



# Knowledge of Spawning Phenology may Enhance Selective Barrier Passage for Wetland Fishes

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## Abstract

Within the Laurentian Great Lakes, many native fishes use wetlands for spawning; however, these areas are also used by non-native common carp (*Cyprinus carpio*) that may impart negative ecological impacts. There is interest in managing common carp using physical barriers to decrease passage to specific habitats (e.g., their spawning sites), but these barriers could also exclude native wetland spawners such as largemouth bass (*Micropterus salmoides*) and northern pike (*Esox lucius*). Our objective was to determine if differences in spawning movements could be exploited in shallow areas to operate seasonal barriers that are opened and closed to promote selective fragmentation. Using a long-term dataset from the Cootes Paradise Marsh Fishway (Hamilton, Ontario), we generated predictive models for spawning movements based on cumulative growing degree day (CGDD) for all three fishes. These models successfully predicted earlier arrival by all species in a warmer year and delayed spawning movements during a cold year, highlighting the role of temperature as a driver of interannual variation in spawning movements. We then compared the Fishway model predictions to spawning movements within nearby Toronto Harbour, which were derived from acoustic telemetry data. We found that the model outputs were correlated with movements of all three species, but performance was weakest for northern pike. Resource managers could use these predictive models to assist in the operation of seasonal barriers to decrease access of common carp to spawning sites, while maximizing passage to native fishes.

**Keywords** Spatial ecology · Spawning migrations · Conservation · Aquatic invasive species · Invasive species management

## Introduction

Movements by fish are undertaken to fulfill fundamental life history requirements such as foraging, refugia, and spawning, which contribute to individual survival and ultimately population persistence (Lucas and Baras 2008). Many fishes exhibit seasonality in their spawning-related movements (Pankhurst and Porter 2003), for example large-scale migrations undertaken by Pacific salmonids to natal

grounds (Neave 1964), and limitations to these movements could negatively impact populations. Drivers of life history-related movements, including those associated with spawning, can be both internal (e.g., cues from individual growth and development phases) and external (e.g. environmental factors; Cooke et al. 2022). In the latter case, variation in environmental conditions can dictate the phenology or timing of such events. For example, photoperiod (i.e., day length) has been shown to be an important stimulus for fish migration including the initiation and synchronization of spawning movements (Bromage et al. 2001). Similarly, temperature (i.e., the master factor of fish physiology; Brett 1971) synchronizes reproduction in fishes (Fry 1971), acts as an ecological resource (i.e., similar to food; Magnuson et al. 1979), and can be indicative of optimal environmental conditions for the development of embryos (Van Der Kraak and Pankhurst 1997).

Within the Laurentian Great Lakes, coastal wetlands (i.e., those that are under substantial hydrologic influence from Great Lakes waters; McKee et al. 1992) provide important spawning habitat (e.g., littoral backwaters dominated

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by aquatic vegetation) for many wetland fish species (i.e., those fishes that require vegetation for spawning; Jude and Pappas 1992; Midwood and Chow-Fraser 2015; Trebitz and Hoffman 2015). Seasonal movements by some fish species within and among these coastal wetlands are undertaken to complete reproductive activities (Jude and Pappas 1992), but the timing of such movements can vary among species (Kronfeld-Schor and Dayan 2003). For example, northern pike (*Esox lucius*) initiate spawning in the early spring once water temperatures have warmed to 8 °C (Casselman 1995). Comparatively, largemouth bass (*Micropterus salmoides*) undertake spawning activities later, with spawning occurring in early summer when water temperatures are greater than 15 °C (Scott and Crossman 1973). While both of these native species often use coastal wetlands in freshwater systems, so do non-native species such as common carp (*Cyprinus carpio*; Jude and Pappas 1992; Piczak et al. 2023), which typically spawn in late spring or early summer when water temperatures exceed 17 °C (Panek 1987). The use of coastal wetlands by common carp for spawning and foraging can exacerbate the already deteriorated condition of many Great Lakes coastal wetlands, and common carp degradation is well documented in Lake Ontario (Lougheed et al. 1998; Chow-Fraser 2006). Common carp may stir up sediment or uproot aquatic vegetation, which can not only affect local water quality, but also reduce the suitability of the remaining habitat for other native fishes (Parkos et al. 2003). To alleviate the impacts associated with common carp, local management of common carp populations is common (Butler and Wahl 2010) and physical barriers can help limit access by common carp to coastal wetlands (Lougheed et al. 2004).

Physical barriers including gates, fishways, screens, traps, or other exclusion structures, are designed to decrease access of non-native species to specific areas (e.g., spawning sites) (Jones et al. 2021). Limiting access of non-native species to specific habitats with physical barriers can mitigate their harmful impacts on native ecosystems and fauna by limiting their spread (Rahel 2013), reducing recruitment, and ultimately decreasing abundance (Post van der Burg et al. 2021). However, one issue associated with physical barriers is the connectivity conundrum, which refers to the trade-off between improving passage for desirable species (e.g., native fishes), while reducing or eliminating access to invasive species (e.g., common carp; Zielinski et al. 2020). Due to the connectivity conundrum, there has been increased interest in using barriers that facilitate selective fragmentation, whereby certain species are permitted to pass, while access of destructive species is minimized. Selective fragmentation can be achieved by exploiting biological traits of the targeted non-native species (Rahel and McLaughlin 2018) including phenology, morphology (e.g., girth or total length), sensory capabilities (e.g., electric, auditory or visual), or

