

Life outside the fishbowl: Tracking an introduced population of goldfish (*Carassius auratus*) in an embayment on the Laurentian Great Lakes

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ABSTRACT

Invasive species are a key threat to biodiversity in freshwater ecosystems; and, as such, their management can be an important part of ecosystem restoration and conservation. In Hamilton Harbour, an impaired Lake Ontario embayment, invasive species are an important threat. In the early 2000s, an increase in invasive goldfish (*Carassius auratus*) was identified during monitoring surveys. This population of goldfish was studied via acoustic telemetry to gain knowledge about its biology to support management control options. Hamilton Harbour goldfish exhibited seasonal patterns in site and depth use, and clear preferences for over-wintering and spawning areas. Goldfish were largely resident to Hamilton Harbour with the exception of one individual. To predict when goldfish would move into spawning areas, we examined goldfish presence, abundance, and temperature at a fish-barrier connected to the harbour and developed models to predict goldfish presence based on Cumulative Growing Degree Days (CGDD) and Day of Year (DOY). Goldfish were captured in large numbers ($>100 \text{ day}^{-1}$) at the fishway when $\text{CGDD} > 25.0$ and $\text{DOY} > 100$; therefore, we predicted that our tagged fish would move to spawning areas when these thresholds were reached. Both models accurately predicted when tagged fish moved to spawning areas which largely occurred when water temperatures were lower ($\geq 9.7 \text{ }^\circ\text{C}$) than thresholds previously identified in the literature (i.e., $15.0 \text{ }^\circ\text{C} - 22.0 \text{ }^\circ\text{C}$). This suggested that pre-spawn/staging behaviour was detected using telemetry driven by factors including water temperature. Results from this work will inform control strategies for goldfish, including active removal during aggregation prior to spawning.

1. Introduction

Invasive species are organisms introduced (purposefully or accidentally) to a novel ecosystem that have detrimental economic and environmental impacts (NISC, 2006). Freshwater systems are particularly susceptible to non-native species introductions (Sala et al., 2000) and have been implicated in the decline of freshwater biodiversity (Gozlan et al., 2010; Tickner et al., 2020). Although very much a global issue, it is particularly salient in the Laurentian Great Lakes of North America which have suffered a loss of biodiversity associated with the impacts caused by numerous biological invaders now numbering in the hundreds (Mills et al., 1994; Richardson et al., 1995). Two introduced cyprinid species, goldfish (*Carassius auratus*) and common carp (*Cyprinus carpio*), are abundant in a degraded but ecologically important

embayment known as Hamilton Harbour, situated at the western end of Lake Ontario, Canada. Goldfish, native to Eastern Asia (Lelek, 1987), were introduced into North America and the Great Lakes, both intentionally and accidentally (Richardson et al., 1995), through the ornamental fish trade (Chan et al., 2019; Rixon et al., 2005) and the commercial baitfish industry (Nathan et al., 2014). Common carp were first detected in Hamilton Harbour in the late 1880s and had become one of the most abundant species in the harbour by the mid-1950s following the collapse of the native fishery (Holmes and Whillans, 1984). In contrast, goldfish were first detected in the harbour during surveys conducted between 1960 and 1961 (Whillans, 1979). In the late 1970s, there was a massive die-off of goldfish in Hamilton Harbour that was attributed to reproductive failure associated with industrial contamination (Munkittrick and Leatherland, 1984a). Furthermore, goldfish

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were rarely captured (i.e., ≤ 0.02 individuals/transect) in the harbour during routine fish community surveys (1992–2002), until the mid-2000s, when an increase in numbers was observed alongside a decline in common carp (Boston et al., 2016; OMNRF, 2019).

Although goldfish and common carp are both globally invasive (Chan et al., 2019; Halas et al., 2018; Lorenzoni et al., 2010a), there is an abundance of information on common carp biology and their impacts on ecosystems outside of their native range, but the same ecological information for goldfish is limited. Life history strategies for both cyprinids are thought to be similar and contribute to their success as invaders in novel environments; these characteristics include early maturation and rapid growth compared to native fishes (Jones and Stuart, 2009; Morgan and Beatty, 2007), high fecundity (Munkittrick and Leatherland, 1984b; Lorenzoni et al., 2010a, b), tolerance of extreme environmental conditions (Abramenko et al., 1997; Shoubridge and Hochackha, 1980; Spotila et al., 1979; Rowe, 2007; Tang et al., 2020), and a broad feeding spectrum (Lorenzoni et al., 2010a, b; Morgan and Beatty, 2007). Both species are known to drastically alter aquatic ecosystems by causing increased turbidity and nutrient mobilization, resulting in decreased abundance of macrophytes, invertebrates, and native fish (e.g., Richardson et al., 1995; Matsuzaki et al., 2009). In the Laurentian Great Lakes, large populations of common carp have become established in coastal embayments and have had a direct impact on ecosystem health resulting from the degradation of native fish habitat (Lougheed et al., 2004; Hoyle et al., 2012; Boston et al., 2016). Although goldfish have been reported in the lower Great Lakes (i.e., Ontario and Erie; Taylor and Mahon, 1977), populations outside of Hamilton Harbour and their effects on the native fish community have not been well-documented or studied.

Hamilton Harbour was designated as an Area of Concern (AOC) in 1985 under the Great Lakes Water Quality Agreement and therefore, has a Remedial Action Plan to address local impairments related to fish populations and fish habitat (Hall et al., 2006; COA, 1992). In Hamilton Harbour, about 70% of historical wetland habitat was lost due to industrialization and municipal development (Holmes and Whillans, 1984). Native fishes must compete with invasive cyprinids, like goldfish and common carp, for the use of the remaining vegetated wetland habitat concentrated at the western end of the harbour. Management actions to restore important wetland habitat (e.g., spawning and nursery) for native fishes in Hamilton Harbour have focused on the re-establishment of aquatic vegetation in two wetland systems, Cootes Paradise Marsh and Grindstone Creek. Measures to improve habitat in these wetland areas have focused on common carp exclusion from spawning areas at Cootes Paradise Marsh (1996-present) and the floodplain ponds connected to Grindstone Creek, as well as targeted removal. In 1996, a manually operated fishway was constructed at the entrance to Cootes Paradise to help control the natural migration of fish in and out of the marsh during spring and fall (Lougheed et al., 2004; Thomasen and Chow-Fraser, 2012). Any goldfish or common carp captured in inbound baskets would be released back into Hamilton Harbour, while native species would be released into Cootes Paradise (Lougheed et al., 2004; Thomasen and Chow-Fraser, 2012). Fish passage into the floodplain marshes/ponds connected to Grindstone Creek is controlled by Christmas tree berms in the lower ponds and by dirt levees in the upper ponds under normal water level conditions; in addition, all seven Grindstone ponds benefit from passive fish exclusion structures, which are comprised of grates and brushes designed to exclude adult common carp. Targeted physical removal of common carp also occurs during certain times of the year in areas where they are known to aggregate and are accessible; if goldfish are caught alongside the common carp, they are also removed but because of their smaller size, aggregations are not as easily detected. A lack of understanding of the environmental drivers and timing of movements for goldfish also limits targeted removal of this species.

Electronic tagging and tracking of fish is a common technique for understanding the biology of invasive species (Lennox et al., 2016). For

example, acoustic telemetry has been used in multiple Great Lakes AOC to address impairments related to fish populations and habitat and to study wild fish population movements through continuous, remote tracking (Brooks et al., 2017; Midwood et al., 2019). The spatial ecology of common carp is relatively well studied via acoustic and radio telemetry (e.g., Butler and Wahl, 2010; Midwood et al., 2019; Penne and Pierce, 2008; Piczak et al., 2023; Stuart and Jones, 2006; Watkinson et al., 2021) and this knowledge has been used to effectively manage common carp through targeted removal using the “Judas technique” (Bajer et al., 2011; Penne and Pierce, 2008). In North American studies, common carp formed tight winter aggregations in shallow water when temperatures were $<10^{\circ}\text{C}$ adjacent to vegetated habitat (Bajer et al., 2011; Chizinski et al., 2016) and made repeated, annual movements to overwintering and spawning habitat (e.g., Bajer et al., 2011; Penne and Pierce, 2008; Watkinson et al., 2021). Conversely, there are only two acoustic telemetry studies of goldfish; one from its native range in southern Korea (Kim et al., 2014) and one outside of its native range, which was undertaken in a eutrophic river system in Australia. In the Australian study, goldfish migrated from the main channel to off-channel wetlands during their breeding period (Beatty et al., 2016) and based on that information, recommendations for control at the narrow entrance to a wetland identified as a key spawning area were made and included a one-way fish barrier. An acoustic telemetry array deployed in Hamilton Harbour originally for studying the spatial ecology of stocked walleye (*Sander vitreus*; Brooks et al., 2019), provided a unique opportunity to explore the timing and extent of movements by goldfish that can be used to tailor local management strategies.

Currently, there are no studies in the Great Lakes that examine goldfish spatial ecology and movement with acoustic telemetry and globally, there have been only a handful of studies that have explored their basic ecology (e.g., Morgan and Beatty, 2007). Understanding how animals, such as invasive species, are distributed in space and time, and how they move across landscapes is foundational for developing management strategies (Cooke et al., 2022). Therefore, to support the management of invasive goldfish in Hamilton Harbour and other freshwater embayments in the Laurentian Great Lakes and beyond, the objectives of the present study were to: 1) determine their residency within the Hamilton Harbour array; 2) document seasonal habitat residency, movements, and changes in depth distribution; and 3) link movements during the spawning period to physical habitat conditions (e.g., water depth or aquatic vegetation) and environmental drivers (e.g., temperature, day of year). Goldfish are broadcast spawners that have adhesive eggs that need to attach to a form of aquatic vegetation and therefore, have a high affinity for submerged aquatic vegetation (SAV), emergent vegetation, or the undersides of other objects and roots, with fine substrates in shallow, lentic waters (< 2.0 m) (Lane et al., 1996a,b). Additionally, based on studies that describe goldfish spawning and development in both the Great Lakes region and globally, spawning typically commences when water temperatures reach between 15°C and 22°C (Lane et al., 1996a,b; Lorenzoni et al., 2007; Munkittrick and Leatherland, 1984b) and ova and larval development require temperatures of 18°C to 21.5°C (Mackey et al., 2019; Teletchea et al., 2009). Therefore, we predicted that goldfish would select areas during the spawning season that have relatively shallow water (< 2.0 m) and some form of vegetative cover when water conditions, including temperature, were suitable, or when alternate thermal metrics, such as Cumulative Growing Degree Days (CGDD), passed a specific threshold conducive to spawning.

