Canadian Journal of
Fisheries and
Aquatic Sciences

Research Article

Evaluation of post-stocking survival and movement of hatchery-reared juvenile bloater (*Coregonus hoyi*) stocked across bathymetric depths in Lake Ontario

Lydia L. Paulic[a], **Silviya V. Ivanova**[a], **Kyle Morton**[b], **R. Josephine Johnson**[b], **Dimitry Gorsky**[b], **Collin Farrell**[b], **John Sweka**[c], **Timothy B. Johnson**[d], **and Aaron T. Fisk**[a]

[a]School of the Environment, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada; [b]Lower Great Lakes Fish and Wildlife Conservation Office, US Fish and Wildlife Service, 1101 Casey Road, Basom, NY 14013, USA; [c]Northeast Fishery Center, U.S. Fish and Wildlife Service, Post Office Box 75, Lamar, PA 16848, USA; [d]Ontario Ministry of Natural Resources, 41 Hatchery Lane, Picton, ON K0K 2T0, Canada

Corresponding author: **Lydia L. Paulic** (email: paulic@uwindsor.ca)

Abstract

Bloater (*Coregonus hoyi*), extirpated from Lake Ontario in the 1980s, have been stocked annually since 2012 with limited success in re-establishing a self-sustaining population. In this study, hatchery-raised juvenile bloater were tagged with acoustic telemetry high-resolution predation tags and stocked over three depths in Lake Ontario (5, 50, and 100 m) in 2022 and 2023 to quantify survival, causes of mortality, and movement. Time-to-event modelling generated a 3-week survival estimate of 38% (31%–46%; 95% confidence interval) across both years, with lower survival in year 1 (12%; 12%–38%) than year 2 (44%; 33%–59%). The deepest depth (100 m) yielded the highest survival, with mortality due to predation more common at shallower depths, while non-predation mortality, potentially from compression barotrauma, was more prevalent in deeper water. Rapid dispersion following release was observed in both years, with greater distances travelled in 2023. This study revealed low initial survival for stocked bloater that varied between years and stocking depth and highlighted different potential sources of mortality associated with depth, while providing new information for consideration of stocking techniques in large lakes.

Key words: bloater, survival, movement, acoustic telemetry

Introduction

Fish stocking, the addition of hatchery fish to an ecosystem, is a global practice to supplement declining or low natural populations, introduce non-native species for recreation or management, or for re-establishing extirpated species (Pace et al. 1999). In the Laurentian Great Lakes (hereafter Great Lakes), fish stocking practices have been ongoing since the 1800s. Presently, over 20 million fishes are released annually into the Great Lakes basin to supplement valuable commercial and recreational fisheries and to mitigate ongoing ecological changes (Zimmerman and Krueger 2009). Despite this long history of fish stocking, the fate of fish post-release is poorly quantified due to difficulty monitoring them until they survive to an age and size catchable by survey gear, limiting the amount of data from the high-mortality period immediately after release (Brown and Day 2002). Mark–recapture, hydroacoustic surveys, and netting data are common methods that provide initial information on survival and movement but lack the fine scale tracking, behaviour, and post-release fate of fishes, particularly for smaller bodied species preyed upon by larger piscivores.

Acoustic telemetry is a technology well suited to inform immediate post-release mortality and behaviour of small fishes. Small transmitters can be surgically implanted into small hatchery-reared fishes such as bloaters (*Coregonus hoyi*) with negligible effects on survival and behaviour (Klinard et al. 2018; Gatch et al. 2022). Specialized acoustic transmitters can identify habitat use (e.g., depth, temperature), behaviour (e.g., accelerometers), and quantify and differentiate sources of mortality (Klinard and Matley 2020*a*; Villegas-Rios et al. 2020). High residence (HR) receivers have made it possible to release large numbers of acoustically tagged fish in a small area while maintaining maximal detection efficiency and avoiding collisions that can occur with non-HR transmitters. HR acoustic receivers operate at 180 kHz (or 307 kHz) and decode both traditional pulse position modulation (PPM) and HR transmission coding systems. Traditional PPM transmissions require 3–5 s to transmit, followed by a 30 s to 3 min signal delay. HR transmissions require only a few milliseconds to transmit, greatly reducing potential signal collisions while allowing more tags to be released into a study system. Identifying predation of tagged individuals, particularly those vulnerable to predation such as small fish, is key for properly interpreting acoustic telemetry data. Predation tags contain a biopolymer that dissolves in the stomach of a predator resulting in a change in transmission ID that can be subsequently decoded by receivers (Halfyard et al. 2017). Coupling tags with predation sensors with HR-180 kHz high residence systems permits fine-scale auto-estimation of predation-related mortality, in turn improving survival estimates of stocked fish, specifically small juveniles. Acoustic telemetry networks (e.g., Great Lakes Acoustic Telemetry Observation System, GLATOS) have greatly increased collaboration, making it feasible to study movements and interactions of fish and the influence of the environment at fine and coarse spatial scales across the Great Lakes (Krueger et al. 2018). For example, smaller acoustic telemetry tags and systems (V5D tags; 180 kHz) are used to determine sources of mortality and quantify behaviour post-release to inform the restoration potential and assist in broad-scale fishery management decisions regarding stocking of coregonines in the Great Lakes (Bunnell et al. 2024).