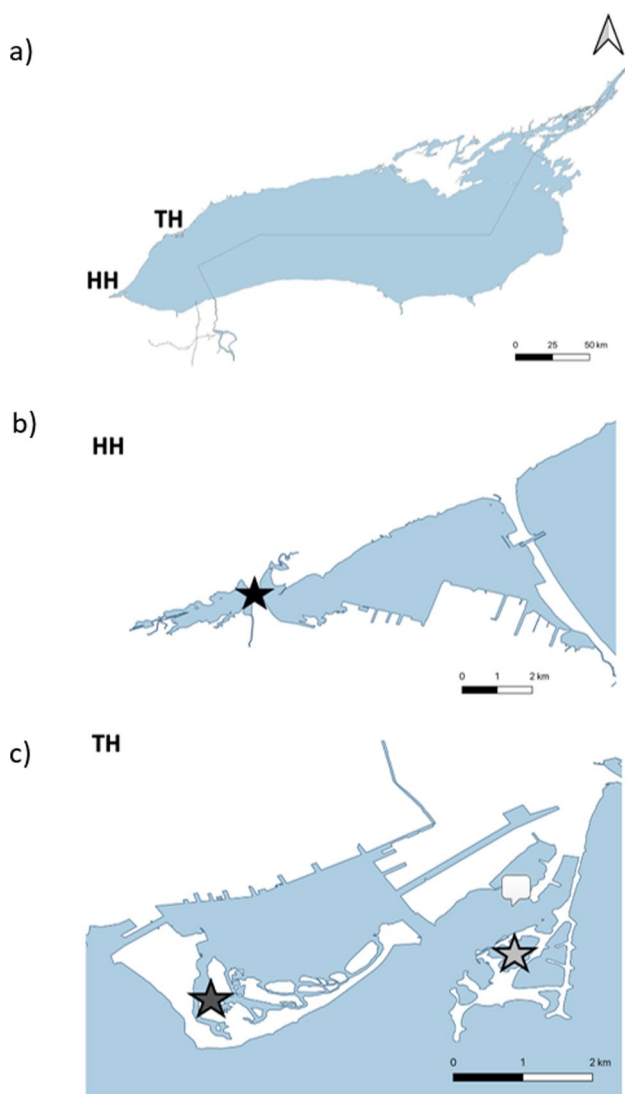
behaviour (e.g., pushing or jumping behaviours; reviewed in Piczak et al. 2022). Specifically, phenology is the timing of recurring biological events such as seasonal migration patterns (e.g., spring versus fall spawning for walleye, *Sander vitreus*, and salmonids, *Salmonidae* spp). Selective fragmentation based on phenologies is reliant on information regarding the timing of movements, including arrival and departure at a site as well as the duration spent therein for both native and targeted non-native species. Additionally, the inherent dynamics of the natural environment results in interannual variability in phenologies. So rather than basing barrier operation on calendar dates, barrier operation could be informed by quantitative models of fish movement and associated environmental variables such as temperature (e.g., Lubejko et al. 2017) that would allow for a more dynamic approach to barrier operation annually.

Our objectives were to develop predictive models for the arrival of common carp and two ecologically important native fishes (largemouth bass and northern pike) at a known wetland spawning area and then apply these models to another nearby system to explore transferability in Lake Ontario. First, we investigated differences in phenologies and peaks in timing of movements by comparing arrivals of native largemouth bass and northern pike versus common carp with a 23 year dataset from Cootes Paradise Marsh (CPM). We then generated models for the phenologies of each species with this dataset to determine which environmental drivers may be influencing these movements across years. Next, using a dataset derived from acoustic telemetry for the same three species, we compared the timing of movements to potential spawning habitat within a coastal wetland complex at Toronto Harbour (TH), Lake Ontario with the timing of movements as predicted from the CPM models. We intend for these models to help managers to adapt the timing of barrier operation to permit access for some native fishes while limiting access to common carp. Ultimately, this knowledge will allow us to explore the potential use of differences in phenologies among three wetland fishes to achieve selective fragmentation.

## Methods

### Study Sites

Lake Ontario has been impacted by anthropogenic activity for well over 200 years, particularly in the densely populated western portion, where both Hamilton and Toronto are located (43.285, -79.843, and 43.631, -79.369, respectively; Fig. 1a). Due to historic and ongoing anthropogenic disturbance (e.g., urbanization, agriculture, and industrial activities) and habitat impairment and loss, both systems



**Fig. 1** **a** Hamilton Harbour (HH) and Toronto Harbour (TH) are located in the western portion of Lake Ontario. **b** The Fishway (black star) is between Cootes Paradise Marsh (west) and Hamilton Harbour (east) and is designed to exclude common carp (*Cyprinus carpio*) from the marsh. **c** Toronto Islands (dark gray star) are a collection of sheltered embayments and Embayment C (light gray star) is located within Tommy Thompson Park of Toronto Harbour

were identified as Areas of Concern in 1987 and are the focus of considerable remediation efforts (Hartig et al. 2020). Efforts to remediate fish habitat have targeted physical habitat enhancement and habitat creation, with the goal of supporting the recovery of native freshwater fishes and other aquatic organisms (Boston et al. 2016; Barnes et al. 2020).

### Hamilton Harbour and the Fishway

Hamilton Harbour (HH), a 21-km<sup>2</sup> protected embayment, is located at the western end of Lake Ontario (Fig. 1b). The south shore of the Harbour is dominated by industry

(mostly steel or concrete walls), whereas the north and east portions are composed of mostly artificial hard and soft shorelines, with more natural shorelines to the west (Gardner Costa et al. 2020). Situated at the western end of the harbour, CPM is a large (250 ha) degraded coastal wetland. An exclusion barrier, the Fishway (operated by the Royal Botanical Gardens since 1997) designed to exclude common carp was built between the marsh and the main harbour in the Desjardins Canal. Water flow through the barrier is driven by both upstream watershed inputs through CPM and lake-harbour seiches. The goals of the structure were to both prevent access of common carp large enough to physically damage marsh habitat (i.e., uprooting of macrophytes), and to reduce recruitment by eliminating females over 3-years-old. The spacing of the vertical bars is 5.0 cm, which is intended to permit passage of native species; however, larger individuals of native fishes may not be able to pass through (French et al. 1999). The Fishway has cages, where all barrier-excluded fish that enter become entrapped and are then manually sorted; native species are released into the marsh and common carp and other non-native species (e.g., Goldfish, *Carassius auratus*) are returned to HH (Theysmeÿer 1999). The Fishway has been successful at decreasing common carp biomasses by up to 95% in CPM (Theysmeÿer 1999; Loughheed et al. 2004) and has also helped reduce their biomass and abundance in HH (Boston et al. 2016). Despite the success of the Fishway, concerns remain regarding decreased passage for larger native fish species. Further, operating trap-and-sort barriers, such as the Fishway, comes at a steep financial cost in terms of installation, on-going maintenance, and operation, which may reduce the feasibility of such devices in other systems. Given that fishes are actively moved into or excluded from the marsh, data collected at the Fishway supports an examination of the timing of fish migrations and associated movements (i.e., arrivals and departures from spawning habitat in CPM) to facilitate better timing of passive barrier management.