2. Materials and methods

2.1. Study area

Hamilton Harbour is a 21 km^2 sheltered embayment located at the western end of Lake Ontario (43.288, -79.840) with a highly industrialized southern shore (Fig. 1). The harbour is connected to Lake Ontario

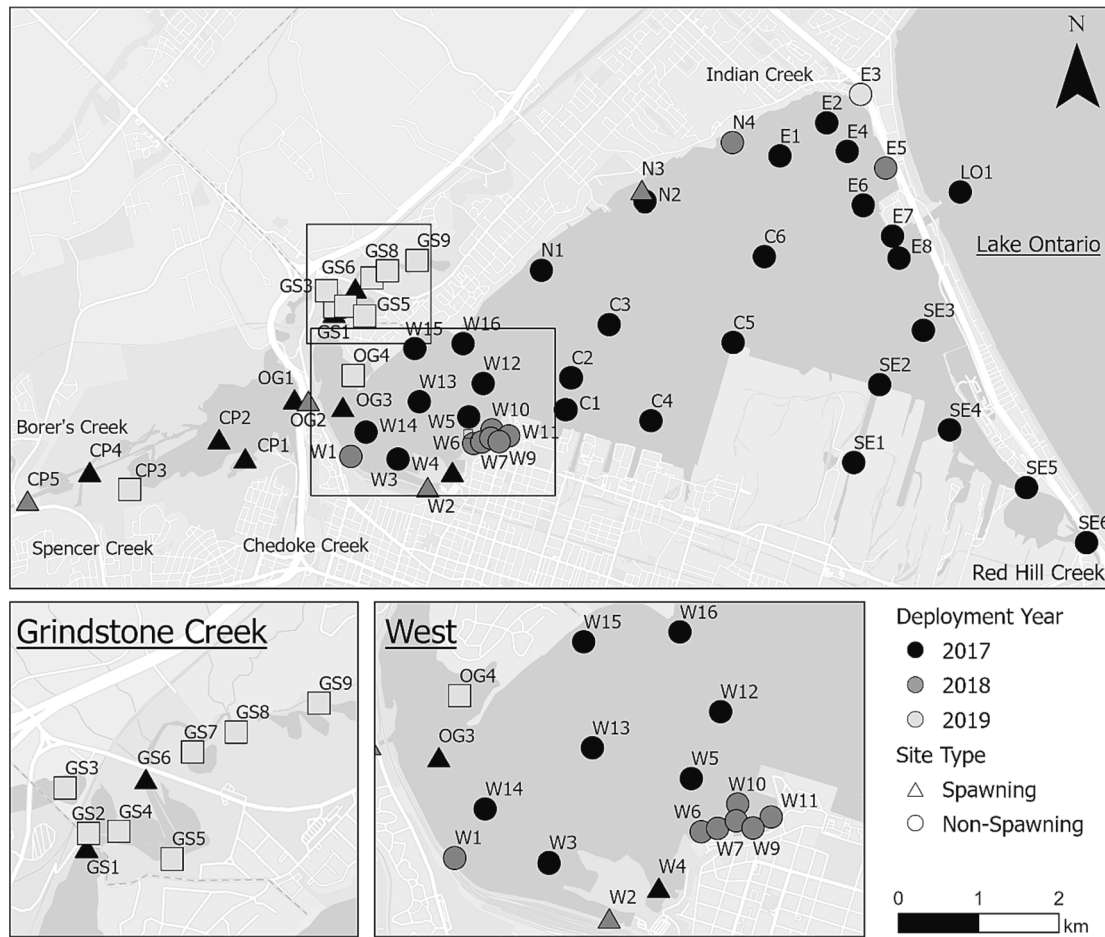


Fig. 1. Location of receivers by deployment year and receivers identified as potential spawning sites (triangle) and non-spawning (circle) sites. Key areas and features are labelled. Receiver groups are labelled as follows: Grindstone Creek (GS), outer Grindstone (OG), Cootes Paradise (CP), Hamilton Harbour west (W), north (N), centre (C), east (E), southeast (SE), and Lake Ontario (LO).

at the eastern end through the Burlington Shipping Canal. At the western end of the harbour, a 2.5 km² wetland complex known as Cootes Paradise Marsh is separated from the harbour proper at Desjardins Canal by a large, manually operated fish barrier. There are three major tributaries that empty into Cootes Paradise (Spencer Creek, Borer's Creek, and Chedoke Creek); general conditions are shallow (< 1.0 m in an average water level year), turbid (Secchi depth < 0.5 m), and sparsely vegetated (< 10% areal extent). The marsh receives effluent from a wastewater treatment plant and multiple combined sewage overflow pipes. Grindstone Creek enters the harbour at the northwest end and the marsh area is about 0.6 km², which includes seven floodplain ponds; the ponds are shallow with a mean depth of 0.44 m with emergent vegetation around the perimeters. Two other major tributaries, Indian Creek and Redhill Creek, flow into the harbour at the northeast and southeast corners, respectively.

2.2. Trends in goldfish and common carp populations

Temporal trends in Hamilton Harbour goldfish and common carp populations were derived from data collected during Fisheries and Oceans Canada's (DFO's) standardized, boat electrofishing monitoring surveys (1988–2018); for more details refer to Boston et al. (2016). In brief, catch data were collected from 100 m transects (~1.5 m water depth) at fixed, nearshore sampling locations along the east, north, and west shores of the harbour. Electrofishing sampling did not occur along the highly industrialized south shore of Hamilton Harbour or Windermere Arm (SE4 in Fig. 1) as water depths were too deep to sample

efficiently (> 10.0 m water depth). The mean catch per transect of goldfish and common carp were generated from data collected during the summer sampling season (June–August).

2.3. Acoustic receiver array

A total of 58 acoustic receivers (Vemco-Amirix, VR2W 69 kHz, Bedford, Nova Scotia) were deployed between 2017 and 2019. Initially in 2017, there were 36 receivers in the array, but additional receivers were deployed in 2018 (13) and 2019 (9), to cover key littoral areas in the harbour proper, Cootes Paradise, and Grindstone Creek system (Fig. 1). A few receivers were deployed from spring till fall and removed overwinter, such that receiver coverage in a few spots varied throughout the year but also as receiver coverage increased with the array expansion over the years (Electronic Supplementary Material (ESM) Fig. S1). Receivers were pooled into nine groups for analyses based on spatial proximity to one another and included Grindstone Creek (GS), outer Grindstone Creek (OG), Cootes Paradise (CP), Hamilton Harbour west (W), north (N), centre (C), east (E), southeast (SE), and Lake Ontario (LO). Four receiver groups were located in the west end of the harbour (GS, OG, CP, W). The OG receiver group included a receiver in the Desjardins Canal (OG2) that connects to Cootes Paradise as well as one at the fishway inside of the CP marsh (OG1; Fig. 1). A study of acoustic signal detection efficiency within the harbour (Wells et al., 2021) found variable detection ranges (350–500 m) with reductions particularly during summer stratification.

2.4. Fish capture, tagging, and detections

Large goldfish (Fig. 2) were captured between June 2017 and October 2018 using a Smith-Root electrofishing boat model SR 21 EH (170 V, 8 A) during routine monitoring surveys that were accessible to electrofishing along the east, north, and west shores of Hamilton Harbour. A total of 19 adult goldfish (> 300 mm in fork length; Table 1; Fig. 2) were surgically implanted with transmitters containing pressure sensors (Vemco V_{13P}-1x-069k-1-0034m, 46 mm length, 13 mm diameter, dry mass 11 g, battery life 1386 days) to determine their depth (m). Tagged individuals ranged in size from 300 to 340 mm (fork length) and 860–1218 g (wet mass; Table 1). Due to logistics of tagging with the thick body wall of goldfish and the size of the transmitter, only large adults could be tagged which limited the number of fish used in our study. These large fish were also not always readily found during monitoring surveys, and as such were tagged across a range of time over four tagging periods (June 2017; October 2017; May 2018; October 2018; Table 1). Fish were immobilized via electro-sedation prior to and during surgeries using Smith-Root Fish Handling Gloves (Vancouver, Washington); goldfish required between 10 and 25 mA for sedation. Transmitters were inserted into the body cavity through 2–3 cm mid-ventral incisions that were closed with 2 interrupted sutures; for more details on tagging methodology, refer to Brooks et al., (2019). The average processing time was 4–6 min and as soon as the fish handling gloves were turned off, the fish recovered and could swim upright in the oxygenated live-well of the vessel. Fish were monitored for about 15 min before they were released back into their area of capture. Fish handling and surgical procedures were approved and followed a Canadian Council on Animal Care protocol (#110723) administered by Carleton University.

All data preparation and analyses were conducted in R version 4.0.2 (R Core Team, 2020). Detection data from the telemetry array were collected from June 26, 2017 to July 19, 2019. Data were filtered to remove fish that were presumed dead ($n = 8$) for a total of 11 goldfish for analyses. Fish were inferred to be dead if they continuously exhibited constant depth-use profiles and stayed within the same area of the array (potentially detected on multiple receivers all within the same vicinity; Klinard and Matley, 2020). All depth values that were zero or negative (in air) were changed to 0.1 m depths, as these erroneous values can be caused by sensor drift in the tag. Lastly, detection data that met the criteria for false detections were also excluded from our analyses (Pincok, 2012), as were data in which tags were detected on the same receiver earlier than the minimum ping rate of the tags, and those that were not spatially possible (e.g., in another lake system).