Bloater, a small bodied coregonid native to the Great Lakes, is an important prey species that once supported commercial fisheries in Lake Ontario. Their extirpation resulted in a disruption of the natural trophic interactions and energy flow within the lake's food web (Christie 1973). Today, non-native alewife (*Alosa pseudoharengus*) are the dominant prey species of piscivores in Lake Ontario (Mumby et al. 2018). A re-established population of bloater would provide native top predators (e.g., lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*)) a prey fish alternative, especially given alewife have high thiaminase activity, a thiamine-degrading enzyme linked to reproduction deficiencies in salmonines (Futia et al. 2019). To address the loss of bloater, Ontario (Ontario Ministry of Natural Resources) and American (U.S. Fish and Wildlife Service (USFWS), U.S. Geological Survey, and New York Department of Environmental Conservation (NYSDEC)) natural resource agencies have partnered to restore self-sustaining populations of bloater through stocking of juveniles, with a goal of increasing prey fish diversity for the benefit of native predator populations and offering greater resilience to the negative impacts of invasive species and a changing climate (Stewart et al. 2017; Weidel et al. 2021).

The initial release of hatchery-raised fish into the wild is a well-known period of vulnerability, with high mortality, particularly predation, occurring in the first days after release (Brown and Day 2002). Offshore stocking practices are believed to increase survival of stocked fish given the lower density of predators (Lantry et al. 2011); however, in Lake Ontario, recent acoustic telemetry studies showed that 61% of juvenile bloater (size range 50–409 g), across four independent stocking events, died within the first 14 days after an offshore release over 50 m, and 81% of the mortalities were associated with predation (Klinard et al. 2020*b*, 2021). Many bloater were also observed to swim quickly to the bottom with limited subsequent movement, suggesting a maladaptation to the environment they are released into (Klinard et al. 2020*b*). Subsequent experiments with hatchery-raised bloater using a hyperbaric apparatus showed significant negative impacts of compression barotrauma on bloater behaviour at 0.5 atm (5 m depth) and >20% mortality at 5 atm (50 m depth) (O. Gorman, U.S. Geological Survey, unpublished data). Stocking prey fish over deeper waters (i.e., 50 m) highlighted multiple sources of mortality at play in the initial period following release; thus, the presumed advantages of deep offshore release of stocked prey fish to minimize predation may be less effective than thought.