### Toronto Harbour and Passive Acoustic Telemetry Array

Toronto, with a population of over five million people, has experienced widespread loss of littoral and wetland habitat along its waterfront (over 400 ha; Whillans 1982) mainly owing to infilling to support urbanization and the expansion of industry (Barnes et al. 2020). To help recover some lost wetland habitat, remediation efforts have been ongoing at Tommy Thompson Park (TTP; Fig. 1c), a constructed peninsula consisting of four embayments (A through D) and a confined disposal facility (CDF) for sediment comprised of three cells (1 through 3; Barnes et al. 2020). Several sheltered areas at

TTP have undergone restoration with techniques including the addition of habitat structure (e.g., through rock shoals, log piles), as well as vegetation planting (Barnes et al. 2020), all designed to enhance their suitability for wetland and sheltered embayment fishes.

Exclusion barriers have also frequently been used at restored sites to limit access to vegetation by common carp (e.g., Embayment C within TTP; Barnes et al. 2020). In contrast, the Toronto Islands are a collection of sheltered areas that have remained relatively natural with aquatic vegetation throughout most of the shallow channels that intersect the islands providing extensive littoral fish habitat (Leisti et al. 2020). To assess the efficacy of restoration efforts throughout TH, an extensive passive acoustic telemetry array was deployed in the system starting in 2011 (Midwood et al. 2019). Key movement corridors, as well as various habitat types were strategically instrumented with VR2W 69 kHz acoustic receivers (Innovasea, Bedford, Nova Scotia). Although the total number of receivers within the TH array has grown since the initiation of the project, we used detections from two specific receiver groupings: Embayment C within TTP (for northern pike) and Toronto Islands 27 (TI 27; for largemouth bass and common carp; see Supplemental 1). The three receivers in Embayment C were deployed in 2010, with detections available from 2010 to 2020. The one receiver deployed at TI 27 was also deployed in 2010, with detections available from 2010 to 2020. Detections were downloaded approximately every six months, once in spring and fall. Previous range testing indicated a conservative estimate of 350 m (see Veilleux 2014).

## Field Methods

### CPM Fishway Operation

Passage of fishes at the Fishway has typically been initiated each year between late-March to early-April and continued until October. The Fishway was not operated during the winter months, at which time the barrier was lifted thus enabling the unimpeded passage to all species. During operation, the six cages are lifted once per week at the start of the season and then increased to twice daily during peak migration periods (typically occurring in April), and finally decreased to once per week in late September. Undesirable species (e.g., common carp and goldfish) are released back into HH, while native species are released into CPM. Prior to release, a subset of entrapped fish are measured (i.e., fork length in mm, mass in g) and sex noted when possible. Data from the Fishway were available from 1997 to 2020.

## Fish Capture and Tagging

Largemouth bass ( $n = 126$ ), northern pike ( $n = 118$ ) and common carp ( $n = 80$ ) were captured from TH using boat electrofishing (SR-18EH, 7.0 A, 340 V; Smith-Root Inc., Vancouver, WA) and then tagged (Vemco V13P-1x-069 k-1-0034 m, 46 mm length, 13 mm diameter, dry mass 11 g, battery life 1386 days; Table 1). After capture, fish were placed in live wells with ambient lake water and either transported to shore for surgery or surgery was conducted on the vessel. Most fish were immobilized for surgery using a Portable Electroanesthesia System (Smith-Root, Vancouver, WA), but some were anesthetized using clove oil emulsified in ethanol (Sigma Aldrich, Montreal, QC; Rous et al. 2015). Next, fish were placed in a trough with ambient lake water passed over the gills to aid respiration. All surgical tools and acoustic transmitters were disinfected with a povidone-iodine (CVS, Detroit, MI) diluted (at ~50,000 ppm) in water and then subsequently rinsed with tap water. Fish size (total length; to the nearest mm) was measured and then weighed to ensure tag burden was less than 2% (Jepsen et al. 2005). An incision (~20 mm) was made with a scalpel and the transmitter was inserted into the body cavity. Incisions were closed with two or three interrupted sutures. Fish were returned to a live well with circulating lake water for recovery. Fish were released at their point of capture after ensuring full recovery (usually within 15 min of completing surgery). Fish handling and surgical procedures were approved and followed a Canadian Council on Animal Care protocol administered by Carleton University (Certificate CU 110723).

## Data Preparation and Statistical Analyses

### Fishway Movements

All data preparation and analyses were completed in R Statistical Environment (version 4.3.0; R Core Team 2023). To examine environmental drivers of fish captures at the

**Table 1** Number of sexually mature individuals per species with acoustic tags in Toronto Harbour at each study site during years where  $n < 10$

Year	Largemouth Bass	Northern Pike	Common Carp
2011	14	NA	NA
2012	10	22	14
2013	NA	20	NA
2017	NA	NA	11
<b>Total</b>	24	42	25

Largemouth bass and common carp were from the Toronto Islands (TI 27), and northern pike were from Embayment C within Tommy Thompson Park

Fishway, we first calculated the total number of individual fish per species per sample year. From there, we only included sample years where more than 10 individual fish per species were captured: specifically, for largemouth bass ( $n = 19$  sample years), for northern pike ( $n = 21$ ), and for common carp ( $n = 23$ ). We then standardized the dataset in terms of effort: since the cage lifts varied (i.e., not uniform lift days) within each season (i.e., starting at once per day in March, to twice daily in June). We calculated a rate of capture per day per species (i.e., total number of individual fish captured per day for each species) with the following equation:

$$NOD_i = \frac{n_i}{(lift\ day_i - lift\ day_j)}$$

where the rate representing the average number of fish captured over days (NOD),  $n_i$  is the number of fish captured on day  $i$ , and  $(lift\ day_i - lift\ day_j)$  is the difference in days between date  $i$  and the last lift day  $j$ . For example, if 20 common carp were captured on day  $i$  on May 22<sup>nd</sup> and the last lift day was May 20<sup>th</sup>, then  $NOD = 20 / (May\ 22 - May\ 20) = 20 / 2 = 10$  for each day. Assumptions regarding the calculation of NOD include uniform capture rates per day across lift dates, which could under- or overestimate some daily rates of capture when there are longer periods between lifts (i.e., early spring and late fall). After this calculation, we converted the daily counts to a cumulative proportion of the total run for each species within a year (e.g., if on May 22, 50 carp had moved into CPM out of 200 over the full year, then the cumulative proportion of the total run for that date would be 25%). The cumulative proportion of total run was used as an indicator of inbound movement from HH to CPM through the Fishway.