Based on the dates of the first and last detection, the total number of detections and days with detections were calculated for each goldfish for

the duration of the study. Daily detection efficiencies were used to examine the performance of the array on a seasonal basis; for more detailed information on detection efficiency refer to Brooks et al., (2019) and Wells et al., (2021).

2.5. Harbour residency, seasonal habitat residency, movements, and depth

Residency within the Hamilton Harbour array was examined spatially by receiver group and temporally by season and year from June 2017 to July 2019; season was defined by temperature dynamics and thermocline delineation: spring (>5°C and warming isothermal), summer (established thermocline), fall (first full water column mixing), and winter (temperature is no longer declining and <5°C isothermal) (Larocque et al., 2020b). Winter and summer were the longest seasons (> 100 days) and spring was the shortest and most variable season; for example, spring 2018 was 31 days (04/30–05/31) compared to spring 2019 which was 41 days (04/21–06/01). Determining residency followed stepwise procedures outlined in Midwood et al., (2019). This study focused on two main activities: residence and movement. Residence at a receiver group was defined as concurrent detections that occurred within six hours of each other and a reset occurred when detections were greater than six hours apart. Movement was defined as a change in residency among receiver groups. Therefore, the proportional seasonal residency represented the proportion of time (%) an individual spent in proximity to a receiver group relative to the other receiver groups in the harbour (i.e., time resident at a receiver group divided by total time detected during that season by year). Mean proportional seasonal residency was calculated from the individual proportional residencies (Midwood et al., 2019). As this metric is focused on residence proximate to a receiver, an important caveat is that low mean proportion residence at a receiver does not necessarily equate to low “use”, rather it suggests that fish detected at that receiver are: 1) either spending shorter periods of time (i.e. <6 hrs) in that area, 2) moving through that area, or 3) being detected on multiple receiver groups concurrently (creates the appearance of movement, when it is more a function of receiver placement).

Abacus plots and depth use plots were generated for each individual goldfish. As each goldfish was fitted with a V_{13P} pressure tag that provided a corresponding depth (m) value for each detection, mean daily depth values were calculated for each individual to determine whether there were relationships with mean daily depth across season and month. Separate linear mixed models were used to assess if mean daily depth (continuous response variable) changed with either season or on a shorter time scale by month (as a categorical factor). Each model included tag ID as a random effect to control for individual variation.



Fig. 2. Photo of the size of goldfish (> ~300 mm fork length) captured and tagged with acoustic transmitters in Hamilton Harbour.

Table 1

Individual fish data including transmitter ID, tagging date, capture location, fork length (mm), total length (mm), weight (g), number of detections, and total number of days detected in study. Sex was unknown at the time of capture.

ID	Tagging date	Tagging location	Fork length (mm)	Total length (mm)	Weight (g)	Number of detections	Days detected (#)	First Detection	Last Detection
14186	10/10/2018	East	330	360	880	49,651	243	10/11/2018	7/18/2019
14187	10/10/2018	East	328	358	1030	43,966	241	10/10/2018	7/19/2019
14190	10/9/2018	North	325	355	860	97,804	259	10/10/2018	7/19/2019
14191	10/9/2018	North	320	350	920	27,210	249	10/11/2018	7/19/2019
14513	10/9/2018	North	323	353	1010	13,639	203	10/11/2018	7/18/2019
14523	5/29/2018	West	340	370	1218	2675	33	5/29/2018	7/3/2018
15851	10/3/2017	West	332	362	1090	51,935	494	10/3/2017	5/26/2019
15863	6/28/2017	West	308	338	990	144,353	596	6/29/2017	6/27/2019
15866	6/27/2017	West	314	344	1150	93,565	680	6/29/2017	7/19/2019
15873	6/27/2017	West	313	343	990	57,821	503	6/27/2017	5/22/2019
15876	6/26/2017	West	300	330	900	133,144	672	6/26/2017	7/19/2019

Assumptions of normality and heteroscedasticity were visually assessed using qqplot and fitted vs. residual plots, respectively. Significance of main effects were determined using a type II analyses of deviance. Post-hoc Tukey pairwise comparison of the least squares means were performed to determine differences in mean depth by seasons and months. Significance was assessed at $\alpha = 0.05$.

2.6. Drivers of spawning behaviour/movement

To investigate the drivers behind goldfish movement during the spawning window, we examined the relationships between both fishway captures of goldfish and acoustically tagged goldfish detections at receivers that match potential spawning habitat with environmental factors including temperature (i.e. CGDD) and day of year (DOY). Temperature, which was included in the models as CGDD, and photoperiod (of which DOY is a surrogate in temperate systems) are both frequently cited as primary environmental cues for the initiation of reproductive processes (Pankhurst and Porter, 2003).

2.7. Physical habitat of spawning

To assess potential spawning habitat at receivers, habitat conditions at each receiver in the array were compiled (ESM Table S1). For each receiver in the harbour proper, mean depth (m), depth range (m), percent cover of SAV, and dominant substrate were determined within a 350 m buffer (i.e., lower end of the receiver detection range) based on spatial layers described in Doolittle et al. (2010). For habitat conditions around individual receivers in Cootes Paradise (CP) and Grindstone (GS), a 50 m buffer was applied from the shoreline due to the smaller size of the Grindstone ponds and reduced detection range. Depth (m) in CP and GS was calculated based on bathymetric surveys carried out by the Royal Botanical Gardens (RBG) in July 2017 and estimates of SAV cover were based on monitoring carried out by the RBG in 2019 (Mataya et al., 2020). The presence/absence of emergent vegetation or an alternate type of vegetative structure was identified within the buffer zone (50 m or 350 m) of each receiver. Other types of spawning vegetation or structure included submergent roots of trees, marsh meadow vegetation, woody debris, or old Christmas trees that are used as berms in between the Grindstone Creek and pond/marshes. It was also noted whether a receiver was placed at an entrance to a wetland or fishway barrier.

Potential spring spawning sites were then identified based on the habitat conditions at each receiver (ESM Table S1, Fig. 1) and included an average water depth or depth range within the buffer of each receiver of ≤ 2.0 m, coupled with the presence of emergent, submergent vegetation, or other types of vegetated cover (e.g., flooded tree roots). In addition, receivers that were placed at the entrance to a wetland or at the fishway barrier (i.e., GS1, GS6, OG1, OG2) were also considered to be potential spawning locations because we predicted that fish would be detected at these locations attempting to gain access to suitable

spawning habitat (ESM Table S1; Fig. 1).

2.8. Cumulative Growing Degree Days (CGDD) and Day of Year (DOY)

To investigate the relationship between goldfish movement, CGDD, and DOY, we used fish capture data from the CP fishway provided by RBG. The fishway provides a way to track fish migration and their timing windows into CP from Hamilton Harbour. A series of cages act as a barrier for excluding undesirable species from migrating into CP. The resulting database contains number of individual fish captured for each species at the fishway from 1996 to 2019. Fishway operations typically start in late-March to early-April and continue until mid- to late-October. As noted previously, any undesirable species, including goldfish and common carp, are excluded and released back into Hamilton Harbour. Cage lifts are variable and may occur from once a week early in the season (March) to twice a day during peak migration periods, which start around mid-April. Captured fish species are measured to fork length (mm), weighed (g), and sex is recorded where possible. For the dataset, we extracted data from the RBG fishway database to include the total number of goldfish captured as well as the presence of goldfish by date. DOY was also determined for each year starting on January 1st. Because lifts were not uniform across an entire season and may happen twice a day during peak season, a rate of capture per day was calculated using the following equation:

$$NOD_i = \frac{n_i}{(liftday_i - liftday_j)}$$

where NOD is the rate representing “number of fish captured over days”, n_i is the number of fish captured on day i , and $(liftday_i - liftday_j)$ is the difference in days between date i and the last lift day j . For example, if 10 goldfish were captured for day i on April 1st and the last lift day was on day j on March 30th, then $NOD = 10 / (\text{April 1st} - \text{March 30th}) = 10/2 = 5$. As such, NOD assumes that goldfish capture rates per day were uniformly distributed across lift dates, and therefore may underestimate the rate of capture when there are longer gaps in life dates (e.g., spring and fall periods).

DFO has been collecting water temperature data in Hamilton Harbour since 2006 as part of a fish habitat assessment program (Gertzen et al., 2016). Loggers were generally deployed in various locations across the harbour to provide good spatial coverage, including CP and GS depending on specific project needs, and in this case, in support of the fish telemetry project. Temperature loggers (Onset HOBO U22-001) were deployed mainly during the growing season (April to October), but overwinter monitoring data were also available for some sites (November to March). Loggers were set to record at 30-minute intervals and later after 2018, at 15-minute intervals for better temporal resolution. The data were subjected to standard quality assurance and quality control process outlined by DFO (Larocque et al., 2020a). Temperature data were available for the fishway from 2015 to 2019

from the dissolved oxygen and temperature loggers deployed at the site; temperature data were then merged with the RBG fishway database to determine mean water temperature by date. As the logger at the CP fishway did not have temperature data for winter 2019, we used a temperature logger on a receiver at Bayfront Park (W2 in Fig. 1). The Bayfront Park logger site was chosen for a number of reasons, including data availability for 2019, its location in the west end of Hamilton Harbour where goldfish mainly overwintered, and its proximity to majority of predicted spawning sites as well as the fishway. As goldfish are ectotherms, their life history and reproductive strategies can be driven by temperature (Neuheimer and Taggart, 2007); it is important to track the incremental heat accumulation within the system as a variable for goldfish movement into CP from Hamilton Harbour. CGDD is a good measure for tracking climatic growing conditions in a system over time through the summation of mean heat accumulation above a base temperature that would contribute to organism growth (Kocovsky et al., 2012; Coulter et al., 2016). Using the daily temperature data extracted from the fishway temperature logger, we calculated CGDD by year for the fishway using the averaging method:

$$GDD_i = T_{mean_i} - T_{base}$$

$$CGDD_i = \sum_{i=1}^n T_i$$

where GDD is the degree day for day i by year, T_{mean_i} is the mean daily temperature, and base temperature (T_{base}) was set at 5 °C. T_{base} was set at 5 °C since little to no growth was expected below this threshold CGDD values were calculated from 2015 to the end of 2019 using temperature data ≥ 5 °C collected at the fishway.

