Walleye exhibited behaviour consistent with staging to spawn or spawning, herein referred to as "presumptive spawning behaviour". We note that direct observation of gamete release was not possible with this approach and that some individuals meeting the presumptive spawning criteria may have exhibited staging or holding behaviour without actively spawning. Walleye have been observed to spawn in Hamilton Harbour throughout the month of April, with most individuals staging in shallow waters (< 2 m) (Midwood et al. 2026). These observations align with reports of Great Lakes Walleye spawning on nearshore reefs at depths < 1.2 m (Busch et al. 1975; Bozek et al.

2011b), although spawning has also been documented on deeper (3–5 m) offshore rocky shoals (Bade et al. 2019; Kalejs et al. 2022; Izzo et al. 2023). We restricted our analysis to nearshore stations that operated from 2016 through 2023 ($n = 10$), ensuring consistent spatial coverage across the 8-year study period and eliminating temporal bias from intermittent receiver deployments. The stations were placed 1060 ± 254 m apart, where their 50% detection range averaged 416 ± 25 m under isothermal conditions [based on the receiver-specific estimates from Wells et al. (2021)]. We first filtered for presumptive spawning behaviours by limiting detections to the month of April, according to prior knowledge of Walleye spawning phenology in Hamilton Harbour, peak egg deposition rates (Midwood et al. 2026), and preliminary data exploration showing peak shallow water activity during this month. This resulted in a dataset of approximately 384,000 detections from 45 individuals. Next, we required that Walleye be at least 2 years of age (390 mm), as this is the minimum age of maturity in males (Scott and Crossman 1973; Bozek et al. 2011a). We predicted age from an age length equation generated for Hamilton Harbour Walleye (Brooks et al. 2025); Age = −[ln(1 − (Fork length/642.5))/0.375]—0.5. Results from a fine-scale Walleye tracking study within a single shoal in the harbour were used to inform additional presumptive spawning behaviour thresholds (Midwood et al. 2026). In that work, Walleye were observed to spawn primarily at night, so we filtered detections to include only those that began during dusk or night periods ($n = 166{,}000$ detections). Diel periods were calculated using {suncalc} (Thieurmel and Elmarhraoui 2017), which identifies solar positions though the date, time, and geographic coordinates of each receiver. This a priori diel spawning threshold was supported by the dataset, as spawning events occurred more frequently during dusk and nighttime (19% and 22% of detections, respectively) than during dawn and day (15% of detections when the diel filter is relaxed). Next, we identified continuous residency events by grouping consecutive detections at the same receiver station. Each residency event was assigned a unique movement identifier, which incremented when the fish moved to a different station or the time gap between consecutive detections exceeded 2 h (< 1% of detections). Ultimately, Walleye were identified as exhibiting spawning behavior if the residency event occurred in April at one of the nearshore receiver stations (Fig. 1), during dusk or nighttime periods, and maintained an average depth < 2 m (81% of detections) for the duration of the event. For quality control, spawning events also required at least three consecutive detections over a minimum duration of 20 min and that the fish had been previously detected within 12 h beforehand. This filtering process generated a dataset of 1800 spawning events from 31,000 spawning event detections across 34 individuals over 8 years.

To quantify individual spawning site specialization (i.e., measures of site-level spawning focus), we calculated Shannon diversity indices and derived specialization metrics for each fish-year combination. Specialization analyses included only fish-years with ≥ 2 spawning events and ≥ 10 total detections to ensure adequate sample sizes. For each fish-year, we calculated the total duration of spawning events found at each station. Shannon diversity index (H') was calculated as: $H' = -\Sigma(p_i \times \ln(p_i))$ where p_i is the proportion of duration at station i. We then derived three complementary metrics: (1) specialization index, calculated as 1—Shannon Equitability Index or 1—(H' / ln(S)), where S is the number of receiver stations, and H' is the Shannon diversity; (2) effective number of stations, calculated as exp(H'); and (3) concentration ratio, the proportion of detections at the most-used station.