We then paired environmental variables with the Fishway cumulative proportion of total run dataset. As water temperature data were not available for the entire study duration (i.e., 23 years), we used air temperature data derived from a weather station nearby (Hamilton Airport; 43.171, -79.932), which covered the entire study period. Given that fish are ectotherms, their growth (Neuheimer and Taggart 2007) and reproductive activities including spawning movements are regulated by environmental drivers including temperature (Pankhurst and Porter 2003). Specifically, we calculated cumulative growing degree days (CGDD), which provides an estimation of mean heat accumulation over time (Kocovsky et al. 2012). Using the air temperature data, we calculated CGDD for each sample year using the averaging method:

$$GDD_i = T_{mean\ i} - T_{base} \quad CGDD_i = \sum_{i=1}^n T_i$$

where growing degree day (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. For days when the air temperature was negative, a value of zero was assumed. The result was a value of CGDD for each calendar day per sample year. We included Julian day (JD) in analyses, and calculated photoperiod (Pankhurst and Porter 2003; using the package *geosphere* *day\_length* function; Hijmans et al. 2021) and moon phase (using package *lunar*; Lazaridis 2022).

## Modelling & Model Predictions

The fixed effects including JD (continuous), photoperiod (categorical), CGDD (continuous), moon phase (categorical), and the interaction term CGDD \* photoperiod on the cumulative proportion of total run (response variable bound between 0 and 1) for each species (largemouth bass, northern pike, and common carp) were tested using a generalized linear mixed model (GLMM; package *glmmTMB*; Brooks et al. 2017) with a beta distribution (with a logit link function). We included year as a random effect to account for repeated measures. We tested for collinearity across variables by calculating the variance inflation factor (VIF; package *performance*; Lüdtke et al. 2021). We only included variables that were not collinear in further analyses. We determined that photoperiod, JD, and moon phase were each highly correlated with CGDD (VIF of 175.62, 41.62 and 81.35, respectively) and therefore these three terms were subsequently dropped from further analyses. Diagnostics for the GLMMs were performed for validation and included plotting the residuals (with a Q-Q plot for normality), residuals versus explanatory variables (for independence), and the residuals against fitted values (to verify homogeneity) to visually inspect model fit (Zuur et al. 2009). For all statistical modelling, a significant level of 0.05 was accepted.

Once the models for each species were finalized, we predicted the cumulative daily proportion of total run at the Fishway for two scenarios. First, we took an average of CGDD per JD across all years of available data for the Fishway to determine the average peak (assessed from here on as 50% of the cumulative daily proportion of total run) for each species. Second, to investigate the ability of the models to account for interannual differences in temperatures, we identified a cold and warm year, 2018 and 1998, respectively, and used the associated CGDDs to predict the cumulative daily proportion of total run for each day in each year.

## Acoustic Telemetry Movements

Erroneous detections were removed if they met criteria for false-positive detections (single occurrences with > 3600 s between successive detections; Pincock 2012). The dataset was also filtered to remove fish that died, or possibly expelled their transmitters, which was presumed to have occurred when consistent depth profiles and locations were recorded for an extended period (Klinard and Matley 2020). Individual fish that were not of spawning age for that species were not included in further analyses: largemouth bass (TL < 300 mm; Scott and Crossman 1973; Schramm and Willis 2012), northern pike (TL < 350 mm; Priegel and Krohn 1975), and common carp (TL < 300 mm; Lougheed et al. 1998). To examine movements into spawning areas, we identified potential spawning sites for each species based on previous telemetry studies (see Midwood et al. 2019): TI 27 for largemouth bass and common carp and Embayment C for northern pike (see Fig. 1c). Additionally, throughout TH there are highly variable water temperatures owing to upwellings from Lake Ontario; however, these sites were chosen because they were generally warm, with relatively constant temperatures (Hlevca et al. 2018). We selected years where there was a sample size greater than ten individuals within spring and summer): for largemouth bass  $n = 14$  for 2011 and  $n = 10$  for 2012, for northern pike  $n = 22$  for 2012 and  $n = 20$  for 2013, and for common carp  $n = 11$  for 2012 and  $n = 14$  for 2017 (Table 1). We then calculated the cumulative proportion of individuals accessing each spawning site each day based on an individual's first detection at the site and divided by the total number of individuals detected at the site within the first 200 JDs of each year. For example, by May 22 a total of 2 different individuals had accessed Embayment C out of a total of 14 throughout the first 200 JDs of that year, then the cumulative proportion of individuals would be 0.14.

## Model Predictions

We used the GLMM derived from the CPM Fishway data for each species to predict the cumulative daily proportion of total run within TH. Next, CGDD for TH was calculated using the same methods as previously described but using air temperature data from Billy Bishop Airport in TH (43.626, -79.393). We then predicted the cumulative daily proportion of total run in the spawning areas for each species: largemouth bass (2011 and 2012), northern pike (2012 and 2013), and common carp (2012 and 2017). We assessed the transferability of our models to another system by comparing the model predictions (with CGDD data from Billy Bishop Airport) and the movements derived from acoustic telemetry data. Further, we performed non-parametric Kendall's Tau correlation tests on each available year for each species.

## Results

### Fishway Movements & Model Predictions within Hamilton Harbour

For all three species, CGDD had a significant impact on the cumulative daily proportion of the total run at the Fishway ( $p = 0.0001$ ; Table 2), with the final model equations including CGDD with year as a random effect for all three species. Using the average CGDD per JD across all sample years, the models predicted the average peak (i.e., 50% of individuals) of the cumulative daily proportion of total run for each species as JD 148 for largemouth bass, 107 for northern pike, and 149 for common carp (Fig. 2; see Supplemental 2 for data on all sample years for each species). Therefore on average, the peak run was earliest for northern pike by more than 40 days, with considerable overlap across largemouth bass and common carp. The curve for northern pike initiated higher than the other two species, reinforcing the earlier arrival time of this species (Fig. 2). Further, there was considerable overlap between the largemouth bass and common carp movement curves.