To help determine movement windows based on when goldfish were captured at the fishway, we utilized Kernel density estimation (KDE) to visualize relationships between days with goldfish catches (and display the NOD values under the curve) at the fishway and CGDD and DOYs. KDE is a non-parametric estimation of the probability density function. Based on KDE plots, the fishway goldfish captures show a bimodal influx of goldfish movements into the fishway in which the first/primary spawn run is completed before DOY 200 and a smaller movement occurs later in the year.

2.9. Spawning movement models

To determine the relationship between CGDD and DOY with goldfish captures at the fishway in relation to the largest spawning run, we restricted the data to those capture events occurring prior to DOY 200 (July 19). This DOY was selected to capture the large influx of goldfish at the fishway noted in the KDE output prior to day 200; limiting the data to before DOY 200 excluded the second, smaller influx that occurred around DOY 250. Based on this cut-off date, we calculated the cumulative proportion of goldfish captures at the fishway from January 1 to July 19, for each year. Due to a non-linear trend and not fitting a logistic curve well, we used two generalized additive mixed models (GAMMs) to determine the relationship between CGDD or DOY (independent variables in separate models due to collinearity) and the cumulative proportion of goldfish captures at the fishway (response variable) from 2016 to 2018 (with year as a random effect) as an indicator of goldfish spawning movement up the Desjardin Canal and through the fishway. Assessing the cumulative spawning movements allowed us to predict the CGDD and DOY when 50, 75, and 95% of the cumulative spawning movements through the fishway had been completed and when goldfish move to spawning locations, based on data from 2016 to 2018.

To determine if environmental factors were also associated with spawning movements of our telemetry tagged goldfish, we focused on the detections of our tagged fish from January 1 to July 19, 2019 (DOY 1 to 200) when the expanded array was in place, when we had a higher number of tagged fish ($n = 10$) in our study, and with the same date

range as the fishway analyses. Unique GAMMs and generalized additive models (GAMs) for CGDD and DOY specific to 2019 were developed for both the goldfish telemetry detections at spawning sites and fishway captures, respectively. For the telemetry data, a GAMM was developed to model the cumulative proportion of daily detections at potential spawning sites (response variable; receivers with appropriate habitat for goldfish spawning described above – Table S1) from January 1 to July 19 based on CGDD or DOY (independent variables using two separate models due to collinearity), with fish ID as a random effect. For the 2019 fishway data, a GAM model was based on the cumulative proportion of daily goldfish captures (response variable) with CGDD or DOY as an independent variable (two separate models). The predicted CGDD and DOY values at 50, 75, and 95% of the cumulative proportion from the 2019 telemetry and fishway capture models were compared to that predicted from the combined 2016–2018-derived fishway capture models. For all GAMMs and GAMs, significance was assessed at $\alpha = 0.05$.

3. Results

3.1. Trends in goldfish and common carp catches

Examination of trends in individual species' biomass and numbers from fish community data collected during electrofishing surveys in Hamilton Harbour (1988–2018) found an increase in goldfish abundance that was concurrent with a decline in common carp abundance in the early 2000s (Fig. 3). Mean common carp abundance peaked in 1997 and was lowest in 2018 (Fig. 3); similarly, common carp biomass was highest between 1988 and 1998 (4.21–7.66 kg/transect) but declined by > 50% between 2002 and 2018 (0.97–3.68 kg). Conversely, goldfish abundance increased between 2006 and 2018 (Fig. 3). Goldfish biomass was on average < 0.10 kg/transect between 1988 and 2002 but increased to 0.39 ± 0.09 kg/transect by 2018.

3.2. Fish capture, tagging, and detections

Eleven fish were tracked in total; five fish that were tagged in the spring of 2017 were tracked for almost two full years while those tagged in the fall of 2018 were tracked for less than a year. Total detections by fish ranged from 2,675 to 144,353 (Table 1) for a total of 715,763 detections over the study period; the number of days that a fish had

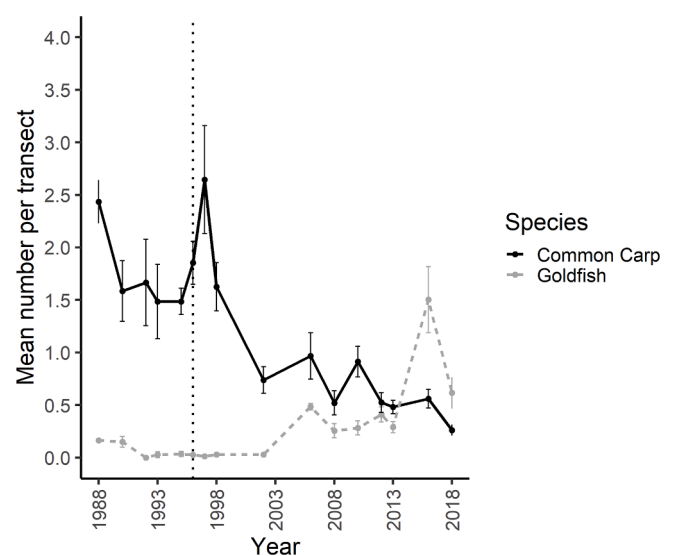


Fig. 3. Mean number (standard error) of common carp (solid line) and goldfish (dashed line) captured per 100 m electrofishing transect in Hamilton Harbour over time; Cootes Paradise fishway carp barrier was built and installed in 1996 (vertical dashed line).

detections ranged from 33 to 680 days. The individual with fewest detections was last detected on July 3, 2018 along the north shore of Hamilton Harbour and was thought to have died based on a lack of activity or change in depth. Sex of individuals was unknown at the time of capture.

3.3. Harbour residency, seasonal habitat residency, movements, and depth

Goldfish were detected almost exclusively within Hamilton Harbour, with only one fish detected outside of the harbour (14 days) at a Lake Ontario receiver (e.g., Fig. 4A) during the winter (2018–19). Residency was also low (0.001; Table 2) indicating that the one fish left the harbour for a short period of time (~5 km from the harbour based on detections in Lake Ontario) before returning. Within the harbour, the spatial distribution of goldfish detections highlighted the importance of the habitat in the west end (GS, OG, and W) for all tagged individuals (Fig. 4A–4C).

Generally, mean residency of goldfish was highest at the W receiver group from summer 2017 to winter 2018; this was true for all seasons and years with the exception of spring 2019. Goldfish that were tagged in 2017 (N=5) were highly resident in the west end of the harbour (W, OG, and GS receiver groups) year-round (Table 2; ESM Table S2; Fig. 4B). In 2018, an additional six goldfish were captured and tagged outside of the west end of the harbour and the array was expanded to increase receiver coverage (2018 – 2019; Fig. 1). As a result of the expansion to the array, our understanding of goldfish residency changed among the receiver groups and these changes were most obvious between the two fall (2017, 2018) and the two spring (2018, 2019) periods (Table 2). Compared to fall 2017, fall 2018 mean residency decreased at W from 0.99 to 0.60 and increased at the N, E, and C groups due mainly to detections from fish tagged outside of the west end of the harbour in 2018. Compared to spring 2018, spring 2019 mean residency decreased at W receiver groups from 0.78 to 0.07 and increased at Grindstone from 0.20 to 0.50 and at Outer Grindstone from 0.01 to 0.41; this change in residency was most likely related to the array expansion and not a change in fish behaviour. In all years during winter, residency for all fish, including those tagged in the east end, was highest at west end receiver groups, OG and W (Table 2). None of the tagged goldfish were detected on any of the CP receivers.

Individuals that were tagged in the west end of the harbour (W, GS, OG receiver groups) were highly resident (0.91–1.0) at west end receiver groups and detections outside of the west end were scarce (Fig. 4B). Fish in 2018 that were tagged along the north and east shores were more mobile and individual residency was generally higher at N and E receiver groups than in the west end in the fall and following summer, as goldfish moved to the west end during winter and spring before returning to their tagging location in the summer (ESM Table S2). Three fish tagged outside of the west end were detected at receivers in the SE group (Fig. 4A, 4C, and ESM Fig. S4) including the fish that was detected in Lake Ontario, whereas fish tagged in the west end did not (Fig. 4B).

Seasonal changes in depth use were concurrent with seasonal shifts in spatial residency and habitat use within the harbour. Goldfish exhibited significant seasonal ($\chi^2_3 = 908.57$; $P < 0.001$; Fig. 5A) and monthly ($\chi^2_{11} = 3086.11$; $P < 0.001$; Fig. 5B; ESM Table S3) variation in mean daily depth distribution. Seasonally, individuals were detected at significantly deeper mean daily (\pm SE) depths during the fall (3.75 ± 0.75 m) and winter (3.65 ± 0.75 m) than in spring (1.76 ± 0.75 m) and summer (1.48 ± 0.75 m). On a monthly time-scale, goldfish progressively moved deeper in the water column from September to their deepest mean daily depths in December (6.08 ± 0.27 m) when days were at their shortest, and in January, started moving upwards in the water column before reaching shallow depths in the spring (April–May; ~0.85 m), coincident with the depths at spawning habitat locations (Fig. 5B; ESM Tables S1 and S3). Goldfish were at the shallowest depths (< 1.00 m) between April and July (ESM Table S3).