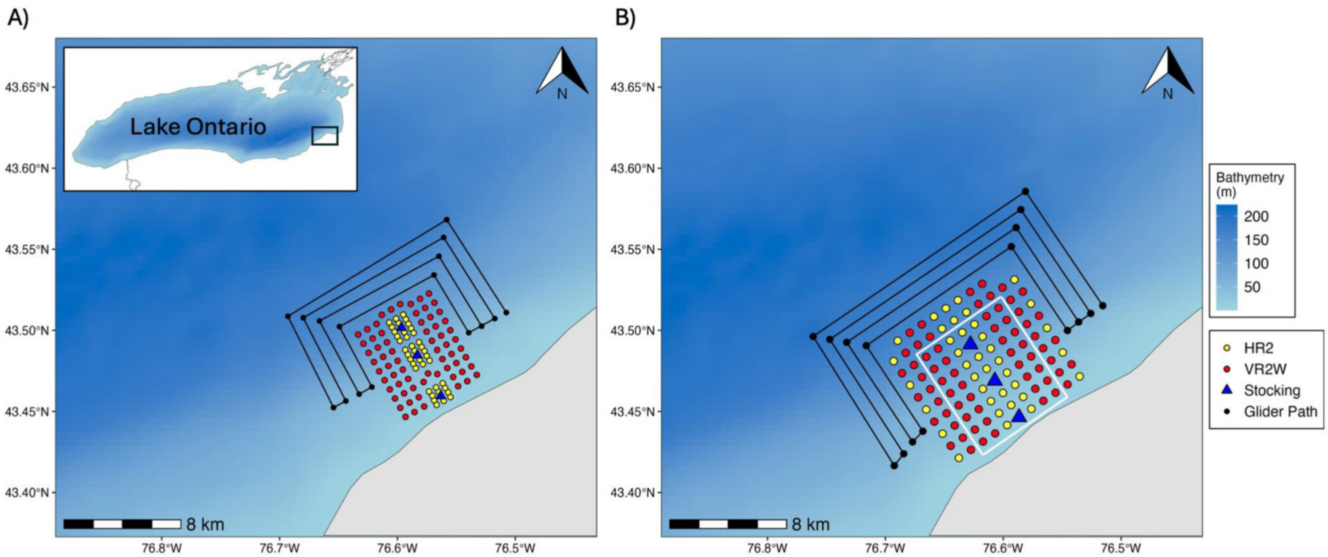
There is a need to better understand and quantify the sources of mortality in stocked juvenile bloater in the Great Lakes, specifically in the initial phase following release and across different depths. To address this, hatchery-reared juvenile bloater (relevant stocking-sizes of ∼11–30 g) tagged with high-resolution acoustic predation tags were released over three bathymetric depths (5, 50, and 100 m) in Lake Ontario to quantify survival, assess sources of mortality associated with depth of release, and movement. It was hypothesized that the shallow depth (5 m) would minimize barotrauma while maximizing predation (cf Lantry et al. 2011), the middle depth (50 m) reflected the approximate release depth of stocked bloater with a mix of predation and barotrauma, while the deepest depth (100 m) would minimize predation and maximize barotrauma. Bloater movement was also assessed to provide insights into habitat depth selection. The presence of acoustic tagged fish predators, of which there is a significant number in Lake Ontario through other projects, within the array following stocking was also evaluated with 69 kHz receivers. By addressing stocking depths and predation, this project directly addressed the key management action (i.e., stocking) used to restore extirpated populations and maintain predator–prey balances, assuming stocked fish survive to contribute to fisheries and/or survive to support natural reproduction. These chosen sites are located within the same area where NYSDEC stocks bloater in Lake Ontario, and encompasses another study's stocking depth (50 m, Klinard et al. 2020*b*) in the Canadian waters of Lake Ontario, providing a basis for survival modelling to be applied to untagged fish stocks.

Methods

Study site and acoustic receiver array

The study was conducted in the southeastern region of Lake Ontario near the Port of Oswego, New York (43.482863, −76.582074) (Fig. 1). The study site is a bathymetric zone that features depth increasing from 5 to 100 m within 10 km of shore, offers habitats that bloater would favour (i.e., depths > 40 m), and is a traditional stocking site for production bloater and other species in US waters of the lake. An array of 108 acoustic receiver moorings, each equipped with both a 180 kHz (either a VR2W-180 (N = 66) or HR2-180 (N = 42)) and 69 kHz (VR2W-AR (N = 108) receiver (Innovasea, Bedford, Nova Scotia, Canada)), were deployed for approximately 5 months in 2022 and 2023 (April to August). In 2022, receivers formed a large rectangle covering approximately 42 km^2 that was expanded in 2023 to cover approximately 150 km^2. Stocked fish were released in the middle of the three depths (5, 50, and 100 m; Fig. 1). The array contained 42 HR2 receivers in the center to ensure high certainty of detecting the initial stocking and movements of bloater

Fig. 1. Location and distribution of the acoustic receiver array within southeastern Lake Ontario in 2022 (A) and 2023 (B). Red points indicate the VR2W-180 kHz receivers and yellow the HR2-180 kHz receivers, blue triangles indicate stocking sites. With the expanded distribution of receivers in the 2023 array, the white box indicates receivers that match the spatial distribution of receivers in the 2022 array and were included in the *Core 2023* analysis. Black lines around the perimeter of the array indicate the path of the glider at 1 km spacing.