Using the GLMMs and CGDD values calculated for both a cold (2018) and warm (1998) year in HH (2018 and 1998, respectively; see Supplemental 3), we predicted the arrivals of each species. There was clear separation in their slopes and the JD of peak runs (Fig. 3) with later predicted peak runs in the cold year and earlier peak runs in the warm year. Relative to the cold year, in the warm year, peak runs were predicted to occur 13 days earlier for largemouth bass (JD 148 vs 135), 33 days earlier for northern pike (JD 122 vs 89), and 13 days earlier for common carp (JD 154 vs 141).

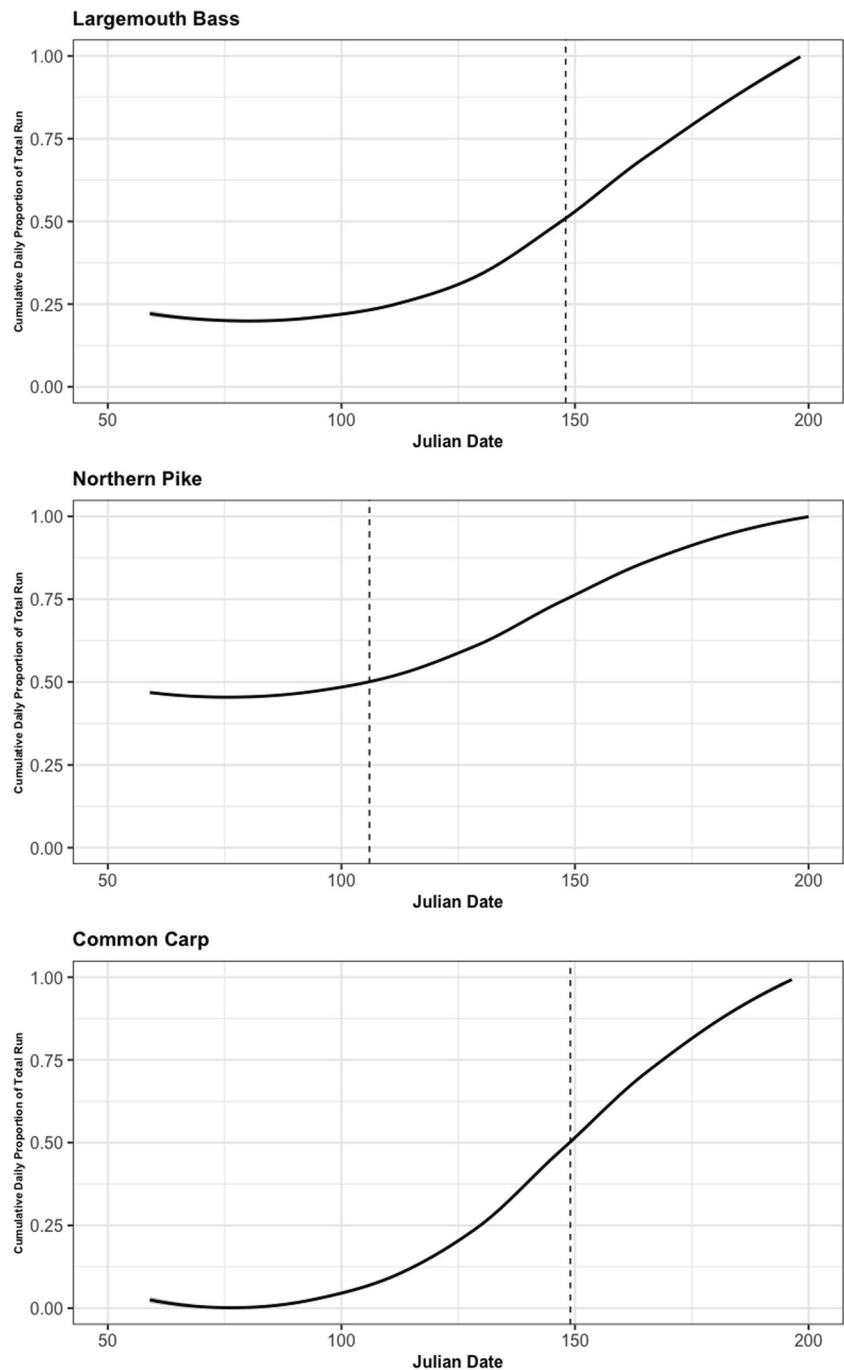
### Acoustic Telemetry & Model Predictions within Toronto Harbour

With CGDD calculated from Billy Bishop airport for each sample year of acoustic telemetry data, we used the models derived from the Fishway to explore their transferability to other similar systems such as coastal wetlands within Lake Ontario (Fig. 4). We found that the models performed generally well for all three species, with the best performance for largemouth bass and common carp and weakest performance from northern pike. Specifically, the cumulative daily proportion of total run for

**Table 2** The effect of cumulative growing degree day on the cumulative daily proportion of total run for each species, with year included as a random effect

Species	Model Terms	Chi Square	df	P value
Largemouth Bass	CGDD + 1 Year	1871.1	1	< 0.0001
Northern Pike	CGDD + 1 Year	2190.2	1	< 0.0001
Common Carp	CGDD + 1 Year	14320.0	1	< 0.0001