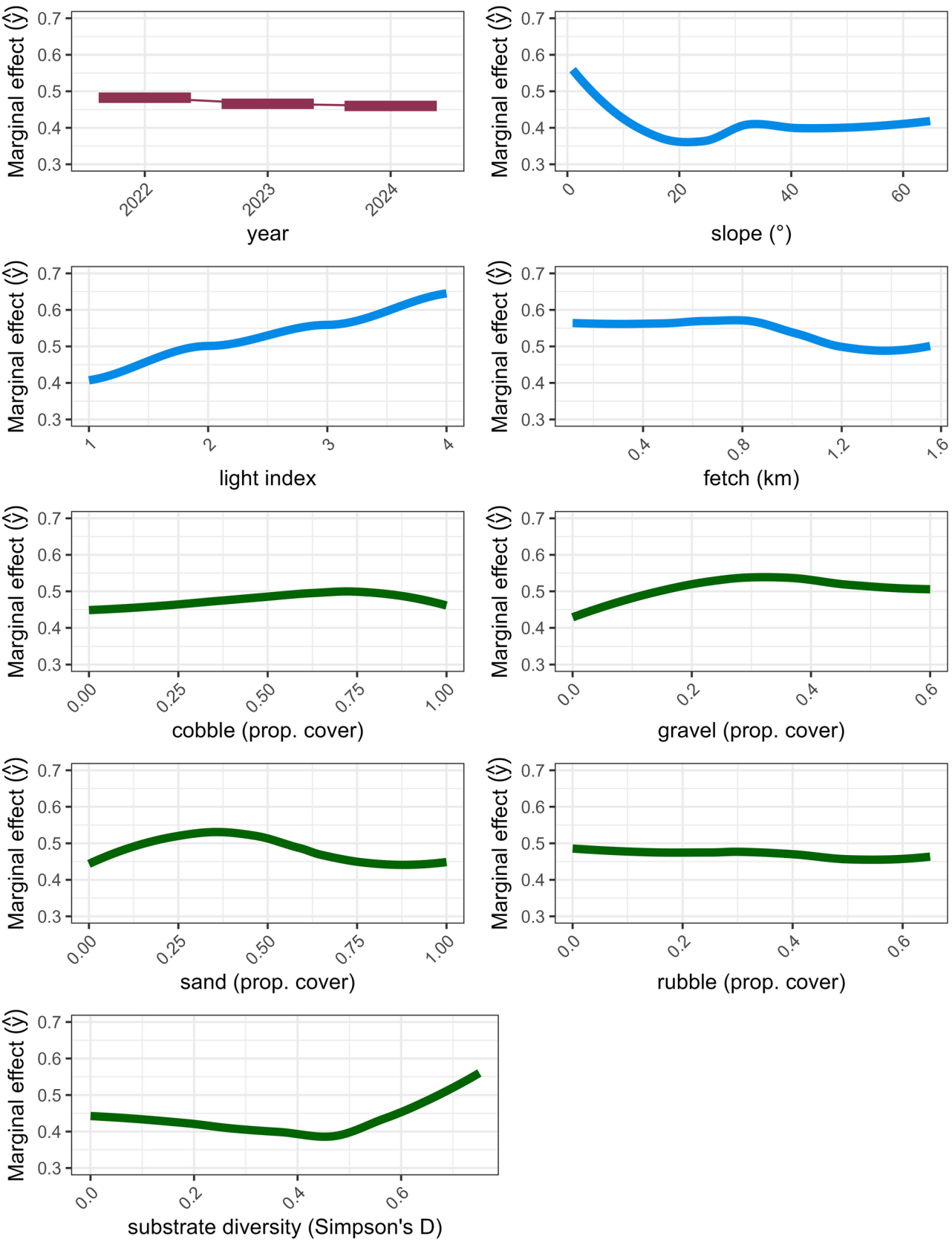
Repeatability analysis

To assess the repeatability of presumptive spawning behaviours, metrics were summarized for each tagged fish per year. Behavioural metrics included: (1) spawning station count—the number of receiver stations where presumptive spawning behaviour was detected; (2) spawning station ratio—the proportion of spawning stations relative to the total number of nearshore stations at which an individual was detected; (3) total residency—the cumulative duration of spawning events; (4) mean depth—the average depth maintained by individuals during presumptive spawning events; (5) specialization index—1-Shannon Equitability Index across receiver stations. The repeatability of presumptive spawning behaviours over the years was assessed using intraclass correlation coefficients where R values were estimated using the R package {rptR} (Stoffel et al. 2017). Fork length, water level, and annual detections per fish were included as fixed effects, while fish identity and year were included as random effects. Confidence intervals around R_{adj} estimates were constructed through model bootstrapping with 1000 iterations. Fork length was updated each year post-tagging by incrementing predicted age and recalculating fork length according to the age-length equation.

Results

Habitat survey

A total of 50 survey points were assessed across the north, east, and west shorelines of Hamilton Harbour. Substrate composition varied substantially among sites, with cobble being present most frequently (58% of site) followed by sand (48% of site). Armourstone had the highest average coverage


Marginal effect (ŷ)
0.7
0.6
0.5
0.4
0.3
2022
2023
2024
year
0
20
40
60
slope (°)
1
2
3
4
light index
0.4
0.8
1.2
1.6
fetch (km)
0.00
0.25
0.50
0.75
1.00
cobble (prop. cover)
0.0
0.2
0.4
0.6
gravel (prop. cover)
sand (prop. cover)
rubble (prop. cover)
substrate diversity (Simpson's D)

◂**Fig. 3** Marginal effect (y-hat) of predicted Walleye occurrence across key univariate predictors. Colours indicate temporal (red), environmental (blue), and substrate (green) habitat features. For example, Walleye are predicted to have higher occurrence at sites with greater substrate diversity

(23%) as it often comprised 100% of substrate coverage when found (9/50 sites). Shoreline slope ranged from 1° to 65°, with an average slope of 14°. Substrate diversity ranged from 0 to 0.75, with an average of 0.42. Full habitat survey data are presented in Supplementary Table 1.