post-release at a fine scale. An additional 66 VR2W receivers were spaced around the central HR2's to extend the array to detect movements into shallower or deeper water. In 2022, the HR2 receivers were spaced at ∼500 m and the VR2W receivers were spaced at ∼750 m apart, but this spacing was expanded in 2023 to a uniform 1 km spacing based on detection ranges. This dense array ensured numerous detections to record fine-scale movements upon initial release as well as detect predation events as instantaneously as possible.

Bloater tagging and stocking

Bloater were reared in captivity at the USFWS, Northeast Fishery Center (Lamar, Pennsylvania) from fertilized eggs collected by the USFWS from northern Lake Michigan (Blo-Lm strain). We selected individuals >11 g to minimize tag effects following surgery based on studies of tag retention and mortality in bloater (Gorsky and Sweka, unpublished data). Bloater tagging took place on 20 and 21 April in 2022 and 24 and 25 April in 2023. A total of 240 juvenile bloater were chosen from rearing tanks containing ∼18 000 age-1 bloater and tagged in spring 2022 and 2023 ($n = 120$ for both years). For tag insertion, tags were activated and confirmed to be transmitting prior to surgery, and fish were anesthetized in a buffered solution of tricane methanesulfonate: sodium bicarbonate (MS-222:$NaHCO_3$; 0.4 g/0.8 g) for 90–120 s to reach stage III anesthesia (Summerfelt and Smith 1990). For each anesthetized bloater, wet mass was measured to the nearest 1 g, and total length to the nearest 1 mm, and were then placed into a cradle for surgery with their gills irrigated with hatchery water. An incision of ∼10 mm in length was made adjacent to the linea alba and a V5D-180 kHz transmitter (5.8 mm width, 12 mm length, wt. in water = 0.38 g, power output = 143 dB, nominal delay 5/30 s for HR/PPM, Innovasea, Bedford, NS, Canada) equipped with a predation sensor was inserted into the coelomic cavity and the incision was closed with a 2-1-1-1 suture (Sharpoint polydioxanone monofilament antibacterial suture, size 5-0). In 2022, acoustic tags were programmed to transmit signals at 180 kHz every 3 s in HR and randomly between 150 and 210 s in PPM, with a battery life of 31 days. In 2023, the tags were programmed to transmit signals every 10 s in HR and 150 and 210 s in PPM to increase battery life for up to 78 days following activation. Differences in transmission delays between 2022 and 2023 were not considered in the statistical analysis as the focus of this paper was to address potential sources of mortality rather than the fine-scale time period in which mortality occurred.

Surgery took <1 min and tagged bloater were then placed in three quarantined holding tanks ($n = 40$ per tank) separate from untagged juvenile bloater and monitored for signs of post-surgery stress and mortality. After 14 days (5 May 2022 and 10 May 2023), all bloater had retained their tags, resumed normal feeding behaviour, and appeared visibly healthy. At this time fish were anesthetized as above and sutures were removed, as rapidly growing juveniles tend to tear at suture insertion points prior to healing, causing injury, dropped tags, and additional stress and mortality (Gorsky and Sweka, unpublished data).

Bloater were moved ∼364 km from the fish hatchery to Oswego, NY, in hatchery transport vehicles equipped with aeration tanks, along with ∼18 000 conspecifics. Tagged bloater were kept separate from conspecifics during transport by a perforated basket to ensure these fish survived, and all fish were released together to have similar stocking numbers at each depth treatment. Bloater were hand-netted off the transport truck into holding tanks on a vessel equipped with aerated tanks and were released mid-day offshore over the three bathymetric depths on 10 May 2022 and 18 May 2023. At each stocking site, bloater were hand-netted for surface release along with ∼6300 untagged conspecifics at each treatment depth. All USFWS Northeast Fishery Center sampling and handling of fish during research were carried out in accordance with guidelines for the care and use of fishes by the American Fisheries Society (http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf).