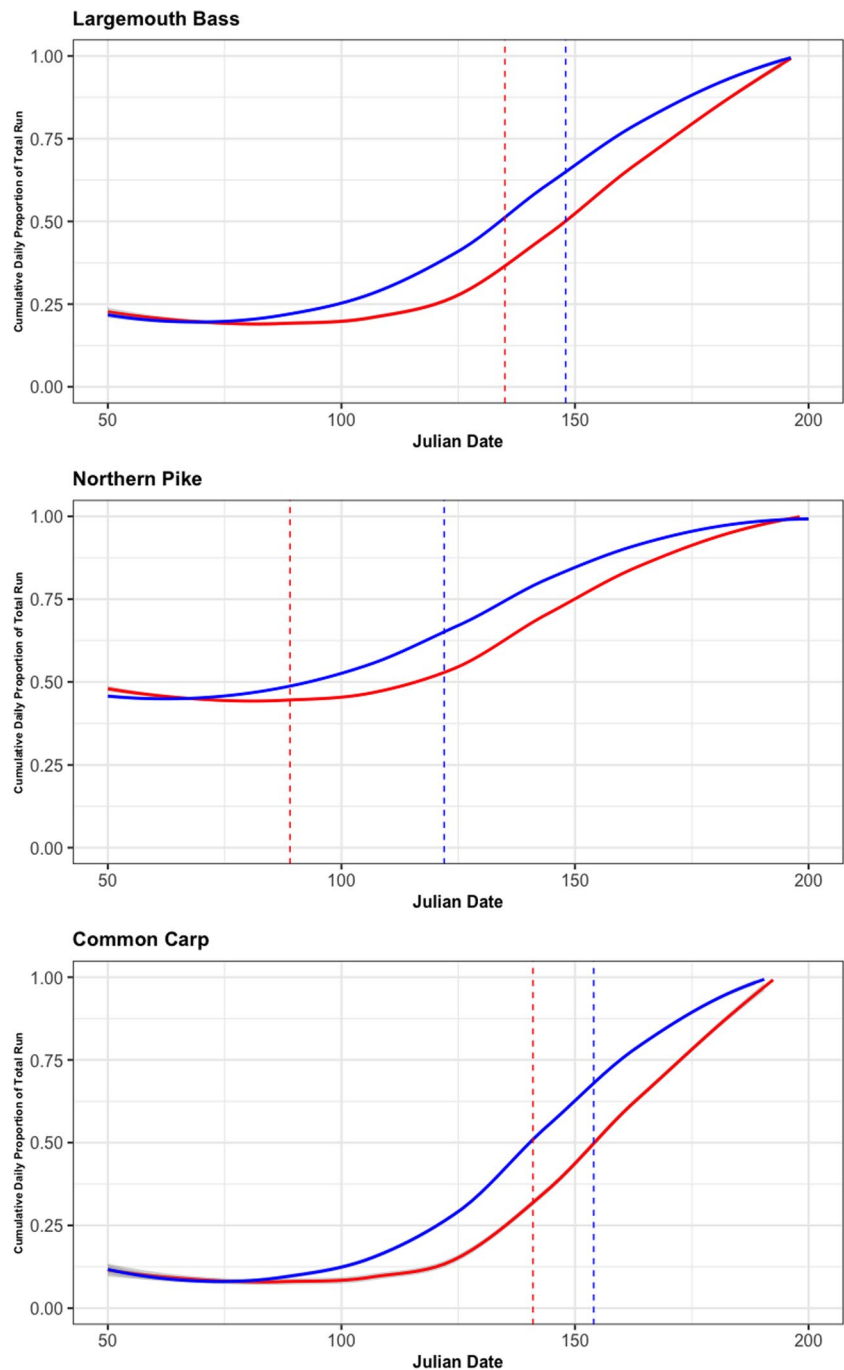
**Fig. 2** Cumulative daily proportion of total run for each species at the Fishway as predicted by the average of all cumulative growing degree days per Julian date from 1997–2020. The peak of the runs (50%; dashed lines) was at JD **a**) 148 for largemouth bass, **b**) 107 for northern pike, **c**) and 149 for common carp (see Supplemental 2 for all sample years for each species)



each species in TH as predicted by the CGDD models and the cumulative daily proportion of total run for each species in TH derived from acoustic telemetry data were correlated for each species and each sample year, with northern pike having the lowest Kendall's Tau value (Table 3). Further, the acoustic telemetry data for largemouth bass at the Toronto Islands for 2011 and 2012, showed similar slopes to the predictions from the Fishway in HH (Fig. 4). Northern pike had the largest separation in curves across all species and all sample years,

specifically for 2012 (Fig. 4; see Supplemental 4 for the temperature data for each acoustic telemetry sample year). Relative to 2012, the predictive model for northern pike performed better for 2013, as depicted by the similarities in curves. Both years of data derived from acoustic telemetry performed well for the model predictions for common carp (Fig. 3). Differences in the curves across years within species demonstrate the ability of the predictive models to detect interannual differences in TH (Fig. 4).

**Fig. 3** Cumulative daily proportion of total run for each species at the Fishway as predicted by a cold (blue; 2018) and warm (red; 1998) years. The vertical lines represent the peaks of the cumulative daily proportion of total run for the cold and warm years, respectively: largemouth bass 148 and 135, northern pike 122 and 89, and common carp 154 and 141



