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Fine-scale behaviour of walleye (*Sander vitreus*) on a spawning shoal in Hamilton Harbour, Ontario

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ABSTRACT

Re-establishment of a naturally reproducing walleye (*Sander vitreus*) population is a management objective for Hamilton Harbour, western Lake Ontario. Though mature, stocked walleye have been captured during the spawning period on littoral shoals of the harbour, there is no evidence of natural recruitment. Fine-scale walleye positions derived from acoustic telemetry data on a known spawning shoal were aggregated into discrete, presumptive spawning events, where spawning conditions (e.g., Distance to Shore, Movement Rate), timing (e.g., Photoperiod), and their spatio-temporal distribution (e.g., Duration, Kernel Density Estimates) were described. A selection of these metrics were used to characterize seven unique spawning behaviours ranging from spatially focused nearshore events that are consistent with previously described spawning behaviour to short and fast transitory events. The location of some spawning events aligned with areas of high egg deposition, but additional events were found to be deeper and further offshore than expected, but still consistent with other Great Lakes populations. Confirmation of egg deposition at these deeper locations is required as it may indicate a potential remediation measure (i.e., addition of aggregate materials at these depths). The range of behaviours observed is indicative of both individual variation and differential habitat preference for the spawning shoal.

1. Introduction

Walleye (*Sander vitreus*) is a piscivorous species of considerable ecological, commercial, and cultural importance in North American freshwater ecosystems (Bruner and DeBruyne, 2021). Understanding their life history, particularly related to spawning, is important to ensure sustainable populations. Though many aspects of walleye life history have been studied, particularly those related to recruitment and fisheries productivity (Barton, 2011; Krabbenhoft et al., 2023; Raabe et al., 2020), significant knowledge gaps exist in how walleye select and interact with spawning-habitat features. Walleye are broadcast spawners that often prefer shallow habitat (< 2 m) where they can use gravel and cobble substrates (Crane and Farrell, 2013; Kerr et al., 1997; Raabe, et al., 2020), flooded wetland vegetation, or rocky wave-washed shorelines (Bozek et al., 2011a). The availability of high-quality spawning habitat is known to be an important factor in walleye production (Raabe and Bozek, 2012). Walleye also exhibit different spawning strategies, with some populations migrating into rivers to spawn and others spawning on shoals in lentic systems (Bozek et al., 2011a). In the latter situation, past studies have documented walleye spawning near the shore, in shallow waters (< 1.2 m; Bozek et al., 2011a), and primarily over gravel, cobble, or rubble substrates (Raabe and Bozek, 2012; Roseman et al., 2002). In the main basin of larger lentic systems, however, walleye are known to spawn in deeper waters (3–5 m) over rocky shoals that are situated further offshore (Bade et al., 2019; Izzo et al., 2023; Kalejs et al., 2022).

As with many temperate fishes, the timing of walleye spawning is influenced by water temperature and photoperiod, with temperature being the cue to initiate spawning and photoperiod regulating gonadal development (Bozek et al., 2011b; Farmer et al., 2015; Pankhurst and

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Porter 2003). Walleye spawn during the spring, generally at night when water temperatures warm to between 4.0 and 14.0 °C (Bozek et al., 2011a), with optimal conditions reported around 7.5 °C (Hasnain et al., 2010). There is evidence for behavioural differences between male and female walleye, with males typically ripening first and spending more time at a spawning site to maximize reproductive opportunities with multiple females (Bade et al., 2019; Hayden et al., 2019). Females initiate post-spawning migrations soon after oviposition and may only remain at the site for one night (Bade et al., 2019; Ellis and Giles, 1965).

Due to their importance, walleye have been the focal species in numerous acoustic telemetry studies in the Laurentian Great Lakes that have explored their migration patterns (Elliott et al., 2022; Hayden et al., 2014; Raby et al., 2018), spawning habitat selection (Izzo et al., 2023), and spawning site fidelity (Hayden et al., 2018), among other topics. Furthermore, when deployed in close proximity, fine-scale positioning acoustic telemetry arrays can provide sub-meter positions of tagged fish (Binder et al., 2018; Espinoza et al., 2011; Whoriskey et al., 2022), and such arrays have been used to contrast the timing of arrival and duration on spawning shoals between male and female walleye (Bade et al., 2019) or provide insight into size-based seasonal changes in gill net encounter probabilities (Gorman et al., 2019; Kinter, 2022).

In the Great Lakes, walleye support critical fisheries such as those in Lake Erie (Hartman et al., 2024) and the eastern basin of Lake Ontario (Hoyle et al., 2012). However, in some areas, loss and degradation of nearshore habitats, overexploitation, and water quality degradation have led to population declines and, in some cases, regional extirpation (Schneider and Leach, 1976). The latter is the case for Hamilton Harbour, a large (21 km^2) freshwater embayment situated at the western end of Lake Ontario. The harbour has a long history of anthropogenic disturbance that has resulted in its listing as a Great Lakes Area of Concern (HHRAP, 1992) due to extensive habitat loss, water quality impairment, and resulting decline or extirpation of native fishes (Midwood et al., 2024). Historically, walleye were frequently encountered spawning in the tributaries of Hamilton Harbour (Dymond et al., 1929; OMNR, 2020). While a remnant population was still present in the harbour into the 1930 s, Whillans (1977) noted no evidence of spawning activity by the 1970 s, and they were considered rare in the system by the 1980 s (Holmes, 1988) and early 1990 s (Turner et al., 2025).

Recovery of walleye in Hamilton Harbour has been an objective of fisheries managers since the 1990 s when a stocking program was implemented by the Ontario Ministry of Natural Resources (OMNR). Initial efforts met with limited success, but in 2012 and again in 2016, stocking of summer fingerlings produced strong year classes and an increase in catch of adult walleye (OMNR, 2020; Turner et al., 2025), with telemetry confirming high residency of adults during the spawning season (Brooks et al., 2019). The source of these stocked walleye was a population from the Bay of Quinte in eastern Lake Ontario. Both river and littoral shoal spawning behaviours are observed in this donor stock (Elliott et al., 2022) with little variation in genetic structure such that they are managed as a single stock (Wilson and Gatt, 2001). In Hamilton Harbour, stocked walleye have not been observed moving into tributaries during the spawning period (Larocque et al., 2023; Larocque et al., 2024a, 2024b), but boat electrofishing surveys have found spring walleye aggregations in littoral areas throughout the system (OMNR, 2017). Despite aggregations on littoral shoals indicating potential spawning activity, to date, there has been no evidence of natural recruitment (J. Midwood, unpublished data). Outside of the spawning period, stocked walleye have shown both resident (Brooks et al., 2019) and migratory (i.e., movements along the south shore of Lake Ontario; Larocque et al., 2024a) behaviours, which suggests that if naturally reproducing walleye can be re-established in Hamilton Harbour, walleye fishing opportunities in western Lake Ontario may return. As such, research that supports the re-establishment of a naturally reproducing walleye population in the harbour is beneficial.