Spring spawning surveys

A total of 440 Walleye were encountered throughout Hamilton Harbour over 3 years of spring spawning surveys. After a 25-m buffer was applied to habitat survey sites, a total of 161 Walleye were observed during annual spawning electrofishing surveys conducted in 2022 (n = 19/137, 100% male; Walleye within habitat buffer/total Walleye, sex ratio of Walleye within buffer), 2023 (n = 62/143, 100% male), and 2024 (n = 80/160, 97% male). These counts represent > 4% of the estimated adult population of approximately 1500 (550-3700) individuals within Hamilton Harbour (Larocque et al. 2023). Observed Walleye were captured and measured in 78% of cases. Mean fish mass was 3190 ± 870 g (mean ± standard deviation). Fish fork length (644 ± 61 mm) varied substantially among years, but there was not a clear trend in mean length (df = 64, t = 1.32, p = 0.20). Walleye observations were typically highest along the southeastern shore followed by moderate densities along the western and, to a lesser extent, the northern shore (Fig. 1).

Random forest model

Walleye occurrence was modelled with 80% accuracy in test data with the random forest model. The model performed with 78% balanced accuracy, 73% sensitivity, and 84% specificity. The most important predictors of Walleye occurrence were shoreline slope (pR^2 = 0.18; negative association), followed by substrate diversity (pR^2 = 0.11; positive association) (Fig. 2). Walleye occurrence increased with higher cobble cover (pR^2 = 0.10), where occurrence rates exceeded 45% for > 50% cobble coverage (Figs. 3 and 4). The Walleye abundance random forest model performed with a mean error of 0.36, a root-mean square error of 0.76, and an r2 of 0.44 in test data, demonstrating moderate predictive performance. Site-level abundance ranged from 0 to 5 Walleye. pR^2 values were generally lower in the abundance model than in the occurrence model.

Walleye behaviour

The frequency of presumed spawning events displayed a diel pattern, peaking at 20:00 with 23% of hourly detections and falling to a minimum at 06:00 with 13% of hourly detections (Supplementary Figure 6) in the full dataset when the diel filter is relaxed. Spawning event proportions during daytime hours (15%) were approximately two-thirds of nighttime proportions (22%), and inter-receiver movement counts showed a similar diel pattern with total hourly movements during the day representing 80% of nighttime levels. Because Walleye typically spawn under low light conditions, our presumed spawning filter restricted the dataset to events that began during dusk or nighttime (19:08–19:41 to 05:43–06:34). After applying both diel and behavioural filters, 8.0% of all April detections were retained as candidate detections in presumed spawning events for subsequent analyses. Presumed spawning events lasted an average of 3.01 ± 5.52 h (mean ± SD) and consisted of 24 ± 48 detections. Detection efficiency averaged 0.58 ± 0.35 (mean ± SD) across presumed spawning events and was calculated as the ratio of detected pings to the number of transmissions expected based on an assumed ping rate of 200 s, corresponding to the midpoint between the minimum and maximum programmed ping delays of 130 s and 270 s. Most tagged fish (34 of 45) exhibited presumed spawning events in at least 1 year, with an average of 25 ± 19 events per fish in each year they were inferred to be spawning. Twenty fish (44%) spawned in every year they were monitored, 14 fish (31%) skipped spawning for at least 1 year, and 11 fish (24%) showed no evidence of spawning across all years.

Shannon diversity indices revealed substantial variation in spawning station specialization among individual Walleye (mean H' = 0.72 ± 0.42 SD, range: 0.00–1.70). The specialization index averaged 0.38 ± 0.24 (range: 0.00–0.95), indicating that fish varied from generalists using multiple stations relatively evenly to specialists with concentrated spawning activity at one location. On average, fish concentrated 70% ± 19% of their presumed spawning duration at their most-used station, with the effective number of stations averaging 2.26 ± 1.00 SD stations.

Presumed Walleye spawning behaviours differed in their degree of individual consistency across years (Fig. 5). Total spawning time showed low repeatability across years (presumably reflecting environmental heterogeneity) and was not statistically significant (n = 74, R = 0.08 ± 0.11 SE, p = 0.24), whereas station specialization was nearly statistically repeatable (n = 66, R = 0.29 ± 0.16 SE, p = 0.06). In contrast, spawning station count (n = 110, R = 0.41 ± 0.12 SE, p < 0.01) and spawning station ratio (n = 110, R = 0.32 ± 0.11 SE, p < 0.01) were both repeatable. Finally, average spawning depth showed the highest repeatability among the behaviours assessed (n = 74, R = 0.47 ± 0.15 SE, p < 0.01).