3.4. Environmental drivers of spawning behaviour

KDE plots were generated to show the density of goldfish on days that they were captured (and associated NODs) at the fishway cages by DOY and GCDD from 2015 to 2019 (Fig. 6). The KDE plots generally followed a bimodal distribution of when goldfish were captured; the main influx had a higher peak and showed high NOD occurrences (≥ 100 fish captured) of goldfish at the fishway between days 101 to 148 (~April 11th – May 28th) from 2015 to 2019 (Fig. 6A, ESM Table S4). A second but much smaller influx of goldfish being captured was also observed later in the season between DOY 204 to 261 (~June 23rd and September 18th). The only exception was 2018, when goldfish continued to attempt to enter Cootes Paradise fairly regularly throughout the season after the initial influx and had one instance of NOD >100 on September 18, 2018 (ESM Table S4).

The highest influx of goldfish (≥ 100 fish) occurred at the fishway between April and May between a CGDD range of 25.5 to 285.2 °C (Fig. 6B). First catch of goldfish at the fishway occurred between March 8 to March 27 from 2015 to 2019; however, early season capture of goldfish can be affected by the start date of fishway operations (i.e. ice out), and thus may not be representative of exact timing windows of goldfish movement. The maximum number of goldfish captured for a single day between 2015 and 2019 was 493 on May 4, 2015 (ESM Table S4); however, when converted to NOD to account for variable lift effort, the highest single day NOD rate was observed on May 17, 2019 with 368 goldfish reported. Generally, high NOD rates were found between April and May, with mean daily water temperatures ranging from 9.7 to 17.4 °C (mean \pm SD = 13.9 ± 3.0 °C; ESM Table S4).

A GAMM was developed for 2016 to 2018 data to determine the relationship between the cumulative proportion of fish captured at the fishway and CGDD or DOY (as separate models; ESM Table S5; Fig. 7). Goldfish captures at the fishway were significantly related to CGDD and DOY and the majority of captures across years occurred between CGDD 50 to 300, and between DOY 100 to 150 (Fig. 7). Similarly, from the assigned probability of KDE plots, across years, the rate of goldfish captures at the fishway was observed to be greatest when CGDD was < 250 and DOY > 100 (Fig. 6A and 6B).

3.5. Spawning movements

Based on the habitat assessment surrounding each receiver in the telemetry array, we identified 19 potential spawning locations (Fig. 1, ESM Table S1). The fishway-based 2016–2018 GAMM models for CGDD and DOY predicted that a majority (50%) of tagged goldfish would move to these locations when CGDD was ≥ 175 (Table 3) which occurred on May 19 in 2019. Separate GAM models that used only 2019 fishway data and GAMM models with 2019 telemetry data (cumulative proportion of daily detections at spawning locations) were significant for both CGDD ($p < 0.001$) and DOY models ($p < 0.001$; Fig. 8, ESM Table S6). We then compared the predicted CGDD and DOY at different proportions of the cumulative spawning run across the 2016–2018 fishway model, 2019 fishway model, and 2019 telemetry model (Table 3). For CGDD, goldfish telemetry detections at spawning sites in 2019 occurred at lower predicted CGDD values (76 CGDD) at 50%, slightly higher CGDD (275 CGDD) at 75%, and higher CGDD (785 CGDD) at 95% of the spawning run compared to both the 2016–2018 and 2019 fishway models (Table 3). For DOY predictions, goldfish detections at spawning sites in 2019 occurred at slightly lower predicted DOY values (DOY 119) at 50%, slightly higher DOY (DOY 151) at 75%, and higher DOY (DOY 184) at 95% of the spawning run compared to predictions of both the 2016–2018 and 2019 fishway models (Table 3). The approximate dates when 50% of the spawning run was completed were relatively similar for telemetry and the 2016–2018 fishway models (May 1 and May 6) but was later for 2019 fishway model (May 18). Otherwise, the telemetry model had later approximated dates for both 75% and 95% of the spawning run but both fishway models had similar approximated dates

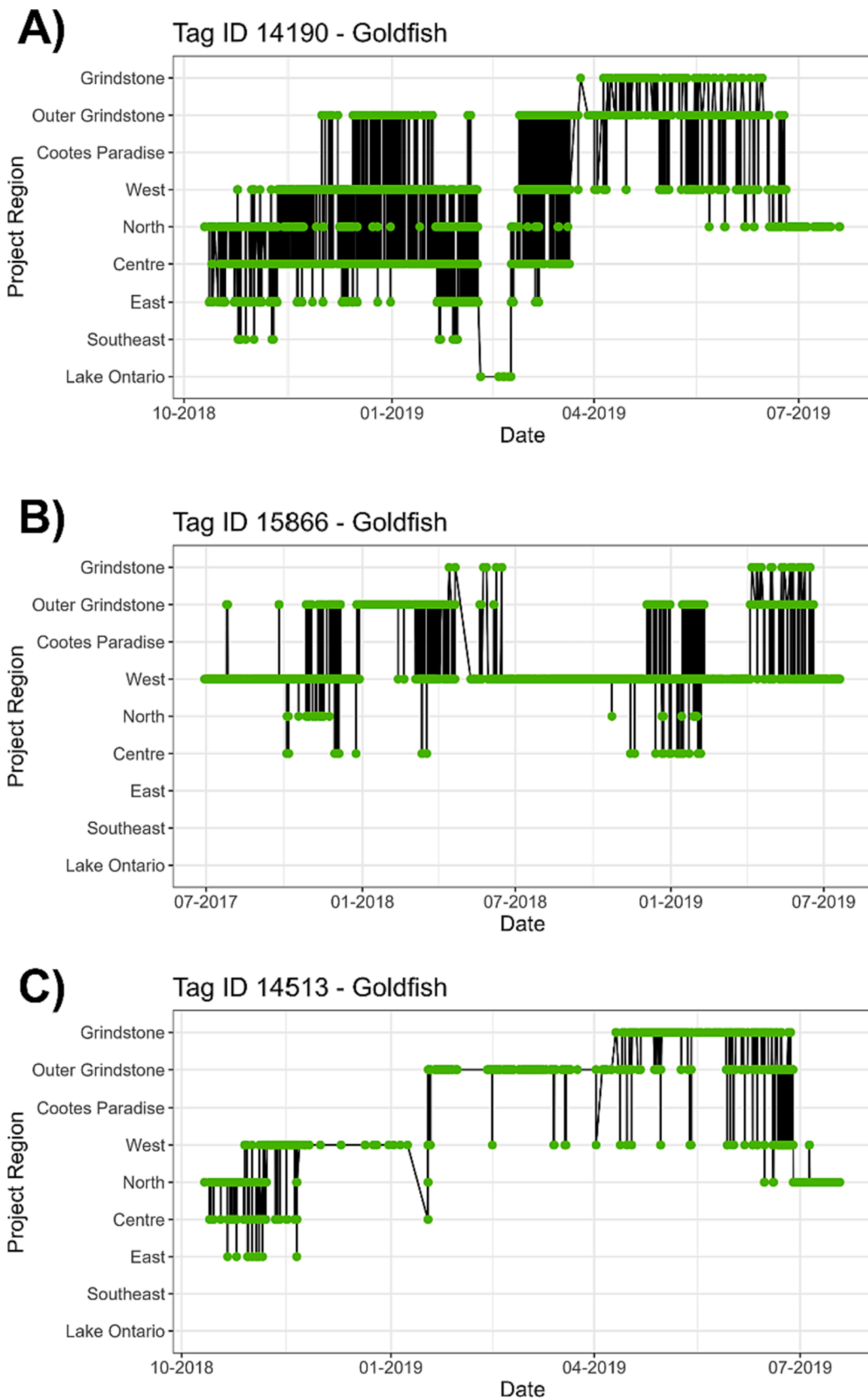


Fig. 4. Examples of Abacus plots indicating different spatial use patterns by receiver group for individual goldfish in Hamilton Harbour. Specifically, goldfish moving throughout the harbour when tagged along the north shore (A and C), or goldfish tagged in the west end remaining in the west end (B). Goldfish 14,190 (C) shows the same movement pattern as 14,190 (A) but was included to show the detection on the Lake Ontario receiver.

Table 2

Mean seasonal proportional residency of goldfish by receiver group. Values were calculated as the mean proportional residency at each receiver group between summer 2017 and 2019. The number of fish used in the analyses varied from 5 to 11. Values in bold represent mean seasonal proportional residence > 0.05.

Location	Area	Seasonal Residency Index								
		Summer 2017	Fall 2017	Winter 2017	Spring 2018	Summer 2018	Fall 2018	Winter 2018	Spring 2019	Summer 2019
Grindstone	GS	0.000	0.000	0.075	0.204	0.005	0.000	0.033	0.501	0.094
Outer Grindstone	OG	0.008	0.004	0.394	0.014	0.005	0.000	0.166	0.413	0.248
Cootes Paradise	CP	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
West	W	0.988	0.989	0.524	0.782	0.937	0.597	0.736	0.073	0.343
North	N	0.001	0.005	0.001	0.000	0.048	0.271	0.037	0.013	0.226
Centre	C	0.004	0.002	0.006	0.000	0.006	0.038	0.022	0.000	0.000
East	E	0.000	0.000	0.000	0.000	0.000	0.093	0.004	0.000	0.088
Southeast	SE	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.000	0.000
Lake Ontario	LO	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000
# Fish		5	5	5	6	6	10	10	10	8

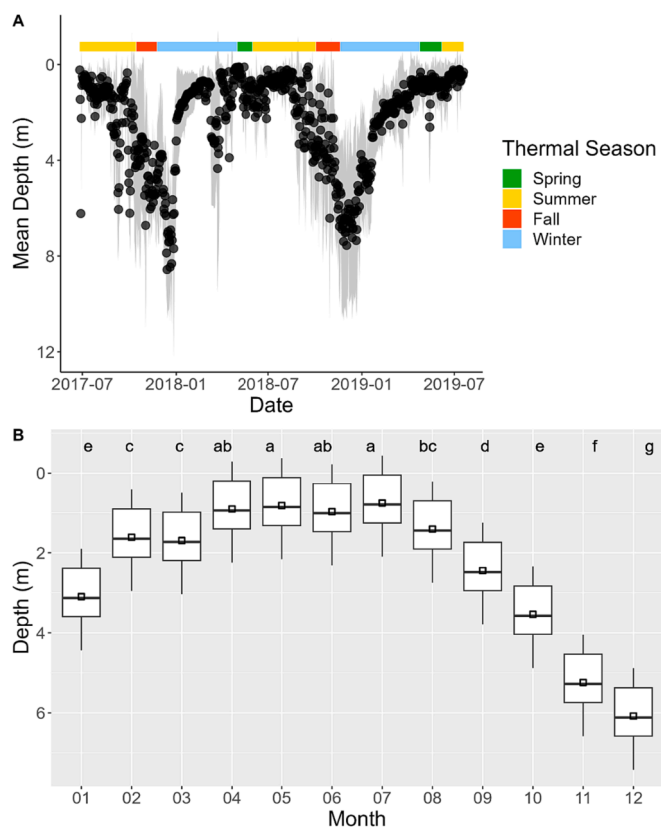


Fig. 5. Depth use of acoustically tagged goldfish in Hamilton Harbour. A) mean daily depth use (\pm standard deviation) of goldfish from June 2017 to July 2019. Colours at the top of the figure indicate the season, which is defined based on water temperatures. B) boxplot (mean = square symbol) of model predicted monthly depth distribution (m) based on mean daily depth use of goldfish. Letters at the top indicate whether monthly depth use were significantly different from each other based on a Tukey least squares difference test ($p < 0.05$).

of 95% of the spawning run (June 5 and June 6; Table 3).