Currently, there is limited knowledge regarding spawning behaviour of stocked populations of walleye, particularly in Hamilton Harbour. The objectives of this study were to describe the behaviour of walleye on a known spawning shoal using fine-scale positional telemetry and explore whether locations within the shoal aligned with areas of high egg deposition. Past studies of lentic-spawning walleye in inland lakes found spawning occurs primarily at night in shallow waters, close to shore, and over suitable substrates (Bozek et al., 2011b; Raabe and Bozek, 2012). While studies in the main basins of other Great Lakes (e.g., Lake Erie; Bade et al., 2019 and Lake Huron; Gatch et al., 2021) have documented spawning on shoals situated further offshore and in deeper waters (e.g., 3–5 m), we predicted walleye in Hamilton Harbour would behave more similarly to individuals in smaller inland lakes for two reasons. First, Hamilton Harbour acts largely as an enclosed basin with limited exchange with Lake Ontario solely via an 89-m wide shipping canal at the eastern end (Flood et al., 2021). Second, the rocky shoals that existed historically at depth within the harbour have been removed or buried by sediment (Bowlby et al., 2010; Holmes and Whillans, 1984), restricting suitable spawning habitats to the margins of the system (Doolittle et al., 2010). Consequently, clustered detections of an individual within the fine-scale positional array that occurred at night, close to shore, and in shallow waters were interpreted as a positive sign that stocked walleye were attempting to spawn in the system. However, intraspecific variation in behaviour is likely (Killen et al., 2016) and informative of the different ways walleye may interact with a spawning shoal. Knowledge derived from this study has the potential to inform habitat management activities in Hamilton Harbour and elsewhere that walleye spawning habitat enhancement and restoration is conducted.

2. Methods

2.1. Telemetry array and study site

Hamilton Harbour (Fig. 1) has been the site of an ongoing acoustic telemetry tracking program since 2015 with walleye one of the focal species (Brooks et al., 2017). The initial objectives of the telemetry program were to explore the large-scale movements of stocked walleye (see Brooks et al., 2019) and document fish habitat associations to inform habitat enhancement or creation efforts (see Larocque et al., 2024a, 2024b). Consequently, at the time of our study, 43 walleye tagged with V13 or V13P acoustic transmitters (min delay = 130 s, max delay = 270 s, V13 = 13 mm diameter, 9.7 g dry mass; V13P = 13 mm diameter, 11 g dry mass; Innovasea, Bedford, NS, see Brooks et al., 2019 for details on tagging) were active within the Hamilton Harbour array. Genetic analysis of walleye captured in the harbour in the mid-2000 s noted they originated from the Bay of Quinte (the source population for all stocked walleye; OMNR, 2020; Wilson and Farrell, 2010); therefore, we assumed all tagged individuals were stocked. We cannot, however, discount the possibility that tagged individuals were from a remnant harbour population of walleye or that they had emigrated from the Bay of Quinte. Sex information was available for only a subset of the tagged individuals, with only one female confirmed, and so was not included as a factor in the analysis.

The site for the fine-scale array used in this study, at the east end of the harbour (Fig. 1), was chosen based on previous observations of spawning walleye in the vicinity (OMNR, 2017). The fine-scale telemetry positioning array consisted of eight receivers (69 kHz, VRTx, Innovasea, Bedford, NS, Canada) and was deployed in 2018 and 2019 between 27 March and 16 May (Fig. 1). Each telemetry receiver had an internal temperature sensor used to derive daily mean, minimum, and maximum temperatures. Within the array, substrates typically associated with walleye spawning (i.e., gravel or cobble) were largely confined to within 4.8 m of shore and in < 1.0 m depth, with sand and silt dominating elsewhere (J. Midwood, unpublished data).

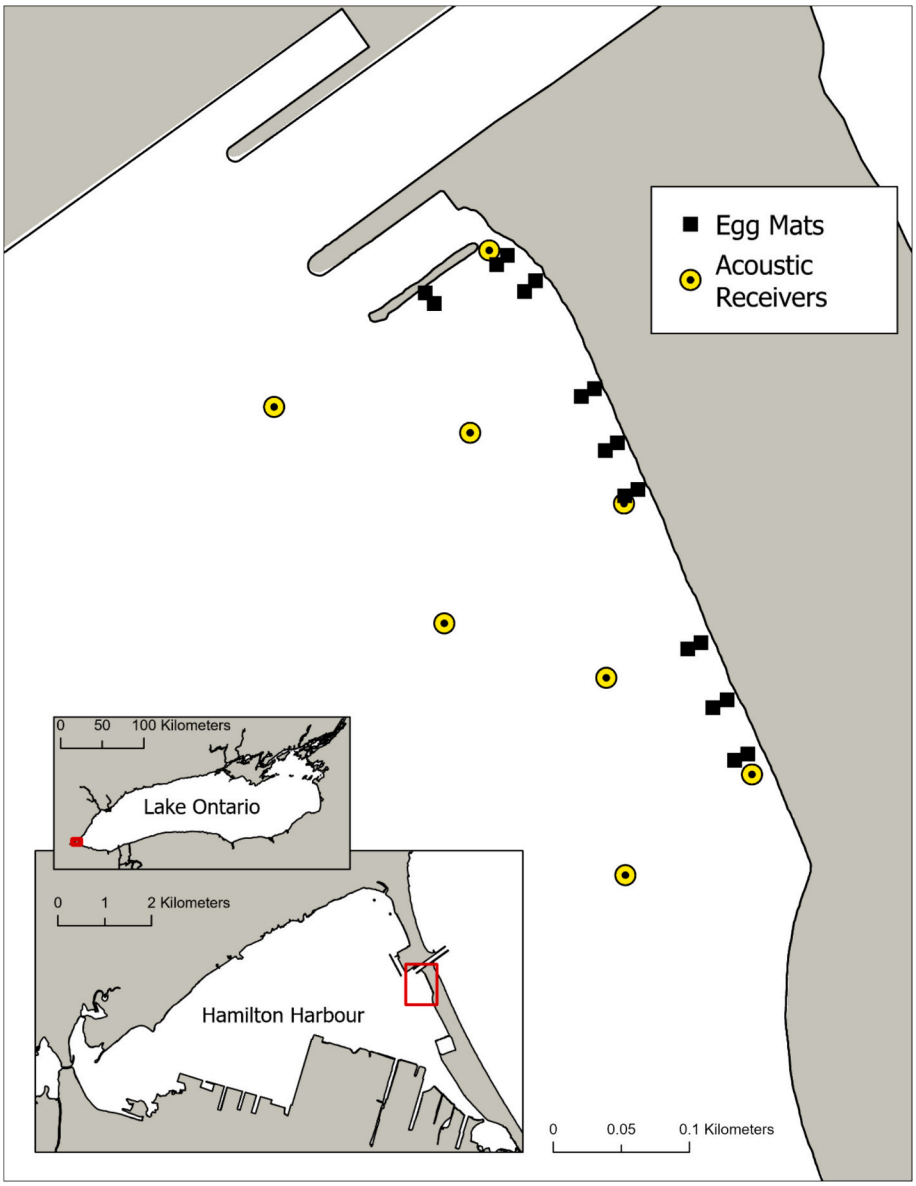

Fig. 1. Location of Hamilton Harbour within Lake Ontario and the positioning of the fine-scale array at the east end of Hamilton Harbour. The position of acoustic receivers that comprised the array (both 2018 and 2019) and deployment locations for egg mats in 2019 are shown.