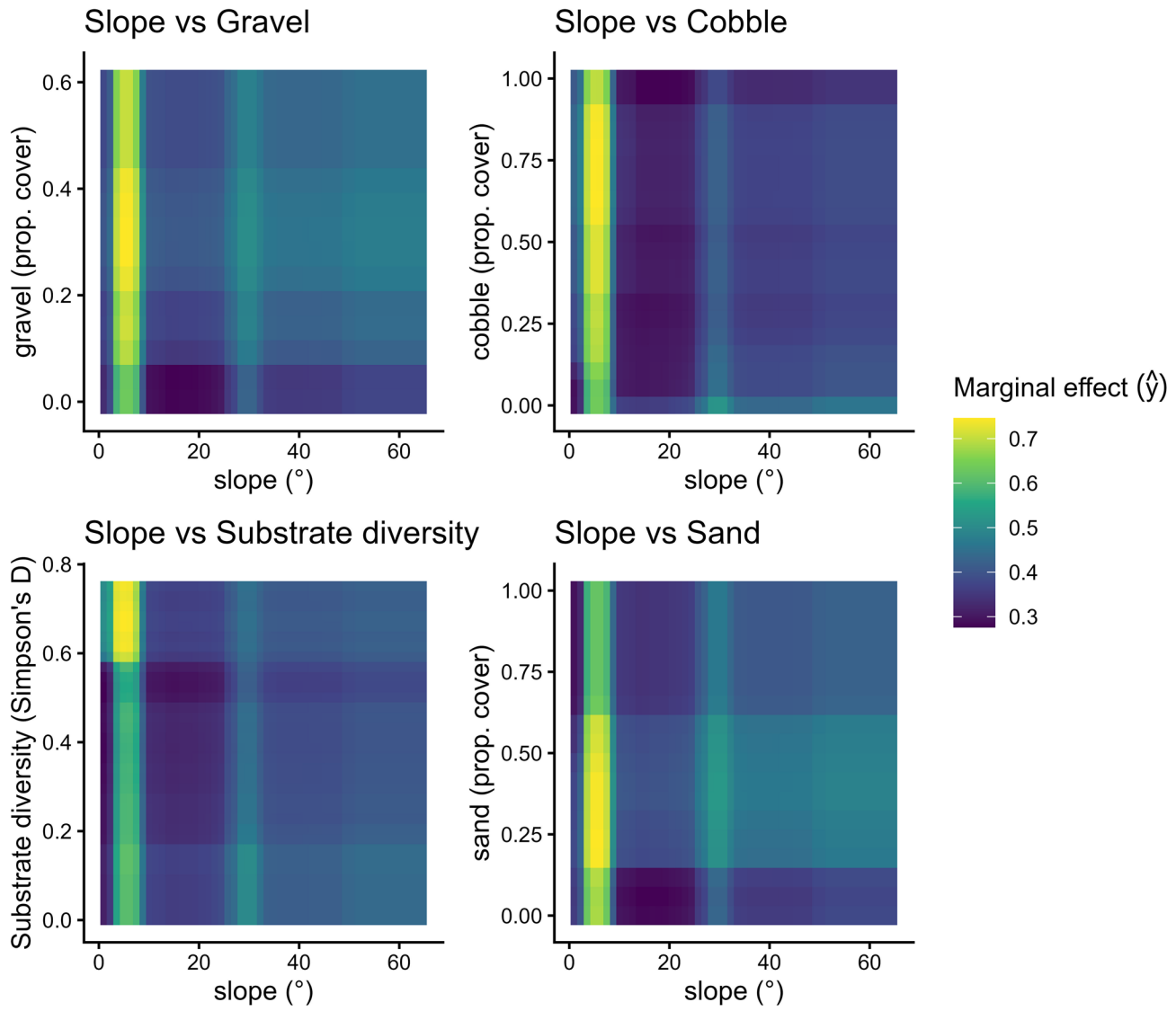


Fig. 4 Bivariate slope and substrate interactions for Walleye occurrence. Predicted Walleye occurrence was greatest at sites with a low slope gradient (<10 °), gravel coverage > 20%, cobble cover > 50%, sand cover < 50%, and a substrate diversity index > 0.6

Walleye fork length was correlated with station count ($p < 0.01$, $r_s = -0.28$; Spearman Correlation) and station specialization ($p < 0.01$, $r_s = 0.32$; Spearman Correlation), such that larger fish visited fewer stations and expressed higher specialization, but was not found to be correlated with total spawning time, spawning station ratio, or spawning depth ($p > 0.10$).