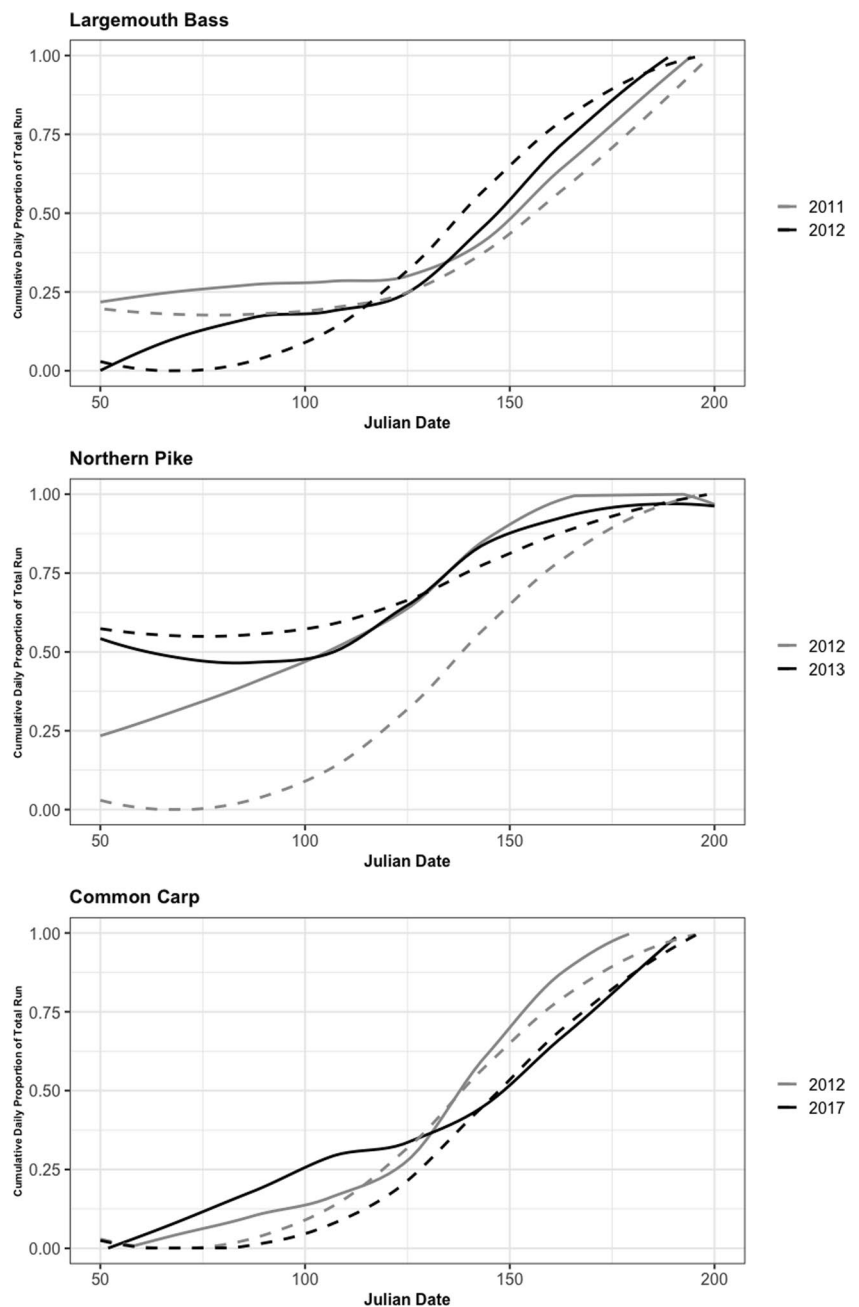
## Discussion

The purpose of this study was to generate predictive models of spawning movements for largemouth bass, northern pike, and common carp to aid in the operation of seasonal barriers aimed at controlling common carp. We found that CGDD was a significant predictor of the cumulative daily proportion of total run for each species at the CPM Fishway. Not surprisingly (based on previous natural history observations; Scott and Crossman 1973),

models suggested that northern pike undertook movements towards spawning sites earlier than largemouth bass and common carp. The predictive models were able to track interannual differences in temperatures in that earlier and later peaks corresponded with a warm and cold year, respectively, for all three species. We explored the applicability of the models to another similar system (i.e., coastal wetlands within TH) based on agreement between model prediction and observed acoustic telemetry patterns. Predictions using TH-specific CGDD data corresponded



**Fig. 4** The solid line represents the cumulative daily proportion of total run derived from acoustic telemetry data in Toronto Harbour at the Toronto Islands for largemouth bass and common carp, and Embayment C for northern pike. The dashed lines represent the Fishway model predictions derived with the cumulative growing degree day as calculated from Toronto Harbour



well to the acoustic telemetry movements for common carp and largemouth bass, but there was greater separation between model predictions and acoustic telemetry-based movements for northern pike. Here we discuss the implications of the phenologies for each species in terms of seasonal barrier operation, the ability of the models to capture interannual differences in temperatures, the suitability of the model for application outside of HH, and potential limitations and avenues for future research.

In both HH and TH there was overlap in timing of movements between largemouth bass and non-native common carp, while northern pike arrived at spawning sites substantially

earlier. These results are consistent with previous findings related to thermal preferences and spawning ecologies, whereby largemouth bass spawn after temperatures reach 15 °C (Scott and Crossman 1973), northern pike 8 °C (Casselman 1995), and common carp 17 °C (Panek 1987). Taken together, these results suggest that operating seasonal barriers according to phenology and temperatures would benefit northern pike more than largemouth bass. Specifically, seasonal barriers could be left open until real-time CGDD data (based off local air temperatures) applied to the common carp model indicates that they are likely to start their spawning movements. This would permit unobstructed passage to northern pike, with

**Table 3** The cumulative daily proportion of total run for each species in Toronto Harbour as predicted by the cumulative growing degree day models and the cumulative daily proportion of total run for each species in Toronto Harbour derived from acoustic telemetry data was tested with a Kendall's Tau correlation to assess model agreement for each sample year and each species

Species	Year	Number of Tagged Fish	Kendall's Tau Correlation
Largemouth Bass	2011	14	0.85
	2012	10	0.88
Northern Pike	2012	22	0.92
	2013	20	0.80
Common Carp	2012	11	0.89
	2017	14	0.88

subsequent closure of the barriers, therefore preventing access to the majority of common carp. Relative to largemouth bass, northern pike require such unimpeded access to spawning areas since they are likely to be more limited by the spacing of bars on barriers given their larger width (see French et al. 1999). Adjusting the timing of barrier use based on seasonal phenology could thus benefit northern pike.

Derived from a long-term dataset, the species-specific predictive models we developed were able to account for interannual differences in temperatures in HH. Specifically, we found that northern pike had the largest temporal separation in peak movements across cold and warm years (more than 30 days), while largemouth bass and common carp had smaller differences (~13 days). These findings have direct management implications in regards to the operation of seasonal barriers to control common carp, while minimizing impacts on native species (Piczak et al. 2022). By incorporating annual air temperature values using CGDD into barrier operation, barriers can be left open longer during cold years to allow early spawning species like northern pike more access with the final closure date dictated by the predicted timing of arrival of common carp. Managers can further use the model predictions to adjust opening and closing dates based on their tolerance to risking entry for common carp (e.g., see Vélez-Espino et al. 2011). Ultimately, the goal would be to operate the seasonal barriers in a way that permits unimpeded access to native species for as long as possible (Zielinski et al. 2020), before common carp undertake their later spawning movements and CGDD-based models support such a dynamic management approach.