2.2. Telemetry data preparation

Data were downloaded from receivers and the files were processed by Innovasea (Bedford, NS) using a proprietary method that yields fine-scale position estimates. Prior to our analyses, the data were filtered for possible erroneous position estimates by removing any that were calculated using less than three receivers or had a HPE (Horizontal Position Error; error sensitivity of a synthesized position) greater than 100. Two walleye in each year of the study were only detected twice and were also removed from the dataset. These initial filters resulted in 15,021 position estimates from 13 fish in 2018, and 13,210 positions estimates from 13 fish in 2019 (Table 1). Position estimates during daylight hours (sunrise to sunset) were then excluded with the duration of daylight ranging from 12.5 hrs (27 March) to 14.7 hrs (15 May) during the study period. This reduced the total number of positions to 6446 in 2018 and 5346 in 2019, with data from 13 individuals in each year (Table 1). The distance from shore for each of these positions was calculated in ArcPro v2.9.8 (ESRI, Redlands, CA). All further analyses were conducted in RStudio v2023.09.1 VX (R Core Team, 2023).

To determine possible spawning events, we first grouped positions that occurred within a defined period. For each individual fish, we calculated the time (s) and distance (m) between each position estimate. Separate events for each individual were then defined when subsequent position estimates exceeded 10x the maximum transmitter delay (i.e., 2700 s or 45 min), which allowed the event to persist even if several transmissions were not detected. The result was a series of unique events for each individual walleye on the fine-scale array that typically reflected all detections that occurred in one night, but in some instances, there were multiple events in one night. Any event comprised of fewer than five position estimates (or less than approximately 20 min in duration) was excluded, which was the minimum number of positions required for a Kernel Density Estimate (KDE; a spatial estimate of the density of detections). Any durations shorter than 10 min would be less than the time expected for a walleye to engage in spawning, especially with staging and courtship behaviour (Bade et al., 2019).

For each event, we then calculated a series of metrics based on known walleye spawning behaviours or preferred habitat conditions (see Bozek et al., 2011a; Raabe and Bozek, 2012). These metrics can

Table 1
Summary of detections of tagged walleye on the fine-scale array in 2018 and 2019. The date tagged, size at the time of tagging, and sex (where available) are presented. The total number of detections (Detect.), number at night time, and number included in groups based on timing of detections are shown. These groups were used to create Night Events, which were then filtered to include events based on more than five detections. Finally, the number of events used in the Principal Component Analysis (PCA) is shown.

Year	ID	Tagging Date	Fork Length (mm)	Sex	Total Detect.	Total Night Detect.	Grouped Detect.	Night Events	Filtered Night Events	PCA Dataset
2018	TH_Walleye_608	Jul-16	608	Unk.	229	116	113	5	5	5
	Wall 15761	Aug-15	460	Unk.	59	49	49	2	1	1
	Wall 16052	Apr-17	554	M	183	47	47	2	1	1
	Wall 16053	Apr-17	581	M	10,157	4046	4021	60	59	6
	Wall 16060	Apr-17	576	M	20	11	11	1	1	1
	Wall 16062	Apr-17	551	M	159	25	25	3	2	2
	Wall 16063	Apr-17	575	M	3177	1621	1615	15	15	6
	Wall 18967	Jun-16	523	Unk.	11	7	3	1		
	Wall 18969	Jun-16	500	Unk.	130	101	86	3	3	3
	Wall 18973	Jun-16	519	Unk.	445	230	227	3	3	3
	Wall 52867	Jul-16	530	Unk.	291	148	148	1	1	1
	Wall 52870	Jul-16	532	Unk.	103	36	36	2	2	2
	Wall 52871	Jul-16	512	M	57	9	3	1		
2019	TH_Walleye_608	Jul-16	608	Unk.	50	18	18	2	1	1
	Wall 14519	May-18	561	Unk.	911	337	337	5	5	5
	Wall 15761	Aug-15	460	Unk.	51	24	24	2	1	1
	Wall 16052	Apr-17	554	M	83	72	71	3	3	3
	Wall 16053	Apr-17	581	M	9899	4066	4047	56	56	6
	Wall 16060	Apr-17	576	M	1039	339	338	7	6	6
	Wall 16061	Apr-17	535	M	68	62	56	1	1	1
	Wall 18965	Jun-16	559	Unk.	35	24	22	2	1	1
	Wall 18967	Jun-16	523	Unk.	564	223	210	6	4	4
	Wall 18969	Jun-16	500	Unk.	266	74	71	3	3	3
	Wall 52870	Jul-16	532	Unk.	63	29	25	3	3	3
	Wall 52871	Jul-16	512	M	101	19	15	2	2	2
	Wall 52874	Aug-16	509	Unk.	80	59	57	2	2	2

largely be categorized as: behavioural characteristics of the overall event (e.g., Duration, Kernel Density Estimation), those reflective of the mean conditions during individual position estimates (e.g., Latitude, Longitude, Distance to Shore, Movement Rate), or overall conditions that day (e.g., Photoperiod). See ESM Table S1 for metric descriptions and methods for how they were derived.

Once compiled, Pearson correlation analysis was used to identify metrics that were collinear, so that only a single metric was retained in cases with moderate (> 0.5) to high (> 0.7) collinearity. This reduced the list from 15 metrics to six (Latitude, Water Temperature, Event Duration, Movement Rate, 50 % KDE, and Distance from Shore), which were then scaled and centered. A Principal Component Analysis (PCA) was run using the *prcomp* function in the 'factoextra' package (Kassambara and Mundt, 2020) on the remaining six metrics to help reduce data dimensionality. The dataset used in the PCA was randomly sub-sampled such that only six events per year per walleye were included. This was the maximum number of events for any individual other than Walleye ID 16053 and Walleye ID 16063 and sub-sampling was used to reduce the influence of these two individuals on the PCA. This dataset included data from both 2018 and 2019 since we assumed the types of potential walleye behaviours would be consistent between years. The result was a dataset that included 69 events (rather than 181; Table 1) that were used in the PCA. Scores for the first two Principal Components (PC) of the PCA were then used in a k-means clustering algorithm applied using the *kmeans* function from the 'stats' package (R Core Team, 2023). The number of clusters to retain was determined based on Elbow and Silhouette plots (see ESM Fig. S1). PCA scores and k-means clusters derived from the sub-sampled dataset were then applied to the entire dataset (i.e., 2018 and 2019 and all 181 events) so that every event could be assigned to a cluster. From this larger dataset, boxplots were created for the six environmental metrics to show the spread of the data within each cluster. Boxplots paired with the PCA loadings informed a descriptive interpretation of the characteristics of each event cluster. For example, spawning events were presumed to be comprised of more tightly clustered position estimates, with low movement rates, which occurred close to shore (Bozek et al., 2011b; Raabe and Bozek, 2012).