Discussion

Assessing the habitat associations and behaviours of spawning Walleye is challenging due to their demanding data requirements and logistical challenges. Fish survey techniques such as electrofishing can identify momentary habitat use at fine spatial scales, making them valuable for detailed habitat assessments. However, these techniques do not determine the amount of time Walleye spend at a given site. Additionally, such surveys are limited to nearshore areas, short temporal windows, and are influenced by site conditions that affect capture success (Brousseau et al. 2005). Conversely, while telemetry arrays can provide broader spatial and temporal coverage, most lack the fine-scale resolution needed to link detections with detailed habitat conditions. Fine-scale positioning arrays overcome this limitation (Binder et al. 2018; Midwood et al. 2026) but require substantial resources, planning, and specialized analysis (Lennox et al. 2023). By pairing electrofishing surveys with harbour-wide telemetry data, we linked Walleye habitat selection to fine-scale environmental features while also examining long-term

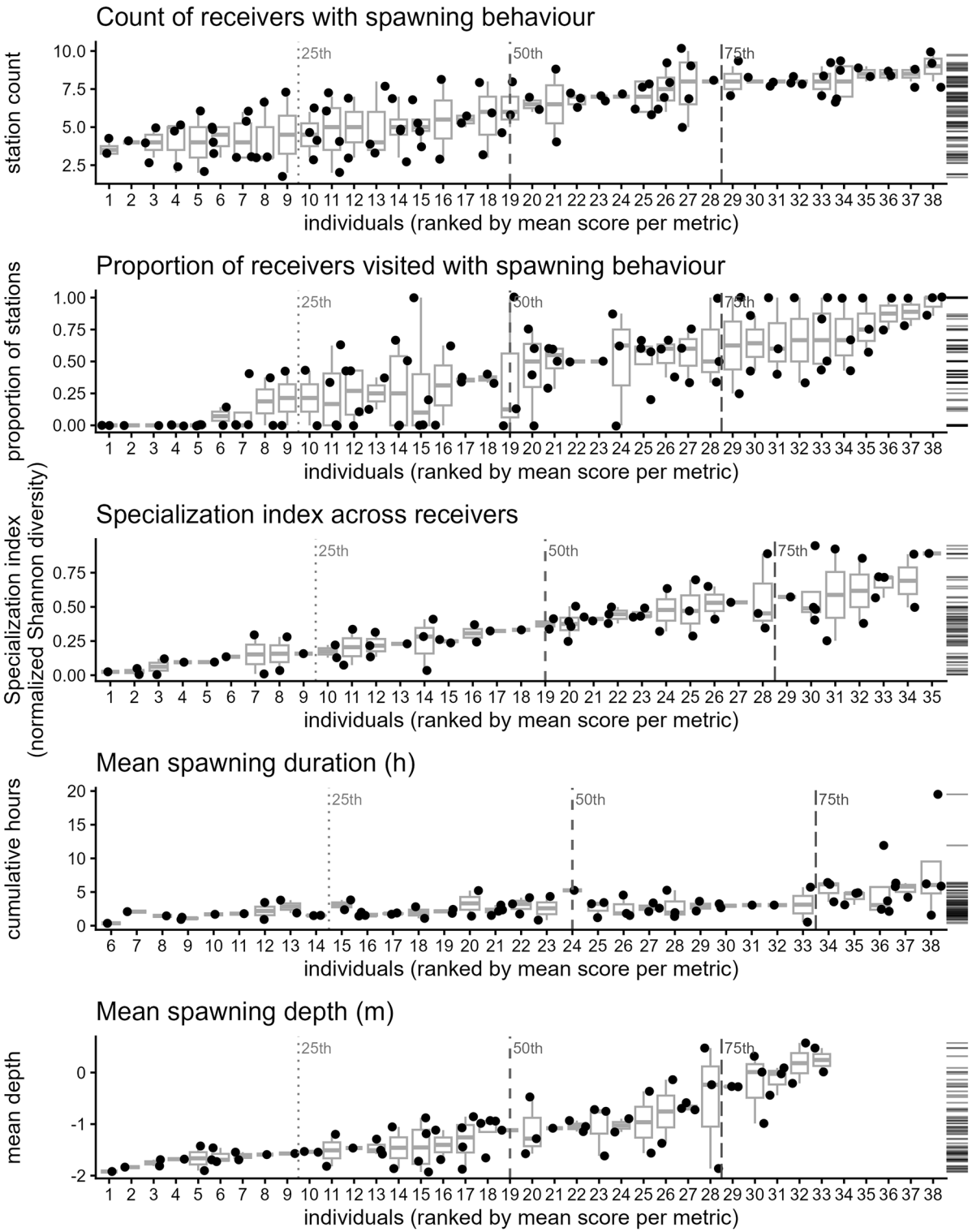


Fig. 5 Repeatability in Walleye presumptive spawning behaviour for station count, station count proportion, specialization index, total residency, and mean depth. Each boxplot represents an individual fish, with individual points representing a year. Fish are ordered along the *x*-axis according to their mean response to a given metric. Inter-individual variation, or behavioural repeatability, is characterized by high variation between fish but low variation across years within a single fish. The metric values are re-displayed along the *y* axis of the right side to display the distribution of behaviours across the tagged fish

spawning behaviour and movement patterns across the full spawning period in Hamilton Harbour.