Based on the 2019 telemetry model when 50–95% of goldfish would be predicted to move to spawning locations (DOY 119 to 184; Table 3), most goldfish were detected in the west end but specifically, near the mouth of Grindstone Creek during this period (ESM Figs S2–S12). In 2019, when better receiver coverage occurred in Grindstone Creek and associated ponds, 80% of goldfish ($n = 10$) were detected in these areas. This movement towards Grindstone Creek was repeated in both 2018 and 2019 by all 2017 tagged goldfish ($n = 5$). Note that we could not determine exact time of goldfish movement into Grindstone Creek as the receiver in this location was deployed from spring till fall and potentially

missed early spring movements with gaps in receiver deployment (ESM Fig. S1).

4. Discussion

Goldfish have been detected in the Laurentian Great Lakes since the 1960s (Scott and Crossman, 1998; Taylor and Mahon, 1977) but more recently they have become a species of interest due to an increased frequency of detections in embayments and watersheds in the basin, coupled with their negative impacts on aquatic ecosystems and native species. In Hamilton Harbour, past aquatic invasive species management efforts have focused on common carp with the adoption of passive management structures (Crawford and Theysmeyer, 2004; Johnston et al., 2001). These efforts have clearly proven to be effective for common carp with marked declines in catch over time during routine monitoring surveys in Hamilton Harbour and at the Cootes Paradise fishway (Crawford and Theysmeyer, 2004; Johnston et al., 2001). However, the goldfish is a smaller cyprinid species that can likely bypass these barriers, and concurrent with the decline in the population of common carp was an increase in goldfish. This suggests that the decline in common carp may have created a niche for the goldfish population in the harbour to expand. In support of developing management strategies for goldfish, here we document their spatial and seasonal residency within Hamilton Harbour and describe physical habitat and environmental drivers related to spawning. Residency of tagged goldfish was almost exclusive to Hamilton Harbour with the exception of one tagged individual that left the harbour to Lake Ontario for a short period of time (~ two weeks) during the winter of 2018/19. Seasonally, residency was primarily in the west end of the harbour, but tagged fish were found in a range of areas during the fall (post-spawning) and clear changes in seasonal depths are well explained by both overwintering and staging for spawning. Although movement was not explicitly addressed, it was partially captured by seasonal changes in residency and depth and both CGDD and DOY were significant predictors of when goldfish moved to presumptive spring spawning locations.

The residency of goldfish within Hamilton Harbour determined from this telemetry study coupled with high catches of goldfish at the western end of the harbour (e.g., Boston et al., 2016; OMNRF, 2019) suggest that goldfish were introduced from a local source (e.g., illegal introductions). However, based on the distances travelled by individual goldfish in the Australian (Beatty et al., 2016), Korean (Kim et al., 2014), and the current telemetry studies, spread and range expansion from Hamilton Harbour into other systems is possible. Beatty et al. (2016) found that invasive goldfish ($N=15$) in an Australian lowland river travelled a minimum of 0.3 km day^{-1} on average during a 365 day period, but one of the 15 tagged individuals travelled 5.4 km over a 24-hour period and 231.3 km in 365 days. Kim et al. (2014) also found that tracked goldfish ($N=6$) in South Korea travelled a minimum of $0.5 \text{ km to } 4.0 \text{ km day}^{-1}$ and one goldfish travelled 191.8 km in 48 days. Goldfish have been

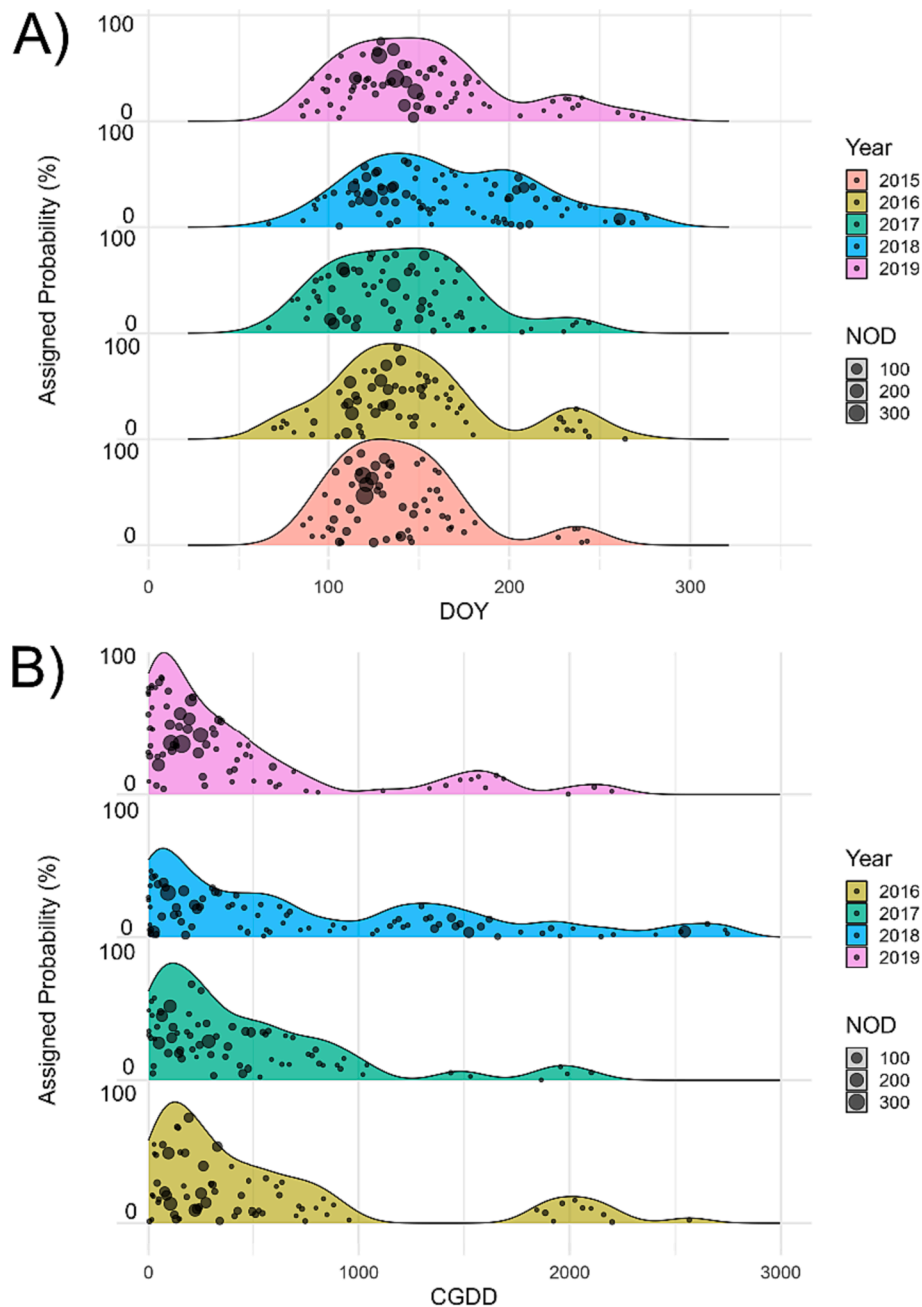


Fig. 6. Ridgeline plots of assigned kernel density estimation (KDE) probability (%) of goldfish capture frequency at the Fishway from 2015 to 2019 by A) Day of year (DOY) and B) cumulative growing degree days (CGDD; °C). CGDD for 2015 was removed due to insufficient data from the first quarter of the year and CGDD for the 2019 distribution was based on Bayfront temperatures. NOD represents the number of fish captured over days to account for unequal effort at the Cootes Paradise fishway.

captured in various DFO monitoring programs both northeast (e.g., Toronto Harbour ~50 km) and southeast (e.g., Jordan Harbour ~ 35 km, Niagara/Welland rivers ~ 50 km) of Hamilton Harbour, therefore, the possibility that goldfish could have originated from elsewhere or have expanded out from Hamilton Harbour cannot be discounted. Given our limited sample size (N=11); however, increased tagging and tracking effort are warranted to determine the frequency and extent of larger-scale movements.