2.3. Eggs mats

To explore egg deposition, egg mats (20 x 40 cm horse-hair furnace filter [2.5 cm thick] attached to a metal plate of the same dimensions) were deployed individually on 5 April 2019 at set water depths of approximately 1.25 m and 1.50 m along a line perpendicular to shore at nine locations (18 mats total; Fig. 1). These shallow depths were selected based on past studies of lentic shoal spawning walleye (e.g., Bozek et al., 2011b; Raabe and Bozek, 2012). Similar mat setups have been used to collect walleye eggs in other areas of the Great Lakes (e.g., Detroit River; Manny et al., 2010 and Lake Huron; Gatch et al., 2021). Mats were checked every 2–5 days and removed on 25 April 2019. Checking the mats included rinsing, visually inspecting, and counting all observed eggs. Given variable set durations, the total number of eggs collected was standardized to eggs/day. All observed eggs were assumed to be walleye eggs as no other spring-spawning species have been detected within the fine-scale array during April walleye spawning surveys (D. Reddick, unpublished data). Egg mats were not deployed in 2018.

3. Results

Of the 43 walleye tagged for the Hamilton Harbour telemetry project, 16 were detected on the fine-scale array during the study period (i.e., 27 March–16 May), with nine detected in both years (Table 1). One additional walleye that was originally tagged in July 2016 in Toronto Harbour (approximately 50 km away) was also detected in both years (see Midwood et al., 2019 for tagging details). After data filtering, night events were retained from 11 walleye in 2018 and 13 walleye in 2019, with seven individuals common to both years (including the walleye from Toronto Harbour). Walleye ranged in size (at the time of tagging) from 460 to 608 mm (mean = 542 mm; Table 1). Sex information was limited, and the sole confirmed female walleye was only detected on the

fine-scale array twice during the day. In total, 181 events were identified (93 in 2018 and 88 in 2019), over half of which (115) were from a single individual (Walleye ID 16053). One other individual had 15 events in 2018 (Walleye ID 16063), but otherwise, individual walleye had 1–6 events within a single year (Table 1). Walleye ID 16053 was detected throughout the duration of the study period and found throughout the array, although it spent the majority of time close to shore (Fig. 2). In contrast, other individuals spent limited time on the array, and night events tended to be concentrated on the northern half and further from shore (Fig. 2).

For the PCA, PC-1 explained 35 % of the variance in the data with positive values associated with longer events situated in the northern portion of the array that were closer to shore and comprised of slower movements (Table 2). PC-2 explained 18 % of the variance and positive values were indicative of events that covered a larger surface area (greater KDE) and occurred early during the study period when water temperatures were cooler. Collectively, these results suggest that presumptive spawning events are likely to have positive values for PC-1 and PC-2.

Interpretation of the k-means clustering results (ESM Fig. S1) indicated there were seven clusters in the events dataset. Clusters 2 and 5–7 all had positive PC-1 values, suggesting they captured events that were close to shore, long in duration, and where fish were moving slowly, all potential indicators of spawning events. Within these, Clusters 2 and 7 were distinct, with Cluster 2 occurring when temperatures were warmer (8.6 °C compared to 4.8–5.5 °C for the other clusters; Fig. 3A) and Cluster 7 having the largest KDE values of any cluster (Fig. 3E). Most events in Cluster 2 also occurred in 2019 (Table 3). The distinctions between Clusters 5 and 6 were more muted, but in general, Cluster 6 was slightly closer to shore, on the more northern portion of the array (i.e., higher latitude), and more consistently of a longer duration (see Fig. 4 for an example of Cluster 6 events). Events within Cluster 5 were more

Table 2
Output from the Principal Component Analysis showing eigenvalues and loadings for the individual Principal Components (PC). Only PC1 and PC2 were retained and interpreted. Loading values in bold were greater than 0.41 (the square root of 1/(number of samples)) and interpreted as being the main contributors to the PC. See ESM Table S1 for descriptions of each of the event metrics.

	PC1	**PC2**	PC3	PC4	PC5	PC6
Standard deviation	**1.44**	**1.03**	1.01	0.97	0.72	0.63
Proportion of Variance Explained	**0.35**	**0.18**	0.17	0.16	0.09	0.07
Cumulative Proportion of Variance	**0.35**	**0.52**	0.69	0.85	0.93	1.00
Loadings						
Event Metrics	PC1	PC2	PC3	PC4	PC5	PC6
Latitude	**0.516**	−0.148	0.472	0.071	0.126	0.684
Distance to Shore (m)	**−0.523**	0.153	−0.410	0.158	0.332	0.633
Temperature °C	−0.076	**−0.711**	−0.065	0.681	0.055	−0.132
50 % Kernel Density Estimate	0.099	**0.668**	0.190	0.700	0.005	−0.134
Movement Rate (m/s)	**−0.510**	−0.038	0.412	0.044	−0.719	0.221
Duration (min)	**0.429**	0.039	−0.632	0.119	−0.595	0.218