We also explored the applicability of our models to other systems with the use of acoustic telemetry data with fish tagged in TH. Specifically, we compared the model predictions based on TH-specific CGDD data predictions with acoustic telemetry data from previously identified spawning sites within TH (see Midwood et al. 2019). We

found that the model predictions and telemetry data aligned well, suggesting that the predictive models were able to determine arrival for all three species in another system. Further, the curves generally tracked interannual differences for all three species, which could contribute to more effective operation of seasonal barriers. There was greatest separation between model predictions and observations from acoustic telemetry for northern pike. While such a discrepancy may reflect inherent differences in northern pike populations between HH and TH, a more likely explanation relates to differences in when and why northern pike use CPM versus Embayment C in TH. Cootes Paradise Marsh is fairly shallow (<2 m; Chow-Fraser 2006) and thus may not have sufficient depths to support overwintering of northern pike, which have been found to overwinter at depths greater than 2 m (Midwood et al. 2019; Larocque et al. 2020). In contrast, the middle basin of Embayment C is deeper (6–7 m) and thus provides suitable overwintering habitat for northern pike (Barnes et al. 2020). An additional complication could stem from our ability to position northern pike in Embayment C relative to where their potential spawning habitat is situated. Acoustic telemetry receivers in this system cannot provide fine-scale information on where a fish is located, so we cannot determine when a northern pike has moved from open waters to a shallower, vegetated spawning area. Such a movement could also result in decreased detectability if the shape of the shoreline, bathymetry, or presence of vegetation impedes the line of sight between the transmitter and receiver (Kessel et al. 2014). Taken together, these factors may limit the utility of Embayment C as a site to fully validate the predictive model for northern pike. Despite the relatively weak performance of our predictive models for northern pike (for 2012 in particular), the models were still able to determine the arrival for largemouth bass and common carp. Finally, it should be noted that the implantation of acoustic transmitters and stress associated with surgery can impact natural behaviour of fishes (Cooke et al. 2013). To mitigate these potentially adverse impacts, we minimized tag burden and surgery time (Cooke et al. 2013). Taken together, these results suggest that our predictive models can be transferred to other systems, indicating their use in the operation of seasonal barrier.

Our findings represent an important step towards operating seasonal barriers in a way that minimizes negative impacts on native species, while decreasing access to coastal wetlands for non-native common carp. Here we generated predictive models for only two native fish species; however, numerous other species, larger bodied fishes in particular, may also need access to key habitat restricted by barriers. Future studies should investigate and generate similar models for other native fishes that use wetlands for spawning. It is also possible that the movements of other aquatic fauna, such as turtles could be disrupted (Conallin et al. 2016),

so the timing and manner of movements for these fauna should also be documented and incorporated into a holistic barrier management plan. While we focused primarily on CGDD as it demonstrates interannual variation, there are other environmental drivers that influence the timing and duration of movements to spawning sites. Such factors could include discharge (e.g., spring flooding), turbidity, water quality (e.g., oxygen levels), and interactions between all drivers (Lucas and Baras 2008). The inclusion of additional environmental factors into predictive models would likely help increase accuracy, but may also pose challenges in terms of broader applicability since not all systems will have access to these types of data. Finally, the approach taken here was specifically focused on control of common carp and native fishes during the spawning period, but these methods could be applied to other systems (i.e., to additional coastal wetlands within the Great Lakes), predictable life history events, and other non-native fish species to help improve the efficacy of seasonal barriers.

## Synthesis

Using a long-term dataset, we generated predictive models with air temperature for largemouth bass, northern pike, and common carp to examine differences in phenology which could help optimize the operation of seasonal barriers aimed at controlling common carp in coastal wetlands. Unsurprisingly, we found that there was considerable temporal overlap between largemouth bass and common carp, while northern pike accessed coastal wetlands much earlier. Our models were able to capture differences in interannual variability in temperatures, whereby all three species arrived earlier in a warmer year, and later in a colder year. We also tested the transferability of the models to other systems using acoustic telemetry data from nearby Toronto Harbour and determined that the models performed well for all three species, with the weakest performance for northern pike model weakest. While there are few examples of physical barriers being managed based on differences in phenology (Piczak et al. 2022), current operations (i.e., opening and closing) could likely be optimized by using real-time temperature data. For all three of our study species, CGDD was found to predict movements to spawning habitat and capture interannual variability. CGDD is ideally calculated with water temperatures located at the site as these are the conditions that the fish are experiencing; however, here air temperature was still a significant predictor (e.g., using data from weather stations or airports) and is likely readily available for most systems. Further, CGDD calculations could be done in real-time, which would allow for dynamic operation of a barrier based on the in-year conditions. The application of the approach taken here would be most effective in areas

where the habitat use of fishes has already been studied. Specifically, the approach would be most effective for sites that are used more exclusively for spawning as opposed to sites that are used continuously throughout the year for multiple life history functions (e.g., foraging or overwintering). Broadly, we recommend operating physical barriers based on real-time temperature data to control common carp, while minimizing obstruction to native species like northern pike. Ineffective operation of seasonal barriers could unnecessarily limit native fishes from gaining access to spawning habitat or provide free access to common carp, therefore not achieving the intended management goal. It is our hope that these predictive models based on temperature could be used by environmental managers to optimize the operation of seasonal barriers aimed at decreasing access to coastal wetlands by common carp. Due to the nature of this connectivity conundrum (Zielinski et al. 2020), there will always be tradeoffs in terms of controlling non-native species, while decreasing negative effects on native species, but these models would allow managers to adapt their use of barriers based on their tolerance of risk from common carp. This study is among a growing number (reviewed in Cooke et al. 2023) that demonstrate how knowledge of fish behaviour can be exploited to benefit management and conservation.

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**Author Contributions** All authors contributed to the study concept and design. Data collection was led by Tys Theÿsmeÿer, Susan Doka and Jon Midwood, with analysis completed by Morgan Piczak with supervision from Steven Cooke. The first draft of the manuscript was written by Morgan Piczak, with all authors providing feedback. All authors read and approved the final manuscript.

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**Data Availability** The datasets generated during this study are available from the corresponding author upon reasonable request. Telemetry data are available through GLATOS.

## Declarations

**Ethics Approval** Not applicable.

**Consent to Participate** Not applicable.

**Competing Interests** The authors have no competing interests to disclose.

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