Our findings on the habitat associations of stocked Walleye within Hamilton Harbour aligned with broader trends in the literature, such as a preference for cobble substrate at shallow shoals (Bozek et al. 2011a; Raabe and Bozek 2012; Raabe et al. 2020), confirming that hatchery origin fish exhibit habitat selection consistent with wild conspecifics. This study extends these observations by producing detailed, quantitatively resolved spawning habitat association curves across a range of environmental and substrate conditions, providing the first quantitative assessment of Walleye spawning habitat in Hamilton Harbour. In doing so, we test the assumption that the adult spawning habitat is adequate for this population (Midwood et al. 2026). Furthermore, by incorporating telemetry data, we investigated presumed spawning behaviour over 8 years to describe how spawning varied over time and among individuals. Walleye spawning was most strongly associated with cobble-gravel substrates, intermediate slopes, and high substrate diversity, and individuals concentrated the majority of their spawning activity at only one or two nearshore receivers. Repeatability analyses revealed that spatial behaviours, such as the number of spawning stations used, the proportion of available stations selected, and preferred spawning depth, were consistent across years, whereas total spawning duration was highly variable. Together, these patterns are useful to restoration efforts by identifying the habitat features Walleye selected for spawning within Hamilton Harbour and how variation in spawning behaviour is structured within a stocked population. These differences among individuals may influence the likelihood that any given individual will sufficiently explore the environment to find and interact with future restored spawning habitat.

Habitat associations

Habitat preference patterns identified here are consistent with established Walleye habitat trends. For instance, Walleye occurrence was most strongly associated with cobble substrate (Raabe and Bozek 2012; Raabe et al. 2020), a well-documented association for shoal-spawning Walleye populations. Secondary associations, such as a preference for gravel cover (McMahon et al. 1984; Bozek et al. 2011a; Raabe and Bozek 2012) or an avoidance of dominant sand cover, are also well established (Bozek et al. 2011b; Raabe et al. 2020). While depth is frequently cited as an important factor influencing spawning habitat preferences, it was not included in our habitat models because boat electrofishing was restricted to depths ≤ 1.5 m to ensure effective capture. In more open areas of Lake Erie, Walleye are regularly observed using spawning shoals situated further from shore and at deeper depths (3–5 m; Bade et al. 2019; Kalejs et al. 2022). Despite some preliminary evidence of Walleye spawning further offshore at deeper depths in Hamilton Harbour (Midwood et al. 2026), rocky shoals at such depths are largely absent in the system due to historic removal or siltation (Bowlby et al., 2010; Holmes and Whillans, 1984), limiting the reproductive potential of such spawning events (Gatch et al. 2020). As noted in Midwood et al. (2026), the frequency and viability of spawning by Walleye at deeper depths warrant further investigation since the addition of aggregate materials at such depths may represent a spawning habitat restoration opportunity. Regardless, for our evaluation of spawning behaviour, we limited depths to < 2 m to align with behaviour of the donor Walleye stock (spawning over shoals of 0.5–2.5 m depths in the Bay of Quinte; Elliott et al. 2022) or Walleye in other small lentic systems (Raabe and Bozek 2012).

Throughout the month of April, Walleye detections in Hamilton Harbour remained relatively shallow (mean depth = 4.4 ± 4.3 SD, 34% of detections < 2 m, Supplementary Figure 7). The environmental factors found to influence Walleye abundance differed from Walleye occurrence in several notable ways. While shoreline slope was of moderate importance for predicting Walleye abundance, it emerged as the strongest predictor of Walleye occurrence. Shallow-slope littoral habitats are generally more productive than exposed, steep shelves (Minns et al. 2023). In our dataset, this pattern likely reflects that Walleye preferentially occupy shallow, gently sloped shoals for spawning, but the slope becomes less informative for distinguishing between sites with moderate or higher spawning abundance once the basic requirements of a suitable shoal are met. Beyond the limited shoals we sampled, much of the Hamilton Harbour shoreline consists of steep shelves and seawalls that provide little suitable spawning habitat, further constraining the availability of moderately sloped environments. A second notable difference between the models was the influence of inter-annual variation. The Walleye occurrence model was insensitive to annual variation, yet sampling year was informative to the Walleye abundance model. Walleye abundances sampled near our habitat survey sites varied widely by year, with only 19 individuals observed in 2022 and > 60 individuals observed in 2023 and 2024 (Supplementary Figure 2). Our results indicate that although the abundance of spawning adults may fluctuate across years, the locations (and conditions therein) where individuals spawn remain relatively consistent.

Substrate diversity was the second-most important predictor of both Walleye occurrence and abundance, highlighting the potential importance of heterogeneous substrates in attracting spawning individuals. Substrate diversity has been previously recognized for its importance in shoal-spawning Walleye (Raabe et al. 2020). Walleye evolved in riverine environments and require equivalent littoral or sublittoral

shoals for spawning in lakes (Kitchell et al. 1977), with suitable oxygenation, light penetration, and interstitial spaces between substrates (Raabe et al. 2020). Interstitial spaces are important in particular as they support improved oxygen and water chemistry, which aids in egg survival and development (Sly 1988; Raabe and Bozek 2012), and also protect eggs that have been pushed off the substrate by wave action (Marsden et al. 1995; Raabe and Bozek 2012). Diverse substrates can provide variation in interstitial crevice size, abundance, and exposure (Marsden et al. 1995), which may support egg development across greater environmental variability. For instance, exposure to wind and wave energy maintains interstitial spaces by pushing silt and sand out of crevices (Raabe et al. 2020); however, stronger wind and wave energy may also push eggs off an ideal substrate (Bozek et al. 2011a) or allow eggs to be buried by fine particles (Croft-White et al. 2026). Diverse interstitial spacing, and the resultant variation in sediment deposition rates, water quality, and protection (Sly 1988), may provide suitable microhabitat conditions for spawning Walleye.