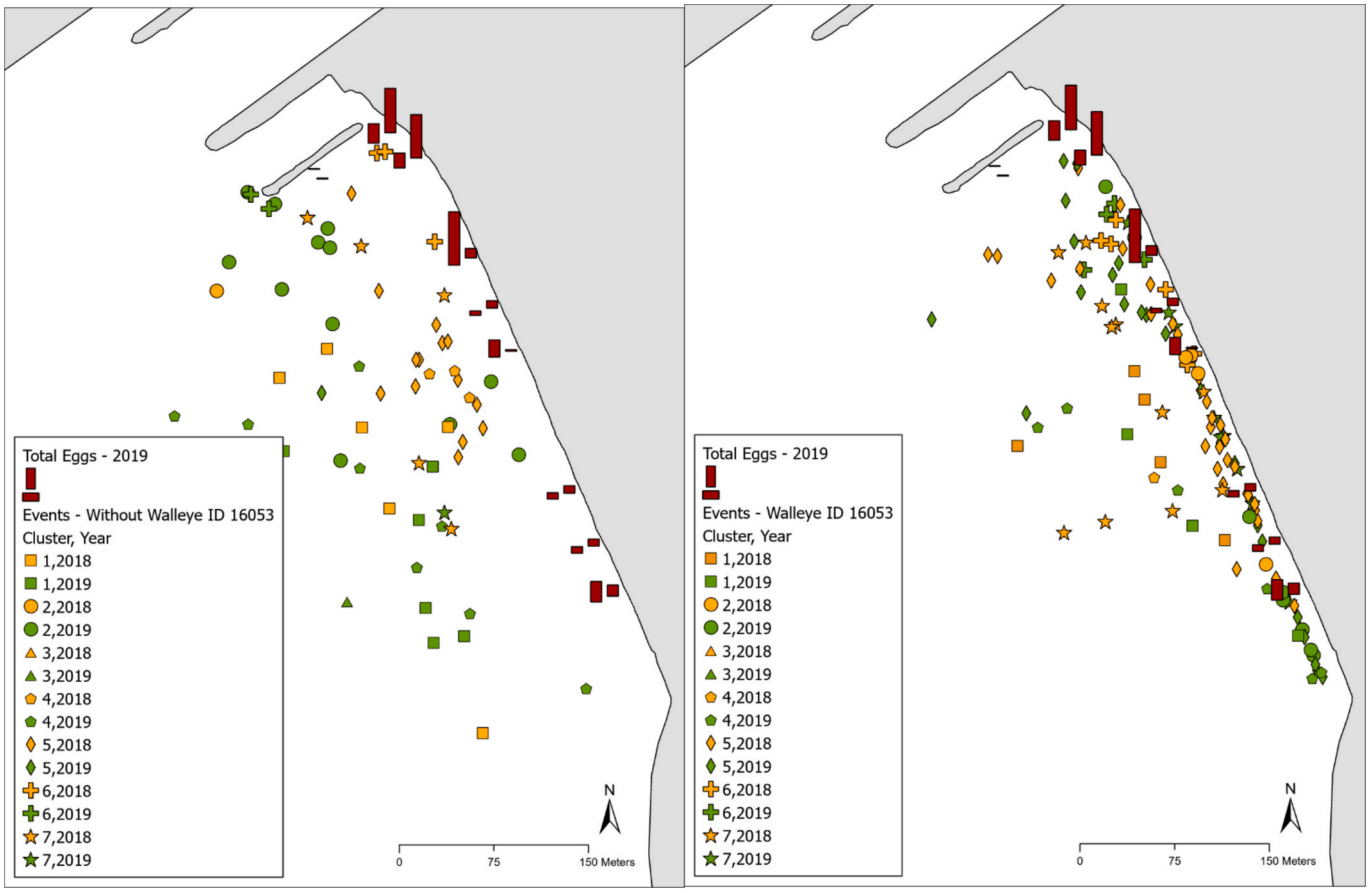

Fig. 2. Location of events (i.e., centroid) on the fine-scale array in 2018 (shades of orange) and 2019 (shades of green) by cluster type (different shapes). The panel on the left excludes Walleye 16053 and the panel on the right is only events for this individual. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

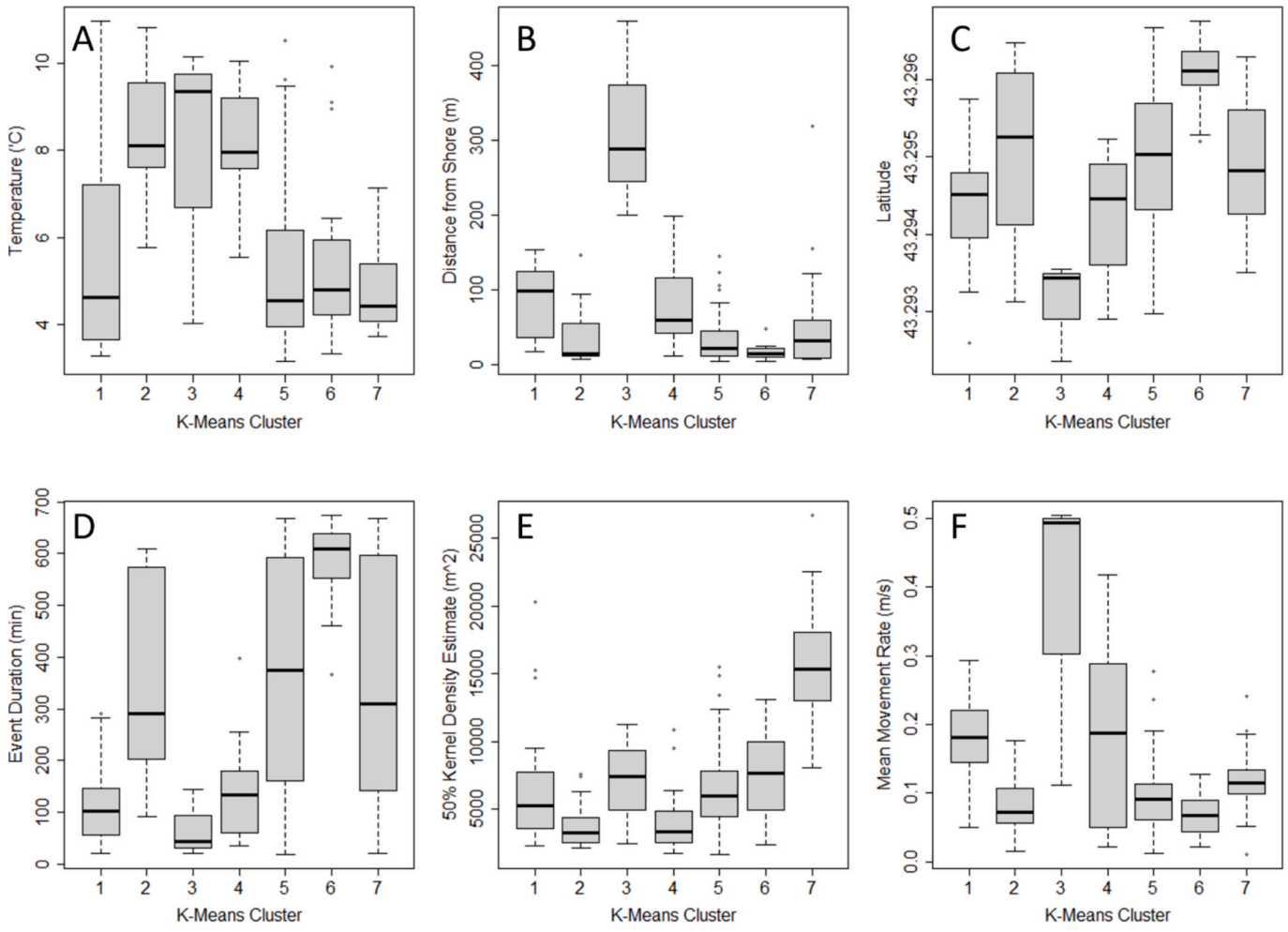

Fig. 3. Boxplots showing the range of metric values for events included in each of the seven k-means clusters. See ESM Table S1 for information on event metric derivation.

Table 3
Number of events assigned to each of the seven clusters for each individual in each year on the fine-scale array.