Despite some variability in individual behaviour, there were clear, spatial preferences for over-wintering habitat and sites that were identified as potential spawning habitat in the west end of the harbour. From October to January (fall to early winter), the residency index for all goldfish was highest at receivers found in moderate to deep (> 6.0 m)

un-vegetated habitat, but as the days became longer and water temperatures increased (>5.0°C and warming), the residency index of goldfish was highest at receivers in shallow, nearshore areas (< 2.0 m) with emergent vegetation or at the entrances to shallow, vegetated wetland habitat (i.e. Cootes Paradise and Grindstone ponds). Winter was the longest season lasting approximately five months (December to late-April) during which transitional movements by goldfish were observed; tagged individuals moved from deeper depth use as early as mid-January towards shallower, identified spawning sites by April. While diurnal detections were not specifically addressed in this paper, Larocque et al. (2020) found that Hamilton Harbour goldfish were detected at deeper depths during the day and shallower depths at night, and Larocque et al. (2023) found a higher proportion of goldfish detections

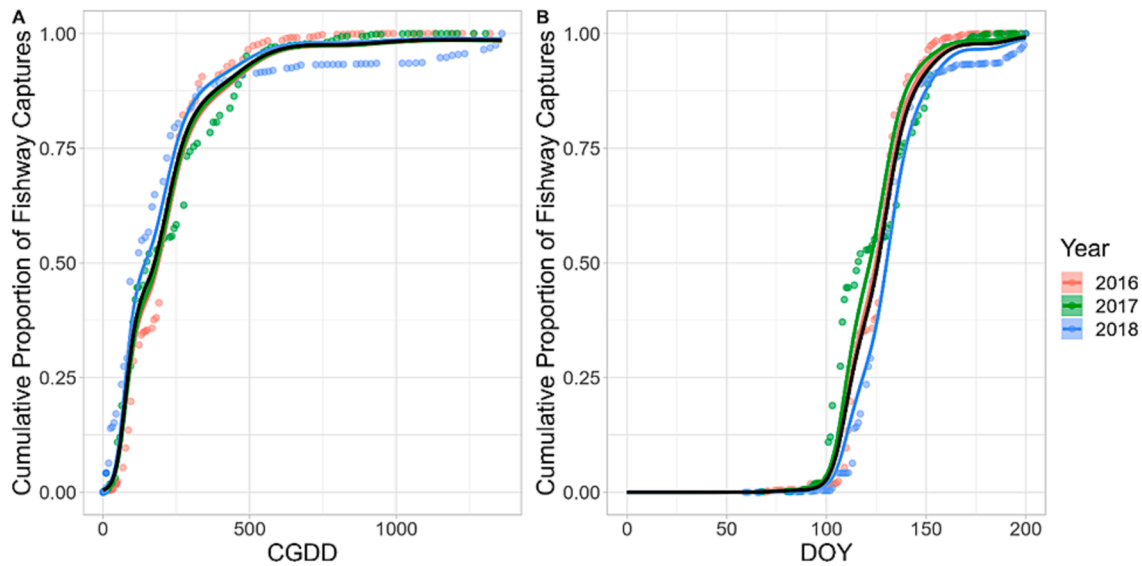


Fig. 7. Generalized Additive Mixed Model (GAMM) models of the cumulative proportion of goldfish captured at the fishway by A) Cumulative Growing Degree Days (CGDD) and B) DOY with year (2016–2018) as a random effect. Data available until DOY 200 for all years.

Table 3

Comparison of Generalized Additive (Mixed) Model (GAM(M) predicted probability (%) of Hamilton Harbour cumulative proportion of goldfish captured at the fishway and cumulative proportion of acoustically tagged fish detected at spawning sites by relative Day of Year (DOY) and Cumulative Growing Degree Days (CGDD) with estimated date based on both model results. Data available until DOY 200 for all years. Re = random effect.

GAM(M) Group	Year		50 %	75 %	95 %
Fishway Proportion ~ s(DOY) + (re - year)	2016–2018	DOY (Day)	126	135	158
		CGDD (°C)	175	265	543
		Date	~May 6	~May 15	~June 6
Fishway Proportion ~ s(CGDD) + (re - year)	2019	DOY (Day)	138	145	155
		CGDD (°C)	173	217	318
		Date	~May 18	~May 25	~June 5
Detection proportion ~ s(DOY2019) + (re - fish ID)	2019	DOY (Day)	119	151	184
		CGDD (°C)	76	275	785
		Date	~May 1	~June 1	~July 5

at night/dawn compared to day/dusk. While Beatty et al. (2016) did not find any significant diurnal differences in goldfish detections in the Australian Vasse River study, Kim et al. (2014) noted that detections were higher at night than during the day in a South Korean reservoir. These preliminary observations suggest that goldfish undertake diel movements into shallower nearshore areas during the night, with increased detections suggestive of greater activity during the night as well.

The expansion of the array in 2019 to cover more areas within and immediately outside of the Grindstone Creek system helped highlight the importance of this area to goldfish, which was not as evident with the more limited 2018 array. Our results were consistent with other acoustic telemetry studies on invasive cyprinids, including the

Australian Vasse River study, where tagged goldfish moved into wetland areas during the spawning season (Beatty et al., 2016) to seek out shallow, vegetated habitat required for egg adhesion (Teletchea et al., 2009). In other North American telemetry studies, common carp also sought out and aggregated in shallow, vegetated areas in the spring (Bajer et al., 2011; Penne and Pierce, 2008; Watkinson et al., 2021) and in some of these study locations, travelled large distances ≥ 50 km to access spawning habitat (Midwood et al., 2019; Piczak et al., 2023; Watkinson et al., 2021). In several studies, common carp formed tight aggregations in the winter when water temperatures decreased to $< 5^\circ\text{C}$ but remained close to shore in shallow water (e.g., 1.0–3.0 m) even though deeper, warmer waters were available (Bajer et al., 2011; Penne and Pierce, 2008; Watkinson et al., 2021). These findings are distinct from our goldfish telemetry study, which found individuals at mean water depths greater than > 4.0 m during the fall and winter and > 5.0 m in November and December, suggesting goldfish may use deeper waters than common carp for overwintering. Their potential for forming tight aggregations during these colder months warrants further study as it may be a behaviour that could be exploited to facilitate population management (Piczak et al., 2023).

In this study, both CGDD and DOY models were important predictors for determining when goldfish would be detected at potential spring spawning locations. CGDD is a measure that combines heat accumulation in a system over time (i.e., rate of warming) or “metabolically relevant thermal energy” (Chezik et al., 2014) and has been found to be a better predictor of spawning movements than both temperature (e.g., Jonsson and Ruud-Hansen, 1985; Neuheimer and Taggart, 2007) and DOY alone (i.e., ordinal or Julian Day – which are not independent from CGDD). We observed a bimodal influx of goldfish at the fishway in all years with the first influx of large numbers (>100) referred to as the “spring spawning event” when CGDD at $T_{base} = 5^\circ\text{C}$ was < 250 . When the 2016–2018 fishway model predictions were compared to 2019 telemetry detections in potential spawning areas, the telemetry model predictions were found to occur at lower CGDD values than the fishway model predicted at 50% of the spawning run but higher CGDD values at 75% and 95% of the spawning run, suggesting that goldfish may be starting to stage prior to the actual spawning run and not immediately leave these areas after spawning. Some annual variability is to be expected and DOY model predictions from the 2019 fishway model started later than the 2016–2018 fishway model, although the CGDD predictions were similar, suggesting that CGDD may be a better predictor of the start of spawning migrations. DOY (> 100) was also a good indicator

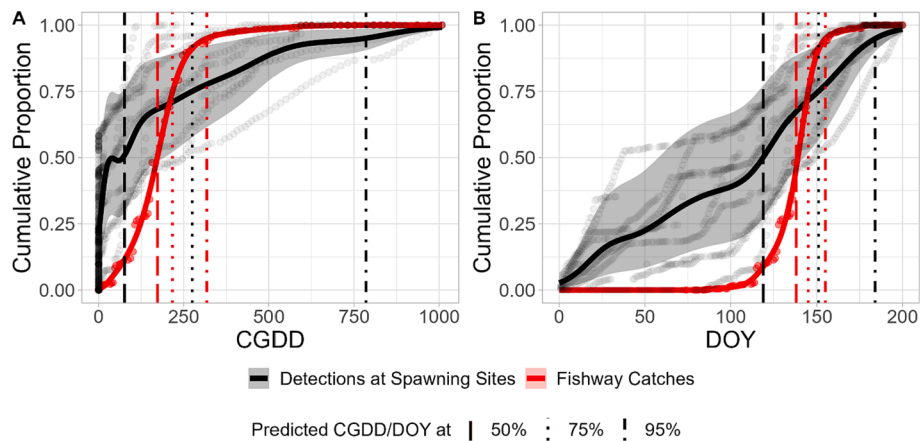


Fig. 8. Generalized additive (mixing) models for the cumulative proportion of Hamilton Harbour acoustically tagged goldfish detections at spawning sites (black) and goldfish captures at the Cootes Paradise Fishway (red) in 2019 using A) Bayfront Cumulative Growing Degree Days (CGDD; °C) and B) Day of Year (DOY). Cut-off for the relationships were set at (DOY 200). Vertical lines indicates the predicted CGDD or DOY at 50%, 75% and 95% cumulative proportions.

of when goldfish first arrived in abundance ($\geq 50\%$) at the fishway and DOY more tightly estimated the end of the spawning run (DOY ~ 150) for the fishway models than CGDD. In a similar study in Lake Winnipeg on common carp, [Watkinson et al., \(2021\)](#) also found that DOY and growing degree days were important in determining when tagged carp arrived in peak numbers at presumptive spawning sites. An advantage of CGDD over DOY in the context of species management, however, is that CGDD can yield more targeted within-year predictions of species arrival in warmer vs cooler years (e.g., [Piczak et al., In Press](#)).