Finally, we did not expect Walleye occurrence to increase with higher light-index values. Walleye are visual hunters that are most effective as predators in low light conditions (Lester et al. 2004; Michels et al. 2025). The Walleye association with light intensity is likely due to the eastern shorelines immediately south of the shipping canal exhibiting both the highest light levels and high quality Walleye spawning habitat. The site has been artificially modified by the addition of armourstone (i.e., large, angular rock used for shoreline stabilization) but has also been shaped by prevailing winds and contains gravel, sand, and some cobble. Walleye were likely attracted to the site because of the gravel and diverse substrate habitat. Additionally, while light intensity and water clarity have been found to influence habitat suitability for Walleye (Lester et al. 2004; Rudolfsen et al. 2021; Michels et al. 2025), the high turbidity of Hamilton Harbour may mitigate potential effects of light pollution. Little is known about the trade-offs between light pollution and spawning in fishes (Bassi et al. 2022), and there remains a clear need to investigate how these dynamics influence Walleye specifically.

Consistent individual differences

The varying levels of repeatability across presumptive spawning behaviours highlight that some aspects of Walleye spawning behaviour are more consistent across years than others. For instance, the cumulative duration of time that individuals spent spawning was highly variable. Individuals ranged between never displaying spawning behaviours across multiple years, to skipping spawning in a given year (Hayden et al. 2018), to expressing presumptive spawning behaviours for the majority of their spawning window (range: 0–88% of candidate detections). Behavioural plasticity in annual spawning effort may allow Walleye to adjust their presence on spawning grounds to match local conditions each year. For instance, water level has been found to influence spawning substrate associations (Bozek et al. 2011a), and impact recruitment strength (Bozek et al. 2011a), but it did not correlate with spawning activity in this study (Supplementary Figure 8). Spawning behaviour may be influenced by other external factors that vary annually, such as environmental conditions (e.g., temperature, wind) (Raabe et al. 2020), social interactions (e.g., mate availability or competition), or energetic constraints.

In contrast, the repeatability of spawning station count, station count ratio, and site specificity suggests that despite the degraded nature of the system, individuals adopt distinct and repeatable strategies during spawning. Specifically, individuals exhibit consistent differences in the spatial breadth of their spawning activity. Some individuals consistently used multiple spawning sites across a broader area of the harbour, while others quickly concentrated their activity at a limited set of preferred locations, even in suboptimal conditions (Midwood et al. 2026). These differences may reflect underlying movement strategies (Turner et al. 2025a) or habitat preferences. Walleye have been observed to exhibit strong spawning site fidelity at broad spatial scales, with fidelity estimates of 70–95% or > 90% in rivers and ~ 95% in lake basins (Hayden et al. 2018; Chen et al. 2020; Zhao et al. 2011). Our findings, together with recent high-resolution tracking (Midwood et al. 2026), extend site fidelity studies into finer spatial scales, revealing spatial fidelity within a single embayment.

Despite being sourced from Bay of Quinte populations that include both riverine and shoal-spawning individuals, no tracked Walleye have entered Hamilton Harbour tributaries (Larocque et al. 2024a, b). Spawning appears restricted to harbour shoals, with individuals not making use of constructed riverine habitats (Hamilton Conservation Authority 2025). This suggests that the stocked population has converged on a consistent shoal-spawning strategy within Hamilton Harbour, regardless of donor stock origin. Spawning site selection generally involves genetic and learned components (Jennings et al. 1996), but there does not appear to be a genetic structuring between the riverine and shoal-spawning source groups in the source population (Wilson and Gatt 2001). Thus, remaining spawning diversity is expressed through variation in shoal spawning behaviour. Maintaining a diversity of shoal spawning strategies may be advantageous at the population level (Bozek et al. 2011b), as a portfolio of behaviours and microhabitat use can increase resilience to stochastic environmental conditions, particularly where recruitment is sensitive to factors such as water level fluctuations.