		Cluster						
Year	**ID**	**1**	**2**	**3**	**4**	**5**	**6**	**7**
2018	TH_Walleye_608	2	0	0	0	0	0	3
	Wall 15761	0	0	0	0	0	0	1
	Wall 16052	0	0	0	0	0	0	1
	Wall 16053	5	4	0	1	32	6	11
	Wall 16060	0	0	0	1	0	0	0
	Wall 16062	0	0	0	0	2	0	0
	Wall 16063	2	0	0	0	11	1	1
	Wall 18969	1	1	1	0	0	0	0
	Wall 18973	1	0	0	0	0	2	0
	Wall 52867	0	0	0	0	1	0	0
	Wall 52870	0	0	0	2	0	0	0
2019	TH_Walleye_608	1	0	0	0	0	0	0
	Wall 14519	0	3	0	2	0	0	0
	Wall 15761	0	0	0	0	1	0	0
	Wall 16052	1	2	0	0	0	0	0
	Wall 16053	4	8	0	6	25	4	9
	Wall 16060	0	4	0	0	0	2	0
	Wall 16061	0	0	0	1	0	0	0
	Wall 18965	0	0	0	1	0	0	0
	Wall 18967	0	1	2	1	0	0	0
	Wall 18969	1	1	0	0	0	0	1
	Wall 52870	1	0	0	2	0	0	0
	Wall 52871	2	0	0	0	0	0	0
	Wall 52874	0	1	0	1	0	0	0

numerous and captured approximately half of the events linked to Walleye ID 16053 (Table 3). Events in the other three clusters (1, 3, and 4) tended to occur further offshore (Cluster 3 in particular; Fig. 3B), have a shorter duration (Fig. 3D), and have more rapid movements rates (Fig. 3F). Regardless of other event conditions, there was clear temporal separation in events with four "early" clusters (1, 5–7) and three "late" clusters (2–4; Fig. 2) within the study duration each year.

For the seven walleye detected on the array in both 2018 and 2019, four showed potential spawning events in both years and two in only one year (Table 3). Of the four that spawned in both years, three were largely consistent in terms of event clusters (e.g., Walleye ID 15761, Walleye ID 16053, and Walleye ID 18969 [although it also spawned earlier in 2019]) with the last individual (Walleye ID 16052) delaying the timing of the spawning event (i.e., shift from Cluster 7 to Cluster 2 from 2018 to 2019; Table 3).

Temperatures within the array remained below 14 °C both years well into May (Fig. 5). Egg deposition peaked between 12 and 16 April 2019 (Fig. 5) and, in total, over 2000 eggs were collected with anecdotal evidence that some eggs were fertilized (ESM Fig. S2). Spawning events were observed both before and after peak egg deposition in 2019 (Fig. 5). There were clear spatial differences in where eggs were collected, with a majority on mats deployed in the northeast corner of the fine-scale array (Fig. 4). Interestingly, with the exception of Walleye ID 16053, no walleye night events were observed in this corner in 2019; however, at least two events were centered here in 2018 (Fig. 2).

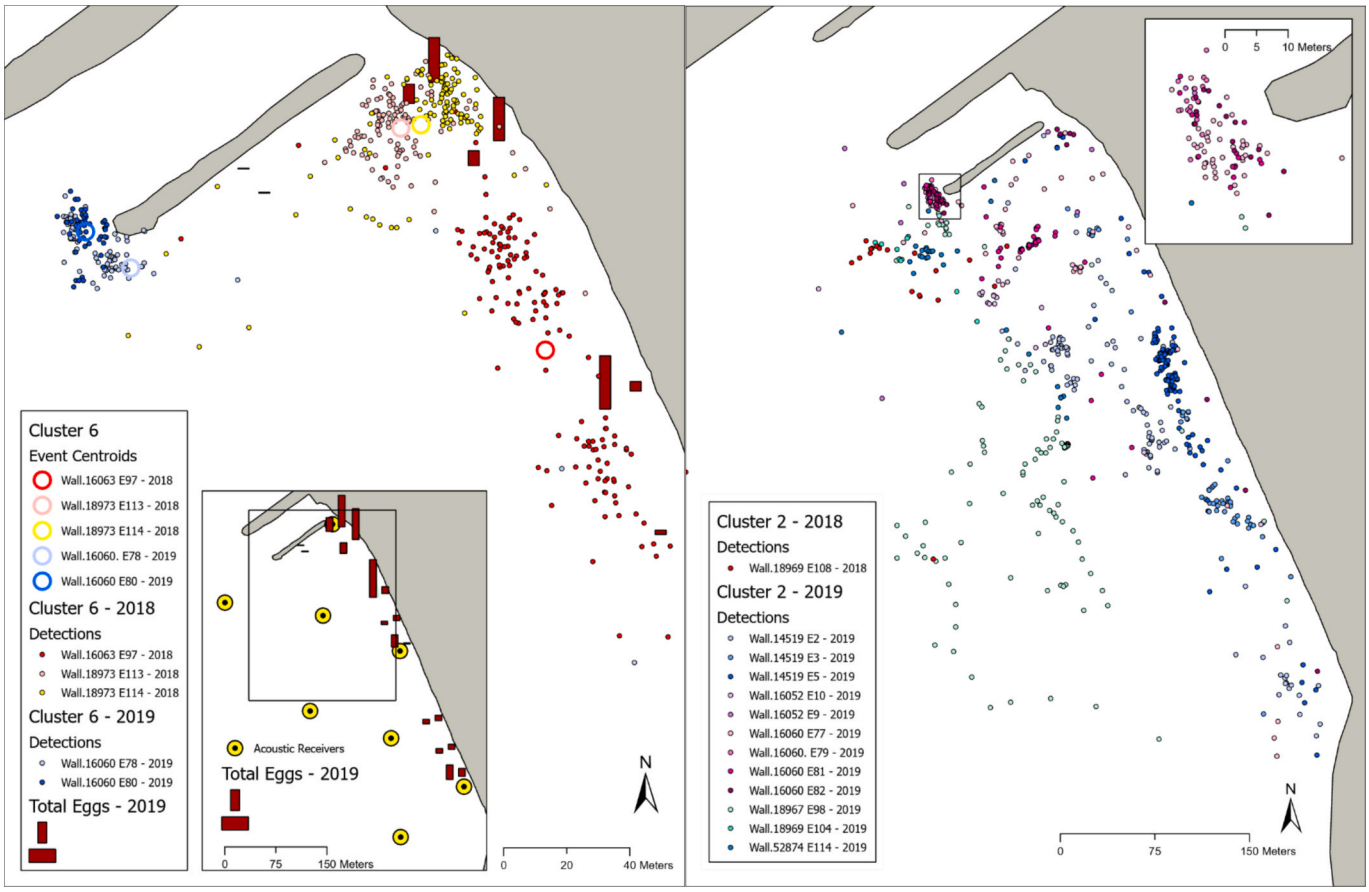

Fig. 4. Left panel: location of Cluster 6 detections and centroids of individual events within the northern portion of the fine-scale array. The total count of eggs collected in 2019 are shown as bars, and the inset maps show the acoustic receiver array and all egg count locations. Right panel: location of Cluster 2 detections of individual events. Inset in top right shows detections clustered near the shore over rubble substrates. These plots exclude Walleye 16053.