The length of the spring season varied considerably among study years, which likely contributed to the differences between the 2016–2018 and 2019 model predictions. In both 2016 and 2018, the temperature-based assignment of spring suggested it started approximately 10 days later than in 2017 or 2019 yet the rate of CGDD increase was slower in 2019, which would have affected the rate of warming and biased the model towards higher catches at a later date in the 2019 model and the similar predicted CGDD at 50% of the spawning run in the fishway models. [Watkinson et al. \(2021\)](#) also observed a similar trend in the Lake Winnipeg study where $> 50\%$ of tagged common carp entered the spawning marsh 13 days earlier when ice out was three weeks earlier. Other sources of variability in our study could be attributed to the fact that CGDD was generated from a temperature logger at a different location in 2016–2018 (fishway) compared to 2019 (Bayfront receiver). Despite these caveats, CGDD and DOY still yielded useful predictive models for goldfish movement to spawning areas that can help guide management actions (discussed below).

Goldfish are iteroparous and can have multiple spawning events in one year ([Teletchea et al., 2009](#)), which can explain the bimodal influx of goldfish observed at the Cootes Paradise fishway. We noted a second smaller influx of fish later in the season when CGDD was approximately 1500 to 2000 (\sim DOY 220 to 250). This smaller summer influx could have represented another spawning event for mature individuals (≥ 2 years), which has been documented in other systems (e.g., [Lorenzoni et al., 2010 a, b](#); [Munkittrick and Leatherland, 1984b](#)), or it could be related to the availability of spawning habitat in Hamilton Harbour during the summer. In the spring, vegetated habitat in Hamilton Harbour is limited to emergent vegetation, submergent roots of willow trees outside Grindstone Creek, or meadow marshes inundated by spring flood waters in the Grindstone marshes ([Mataya et al., 2020](#)). However, by summer, SAV is well established and dense SAV beds can be found along the west and north shores of the harbour providing alternate vegetative spawning habitat options ([Gardner-Costa et al., 2019](#)). Such an increase in the availability of spawning habitat in the harbour during the summer may reduce the number of goldfish attempting to enter Cootes Paradise Marsh for a second spawning event. Confirming

reproductive activity through egg mats, the collection of gravid individuals, or the use of fine-scale acoustic telemetry positioning (after [Binder et al., 2018](#)) could help to further refine the identification of harbour spawning sites and goldfish behaviour therein.

In general, our findings suggest that we have identified a pre-spawn/staging event for Hamilton Harbour goldfish using acoustic telemetry that correlates with the capture of large numbers of goldfish (NOD > 100) at the entrance to the Cootes Paradise Marsh when DOY and CGDD are > 100 and > 250 , respectively, corresponding to mean daily water temperatures of ~ 10 °C or greater. Water temperatures during which goldfish were captured in high numbers at the Cootes Paradise fishway were in general, lower than spawning temperatures ($15.0^{\circ}\text{C} - 22.0^{\circ}\text{C}$) identified in the Great Lakes and other regions (e.g., [Lane et al., 1996a](#); [Munkittrick and Leatherland, 1984b](#); [Scott and Crossman, 1998](#); [Sani et al., 1999](#); [Teletchea et al., 2009](#)) and also lower than water temperatures required for larval goldfish development (e.g., 21.5°C ; [Teletchea et al., 2009](#)). The fishway catch data in this study were collected at a pinch point for fish trying to access spawning areas and therefore CGDD and water temperatures likely reflected the conditions when goldfish are moving into their spawning areas rather than actually spawning. Our results are in line with observations made in European studies regarding goldfish aggregations. For example, in Lake Trasimeno, Italy, goldfish aggregations were detected when water temperatures reached 13°C ([Lorenzoni et al., 2010b](#)), which was lower than the spawning temperature reported (20°C) in another Italian study ([Sani et al., 1999](#)) but in line with the observations made by [Kuznetsov \(2004\)](#) regarding the Volga basin in Russia ($12-14^{\circ}\text{C}$) and by [Paschos et al., \(2004\)](#) in Lake Pamvotis, Greece (12°C). As goldfish arrived at spawning sites when water temperatures were theoretically too cold for larval development, it suggests that water temperature and potentially other drivers could be related to early goldfish aggregations in Hamilton Harbour.

DOY was also an important driver of pre-spawning aggregations and relates to both CGDD and photoperiod (i.e., hours of daylight). Goldfish were detected at their deepest depths (> 5.0 m) in November and December when the number of daylight hours declined to a minimum before progressively being detected in shallower water from January until April when staging for spawning was identified. Goldfish were detected in < 1.0 m waters until the end of August before moving deeper in the water column as photoperiod and water temperatures declined. While not addressed directly in this study, photoperiod is thought to be the principal environmental determinant of reproductive development for many fishes ([Pankhurst and Porter, 2003](#)) and has been identified in laboratory studies as an important factor in gonadal maturation in goldfish and other temperate fishes ([Migaud et al., 2010](#)). Goldfish that

were exposed to more hours of light than dark spawned earlier than fish in a control group (Sarkar and Upadhyay, 2011). Therefore, the observed shift in goldfish depth in Hamilton Harbour as photoperiod increased may be related to the start of gonadal maturation. In addition, goldfish may seek shallower areas prior to spawning since these areas will warm the fastest. This interplay between photoperiod and depth would thus act to first trigger the start of gonadal development and then help to ensure the pace of reproductive development matches the surrounding environmental conditions where they will ultimately spawn (Pankhurst and Porter, 2003; Migaud et al., 2010).

As goldfish have evolved in a wide range of climates, (polar to subtropical), they should be able to colonize and reproduce in a wide range of climates outside of their native range (i.e., Siberia/Russia, China, Hong Kong, Korea, and Taiwan) (e.g., Balon, 2006; Froese and Pauly, 2023). Goldfish have been classified as late-spring spawners in a comprehensive review of freshwater fish reproductive traits in Europe, and although spawning behaviour has been detected at temperatures as low as 13 °C (e.g., Lorenzoni et al., 2010b), egg hatching and growth are more successful at temperatures > 20°C (Teletchea et al., 2009). Goldfish are known to be iteroparous or “repeat” spawners requiring vegetative material for egg adhesion (Scott and Crossman, 1998) but the success of hatching and growth are likely subject to suitable water temperatures. Outside of their native range, Goldfish reproduction was studied in an Australia river (e.g., Morgan and Beatty, 2007; Beatty et al., 2016) and an Italian lake (e.g., Lorenzoni et al., 2010 a), which were characteristic of temperate Mediterranean climate. In the Australian study, peak spawning activity occurred between mid-August to mid-September (Beatty et al., 2016) but peak spawning activity in Lake Trasimeno, Italy was more prolonged and similar to this study, in which the highest numbers of adults were found near suitable spawning habitat between March and June (peak in May; Lorenzoni et al., 2010a). Because goldfish are considered to be highly “eurythermal”, meaning they can tolerate a wide range of temperatures (Ford and Beitinger, 2005), they can likely adapt physiologically to the climate in the region in which they are found to ensure reproductive success.

In our study, tagged individuals expressed an affinity for habitat in the west end of Hamilton Harbour during the winter and spring, suggesting that goldfish are using a specific area for overwintering and spawning. Our habitat assessment revealed that suitable spawning habitat (i.e., shallow with vegetated structure) for goldfish outside of the west end was scarce during the spring and the residency of tagged individuals/concentration of detections in that location confirmed those findings. We found very few goldfish detections outside of the west end during what was identified as the first spawning event and none of our tagged goldfish were detected in or at the mouths of Indian or Redhill Creeks at the northeast and southeast ends of the harbour, respectively. Furthermore, goldfish were detected at the mouth of Grindstone Creek during their spawning movement window and this behaviour was repeated each year, suggesting the potential for high spawning site fidelity which can have management implications for goldfish removal. Our study indicated that the Cootes Paradise fishway was successful at preventing our tagged fish from entering (300–340 mm fork length), which was encouraging, but it is likely that goldfish in Hamilton Harbour are sexually mature at sizes that allow access to spawning areas protected by barriers designed for sexually mature common carp. The spacing of the bars in the passive structures at the access points to Cootes Paradise and the Grindstone ponds are 50.0 mm apart and multiple studies have identified sexually mature goldfish as early as at the end of their first year of life and at standard lengths between 90 mm and 138 mm (Lorenzoni et al., 2010 a, b; Munkittrick and Leatherland, 1984b; Teletchea et al., 2009). Confirming that these smaller goldfish exhibit similar movement patterns as the larger individuals tracked in the present study will be critical for ensuring management actions limit reproduction from all age-classes. Additionally, goldfish currently captured at the in-baskets to Cootes Paradise are not removed from the system and instead are released back into the harbour proper. This

represents a missed opportunity for control of these larger individuals, but passage is still possible for smaller, reproductive fish and alternate control measures may be necessary to limit overall population size.

5. Conclusions

Our telemetry data suggest that goldfish are aggregating in shallow water under certain conditions in specific areas prior to spawning and deeper in the water column during the winter, which presents opportunities for control and management using a “Judas fish” approach (Bajer et al., 2011; Lennox et al., 2016). In the Midwest United States, the “Judas fish” approach has been used to remove winter aggregations of common carp using commercial seine nets resulting in >50 % reduction in the common carp populations in those lakes (Bajer et al., 2011; Penne and Pierce, 2008). In addition, other types of control structures (i.e., a modified box trap net) have been designed to target smaller goldfish in the connecting channels to lakes in the mid-west with good success to date (Jordan Wein, personal communication) and such an approach can be explored in the Grindstone Creek system or in the Hamilton Harbour watershed where detections of goldfish in on-line stormwater management ponds have increased over the last decade. With increasing water levels and climate change favouring species like goldfish that can survive in extreme environments, alternate control measures will be important to protect spawning areas targeted by invasives that are also important for native fishes. These findings provide novel information on the ecology of introduced goldfish and reveal opportunities for management.

There are now three studies that have examined goldfish ecology using acoustic telemetry and the evidence suggests that goldfish have the potential to move greater distances than we anticipated, which has implications for invasion into new areas.

CRediT authorship contribution statement

Christine M. Boston: Conceptualization. **Sarah M. Larocque:** . **Rex W.K. Tang:** Conceptualization. **Jill L. Brooks:** . **Jennifer A. Bowman:** . **Steven J. Cooke:** . **Jonathan D. Midwood:** Conceptualization.

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

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