Caveats

Walleye exhibit marked sex-specific differences in spawning strategy. Males typically locate suitable spawning sites and remain in place to maximise mating opportunities with females, while females hold offshore in deeper water, briefly venture nearshore to spawn, and swiftly initiate post-spawning migrations (Ellis and Giles 1965; Hayden et al. 2014; Brooks et al. 2019; Bade et al. 2019; Midwood et al. 2026). The sex of telemetry-tracked fish was not recorded in this study, and the degree to which observed variation in behavioural metrics reflects sex-specific strategies rather than genuine individual differences remains unknown. This represents a meaningful source of unaccounted variation in the repeatability analyses. For instance, larger Walleye expressed greater spawning site specificity and spawned at fewer stations, but this pattern may reflect an unresolved sex effect rather than a direct effect of body size. Female Walleye grow substantially larger than males and are expected to use fewer nearshore stations during brief spawning forays. Consistent with this interpretation, Hayden et al. (2018) found no independent effect of fish length on spawning site fidelity in Walleye after accounting for sex, suggesting that body size alone may not have driven the observed pattern.

Several methodological limitations should also be considered when interpreting these findings. The three datasets span different temporal windows and were collected at different spatial resolutions, which limits their direct integration. The habitat survey was conducted once in 2021, electrofishing surveys were conducted annually from 2022 to 2024, and acoustic telemetry data span 2016 to 2023. The random forest habitat models therefore rely on the assumption that substrate composition and slope remained stable between the 2021 survey and the 2022 to 2024 electrofishing period. Although this assumption is generally robust for rock and hardened nearshore substrates, it may not hold true for areas dominated by finer sediments. Year was included as a predictor in both random forest models and as a random effect in the repeatability analysis to account for interannual variation, but the datasets are nonetheless comprised of distinct sampling windows and spatial resolutions. This approach reflects the realities of long-term fisheries monitoring, where datasets with different temporal designs are often the primary available data. Additionally, electrofishing provides only a snapshot of fish presence, and capture locations may not correspond precisely to where gametes are deposited, such that observed habitat associations may reflect both pre-spawning staging and active spawning. Additionally, acoustic receivers were not uniformly distributed across the harbour shoreline, so spawning activity in underrepresented areas may be underdetected. Finally, the physical habitat features identified here likely represent necessary conditions for spawning, but unmeasured variables may further refine habitat suitability at finer spatial scales than those captured by this study.

Conclusion

This study combined electrofishing surveys and acoustic telemetry to provide the first quantitative assessment of spawning habitat use and individual behavioural variation in stocked Walleye within Hamilton Harbour. Walleye selected cobble shoals with gentle shoreline slopes and heterogeneous substrates, consistent with associations documented in reference populations across their range. Individuals exhibited strong consistency in spawning decisions across years and displayed site fidelity at a fine spatial scale. Such insights are particularly important in heavily modified or degraded systems like Hamilton Harbour, where habitat availability, water quality, and physical barriers may influence spawning behaviour and ultimately reproductive success. For instance, the observed consistency in spawning site selection suggests that restoration approaches successfully applied in other Walleye systems, particularly those aimed at improving substrate quality and shoal structure, may also be effective within Hamilton Harbour. Restoration efforts may benefit from prioritizing areas already in use to ensure enhanced habitat is readily encountered by individuals that return to the same sites year over year. Alternatively, the presence of highly selective individuals that only used one or two stations emphasizes the value of restoring multiple sites across the embayment, as distributed enhancements are more likely to accommodate the full range of spawning habitat utilized within the population. Recruitment failure in Hamilton Harbour has been attributed to early life stage mortality rather than a deficit of adult spawning activity (Midwood et al. 2026), and the findings presented here confirm that adult spawning behaviour is not a barrier to natural reproduction. Stocked Walleye consistently selected habitats with characteristics associated with successful spawning in the reference systems (Bozek et al. 2011a; Raabe and Bozek 2012), and the spatial repeatability of individual behaviour suggests that habitat enhancements placed at or near existing spawning aggregation sites are likely to be encountered by returning fish. Should restoration measures succeed in reducing early life stage mortality, the individuals and sites identified here as centres of high spawning fidelity and activity represent the most probable focal points for emerging natural recruitment. Furthermore, the patterned and repeatable spawning behaviour documented across multiple years suggests that hatchery-origin fish can exhibit functional spawning behaviour in adults (Binder et al. 2018). This supports the premise that supplementation stocking can contribute to long-term recovery in systems where natural reproduction has been disrupted, or even where the population

was extirpated prior to stocking, as in Hamilton Harbour. Together, these findings provide a quantitative foundation for targeted habitat restoration and adaptive management aimed at restoring self-sustaining natural reproduction of Walleye in Hamilton Harbour.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00027-026-01344-w.

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Author contributions PAB, JLB, SJC, and JDM developed the context and design for the study; MVCW, DTR, NAT, JLB and JDM conducted the data collection; PAB conducted the analyses; PAB and CH wrote the initial draft; all authors assisted with the writing and approved the final manuscript.

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Data availability The data and code supporting this study are publicly available. The analysis code and associated datasets are archived on Zenodo (https://doi.org/10.5281/zenodo.20402858) and available on GitHub (https://github.com/FishEcologyScience/2026_Bzonek_Walleye_Spawning).

Declarations

Conflict of interest The authors declare no competing interests.

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