4. Discussion

Our study is one of the first to document the fine-scale movement behaviours stocked walleye exhibit near a potential spawning shoal during the spawning period. We used fine-scale acoustic telemetry to describe the conditions used by free-swimming stocked adult walleye. There were clear differences in walleye behaviour within the fine-scale array, as exhibited by the data filtering, PCA, and clustering approach. The majority of individuals were only present within the array for a limited period and consequently most yielded only a small number of filtered events. Despite this challenge, a range of behaviours within the fine-scale array were still evident. Confirmation of egg deposition in 2019 paired with anecdotal evidence of egg fertilization indicates both male and female walleye are using the shoal. While night events in 2019 did not align with areas of high egg deposition (i.e., the northeast corner), several events in 2018 did. Here we discuss how our findings align with past studies of walleye spawning behaviour, describe the use of the event-based approach, discuss caveats to the current work, and management implications for the stocked walleye population in Hamilton Harbour.

The range of behaviours as seen by seven event clusters within a single population of walleye during their spawning window is not surprising, with intraspecific variation in behavioural traits documented in fishes (Larson et al., 2025; Muir et al., 2012), including in walleye (Killen et al., 2016). Several event clusters had characteristics consistent with what we expected for a walleye spawning event, that is, closer to shore, focused on a smaller area, and with slow rates of movement (Bozek et al., 2011b; Raabe and Bozek, 2012). However, distinct behaviours on or near the spawning shoal were also evident with some events indicative of transitory movements by walleye along the margins of the array (i.e., rapid movement, short duration, far from shore), others situated an intermediate distance from shore (~100 m) but still with comparatively rapid movements, and a last group that were less focused on a single area (possibly reflective of an individual pausing at multiple locations within the array during one night). These behaviours likely reflect selection patterns among walleye, with more transitory individuals being attracted by some features of the habitat covered by the array, but finding aspects of conditions therein unsuitable and therefore moving on. Those detected further offshore for a short duration could be staging females (Elliott et al., 2022); however, it is difficult to discern spawning activity vs staging without knowledge of the sex, as males tend to arrive to spawning grounds early and stay in shallow portions of reefs for extended periods and females may only come in for as little as 40 min on spawning grounds (Bade et al., 2019). Tagging during spawning can be done to determine the sex of fish (e.g., Hayden et al., 2014), which may further elucidate male vs female spawning activities in Hamilton Harbour.

Based on past studies of lentic spawning walleye, we expected to find most events within 10 m of shore (Raabe and Bozek, 2012), which is similar to the limited information available on shoals used by walleye from the donor population (i.e., littoral areas with gravel, cobble, and boulders at depths of between 0.5–2.5 m; Elliott et al., 2022; S. Beech, Ontario Ministry of Natural Resources, pers. comm.). In contrast, the majority of events observed in Hamilton Harbour were centered further offshore (cluster means ranged from 17 to 316 m, although individual detections < 10 m were observed). Discrepancies between our observations and Raabe and Bozek (2012) may partially be related to the differences in study systems. The study by Raabe and Bozek (2012) took

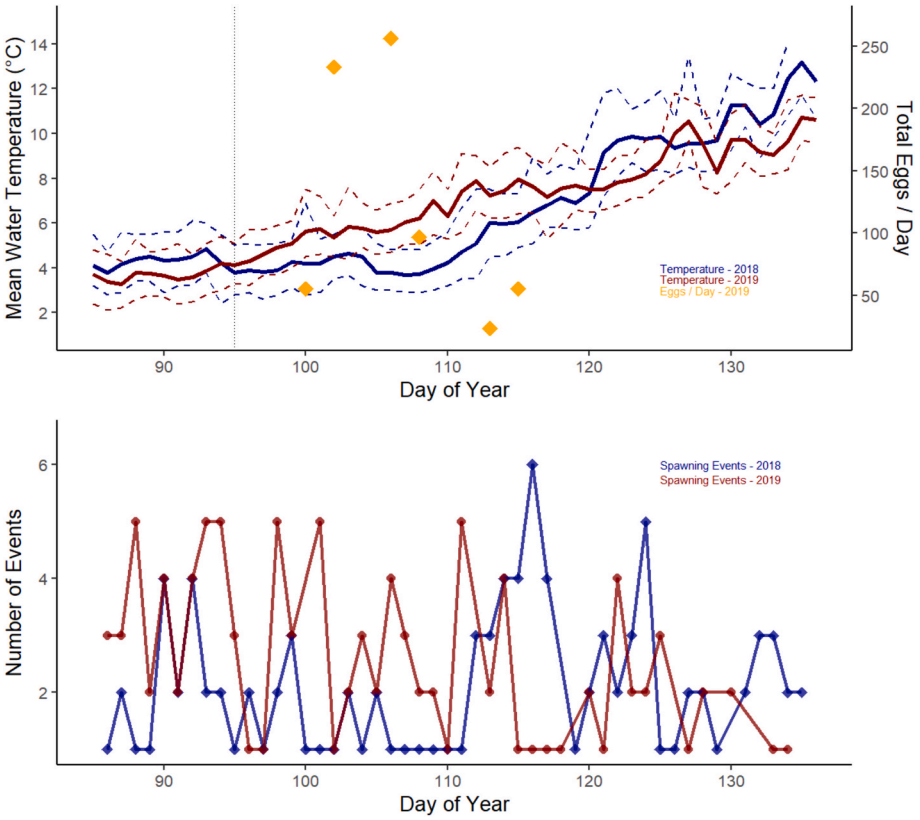

Fig. 5. Top Panel: Daily mean water temperature within the fine-scale array for 2018 and 2019. The dashed lines show the daily minimum and maximum temperature. Values are plotted against day of year (e.g., 01 April = day of year 90 and 01 May = day of year 121). The total number of eggs collected is shown with values standardized by the number of days between egg mat deployment and recovery. The vertical dotted line shows the date when egg mats were first deployed (05 April 2019 – DOY = 94). Bottom Panel: Daily number of spawning events on the fine-scale array for 2018 and 2019.

place in a comparatively small, isolated lake that has a maximum fetch of < 2 km. In contrast, the spawning shoal in Hamilton Harbour has a maximum fetch of more than 7 km that is nearly aligned with prevailing south-westerly winds in the system. As such, the areas immediately adjacent to the shore, despite containing suitable gravel, cobble, and rubble substrates, may be too high energy for walleye. As noted, shoal spawning behaviour in walleye is well documented in other Great Lakes, although shoals are often situated further from shore and in deeper waters (Bade et al., 2019; Gatch et al., 2021); however, to our knowledge, there is no evidence of walleye in the donor population spawning in such conditions. Specific habitat conditions within Hamilton Harbour may therefore be constraining stocked walleye to utilize waters situated further offshore than is typically seen in inland lakes or the donor stock. Regardless of the driver, potential spawning events were observed further offshore and, while substrates in these areas are less suitable (predominantly sand or silt; Doolittle et al., 2010), walleye have been observed spawning over such substrates albeit with poor overall recruitment (Gatch et al., 2020; Nate et al., 2003). It is also possible that if spawning occurs further offshore over less suitable substrate, eggs can drift inshore and find interstitial spaces along the shoreline. A potential risk, however, is that eggs that settle immediately adjacent to shore will be exposed to high wind and wave energy, which has been found to negatively influence egg survival (Roseman et al., 2001). Importantly, the specific location where eggs captured by our mats were released is unknown and a more spatially comprehensive survey is needed to confirm deposition locations.

Peak egg deposition occurred between 12 and 16 April 2019 when water temperatures were consistent with temperatures associated with peak capture of adult walleye (6 °C; Colby and Baccante, 1996). This temperature, however, is cooler than both what has been observed across their range (4.0–14.0 °C; Bozek et al., 2011a) and what has been deemed optimal (7.7 °C; Hasnain et al., 2010). This timing was also earlier than many telemetry-determined spawning events, which frequently occurred later in the season than we had initially expected. While the egg mat study did show an apparent normal distribution, it is possible that the removal of egg mats on 25 April 2019 was too early and potentially missed later spawning events. Water temperatures exceeded optimal spawning temperatures for walleye by early May, but remained within their wider spawning window (i.e., < 14.0 °C) for the duration of the study period. A more protracted spawning period may be beneficial to walleye; however, it also poses a risk for misalignment with larval emergence and the availability of food sources (see Kaemingk et al., 2014; Krabbenhoft et al., 2023). Notably, the period between emergence from eggs and mid-summer has been identified as a common recruitment bottleneck in walleye populations (Raabe et al., 2020), so confirmation of adult spawning and egg deposition are far from sufficient to indicate natural recruitment of stocked walleye.

A major caveat of our study is that the sex of most walleye was not determined at the time of tagging. This is an important limitation because differences in behaviour within the fine-scale array may be a function of sex (especially during the spawning period), with past studies suggesting males arrive earlier, find a suitable location, and wait for females, while, in contrast, females will wait offshore in deeper waters and venture in briefly to spawn (Bade et al., 2019; Ellis and Giles, 1965). The majority of tracked walleye showed a more limited detection pattern (including some that were known to be male) within the fine-scale array; however, we cannot confirm that these patterns are linked to sex rather than some other factor, such as an individual's determination that spawning habitat quality or suitability is limited within the fine-scale array. This pattern may also indicate walleye attempt to spawn at multiple locations in the harbour and so may remain in one spot for a few nights before moving off to try another area. Related

works have found walleye at multiple locations throughout the harbour at night during the spawning period (OMNR, 2017) and habitat surveys within the system have also found suitable spawning habitat in multiple locations (J. Midwood, unpublished data). In a limited spatial study of egg deposition, however, peak counts were observed at the location of the fine-scale telemetry array (Croft-White et al., 2026). In contrast, Walleye ID 16053 and to a lesser degree Walleye ID 16063 (both known to be male) may be opting for a different spawning strategy that is more typical of male walleye, wherein they remain in one general area for the entire spawning period and shift positions within the area each evening. Walleye ID 16053 was resident in both 2018 and 2019 but showed a slight change in the location of night events with the addition of more southern locations in 2019.

For the present study, we were able to opportunistically track walleye that had already been tagged for the larger Hamilton Harbour-wide telemetry study. While this approach reduced our time and effort, it posed a challenge in that prior to data downloads, we did not know the number of tagged walleye that would be detected within the fine-scale array. As an open system, we also could not control their residence within the array, which reduced our overall sample size. That being said, the array being embedded within a larger network allowed us to observe situations where walleye were in proximity to the potential spawning shoal during the spawning window but did not display any behaviours presumed to be indicative of spawning. Similarly, through more expanded tracking, it will be possible to identify other areas within the harbour where walleye also appear to aggregate during the spawning window. Despite a third of tagged walleye being detected within the array, there are likely considerably more un-tagged walleye that use this spawning shoal. The spatial–temporal mismatch between the location of observed nearshore night events and the area with the highest count of eggs (i.e., the northeast corner of the array) implies that our tagged walleye were likely not the source of the eggs. There is estimated to be a large population of walleye in Hamilton Harbour (up to 4500; Larocque et al., 2023), with our base sample of 43 individuals reflecting less than 1 % of this estimate. This underscores one of the main potential challenges with acoustic telemetry, tagging a sufficiently large proportion of a population to ensure spatial and behavioural patterns of the sampled individuals reflect the overall population (Brownscombe et al., 2019), particularly when the area of focus reflects only a small proportion of the overall system. In this case, knowing the sex and age (experience) of all our tagged fish would have ensured better representation of the spawning population and may resolve some of the apparent spatial–temporal mismatch issues with egg deposition.

Habitat creation or remediation efforts in fresh water are frequently focused on spawning habitats because they are presumed to be limiting in some fashion (i.e., limited in availability or limiting because of poor quality). A more spatially focused understanding of habitat selection can help better target such remediation efforts. While we had already confirmed the presence of male and female walleye at the location of the fine-scale array during the spawning period using boat electrofishing (OMNR, 2017), our telemetry approach allowed us to learn more about their fine-scale habitat selection, characteristics of their behaviour, and locations within the area that are most frequented. This information can help guide restoration works in terms of where within this more general area efforts should be focused (e.g., the northeast corner of the array). More targeted habitat management (e.g., restoration, enhancement, creation) has the benefit of reducing costs (i.e., not modifying an entire shoreline) and in theory being more effective because it can involve more minor enhancements to areas already being used. Within our specific array, the absence of suitable spawning substrates beyond 5 m of the shoreline presents a mismatch in the areas where walleye are aggregating and where suitable habitat is situated. The addition of coarse aggregates (i.e., gravel, cobble) in waters further offshore is one possible management action, but it must be guided by detailed modeling of sediment transport dynamics to ensure aggregate material is positioned to avoid burial by sediment. Such additions may help to increase egg retention further offshore and ultimately survival on this spawning shoal, an important step to re-establishing natural recruitment. However, several major knowledge gaps remain, including: the fate of eggs within the shoal, their ability to survive to emergence, and the likelihood that fry can find suitable nursery habitat.

CRediT authorship contribution statement

Jonathan D. Midwood: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jill L. Brooks:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Paul A. Bzonek:** Writing – review & editing, Methodology, Formal analysis. **Steven J. Cooke:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Melanie V. Croft-White:** Writing – review & editing, Methodology, Investigation. **David T. Reddick:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Nicole A. Turner:** Writing – review & editing, Methodology, Investigation. **Sarah Larocque:** Writing – review & editing, Software, Methodology, Investigation, Formal analysis. **Caleb T. Hasler:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2025.102728.

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