Determination of tagged fish fate

All statistical analysis were completed in R version 4.2.2 (R Core Team 2013), with statistical significance determined at $\alpha \leq 0.05$. Determining fate (i.e., dead or alive) of bloater followed approaches used in other acoustic telemetry studies (Klinard and Matley 2020; Villegas-Ríos et al. 2020). If a tagged bloater's last detection occurred at the perimeter of the array, it was recorded as censored (unknown fate, i.e., alive upon emigration out of the array) and not mortality because individuals could still be alive but in areas of the lake without 180 kHz receiver coverage. All other tagged bloater were considered to have died, and date, time, and source of mortality were assigned as

i) *Stress-related* defined as the lack of horizontal movement of individuals between receivers shortly after release and being continuously detected on a single receiver (or neighbouring receivers due to proximity and tag range) at some point and for the entire remaining study duration without detection on additional receivers, consistent with previous acoustic telemetry work with stocked bloater (Klinard et al. 2020*b*). A period of 8 h was subjectively selected to assign death as bloater were detected every 3 s and were not observed to be moving from the initial detection. Mortality was assigned at date and time of the start of continuous detections. The primary mechanism for stress-related morality was assumed to be compression barotrauma.
ii) *Fish predation* based on predation tag signalling a predation event, with mortality assigned based on the date and time since predation reported by the tag. This is the most definitive given the telemetry tags used and have been shown to have a low false positive rate (5%–6%; Halfyard et al. 2017).
iii) *Avian predation* based on tags vanishing from the center of the array without further detection. This fate cannot be confirmed but is highly plausible as these fish "disappeared" from the within the middle of the array shortly after stocking and many avian predators (ringed-billed, *Larua delawarensis*, or herring, *L. argentatus*, gulls, and cormorants, *Nannopterum auritum*) were observed foraging at the time and location of stocking (L. Paulic, personal observation). Mortality was assigned at date and time of last detection prior to disappearance from the array.

In 2022, a total of 107 fish were included in the data analysis as 12 individuals were removed due to a transmitting error that reported a false positive predation event before the fish were released and one individual was removed due to mortality during transport. Of the total 120 fish released in 2023, 117 fish were included as three individuals were never detected, and as their fates were unknown, they were removed from further analysis.

To search for tags outside the array, a Slocum Glider equipped with a 180 kHz receiver was piloted along the perimeter of the array, at distances of 1–4 km from the outside edge of the array from before the time of fish stocking until 3-weeks post-stocking., a total of 42 days in 2022 and 2023 (Fig. 1). As the existing GLATOS receiver arrays (69 kHz) differ from the tag frequency (180 kHz) used here, tagged bloater could only be detected outside the array by the glider. Note, no glider data were used in modelling as it was not a comprehensive dataset, only used to confirm live fish outside the array. During each deployment, the glider moved at a velocity of 0.24 m h^{-1} in descending and ascending profiles between ∼5 m below the surface to several m above the bottom, with occasional surfacing's during ascending profiles for satellite communications (data uploading and location identification).

Survival analysis

For all statistical analyses, only detections of individuals that were considered alive at the time of detection were included. The Survival, SurvMiner, and KMsurv packages in R (version 4.2.2) were used to calculate Kaplan–Meier survivorship functions (Kaplan and Meier 1958; Sweka et al. 2017) to estimate the survival of bloater over the entire study period post-stocking. The Kaplan–Meier survivorship function calculates the likelihood that an individual will survive for *t* units of time after an individual is introduced to the study and the variance around that estimate. The Kaplan–Meier survival function allows for censorship of individuals that have an unknown fate (i.e., emigrated the array), for a staggered entry design, and does not assume distribution of data (Sweka et al. 2017).

The survival data of all treatment depths combined was first analysed using a Kaplan–Meier survival model, and then by a Cox proportional hazards model to determine whether the covariates of year, treatment depth, fish size (weight, 11.0–30.0 g), and movement rates influenced survival, with each covariate tested independently (Cox 1972; Pollock et al. 1989). In 2023, the survival analysis was run two ways: (1) including the entirety of the 2023 array (i.e., 2023); and (2) limiting the array coverage to the same area as the 2022 array (i.e., *Core* 2023). This allowed for direct comparison of survival across years for the same array area (the coverage of the array increased in 2023), regardless of the distribution of receivers. Combined temporal (year) and spatial (treatment depth) trends in survival were assessed using a pairwise comparison to assess specific interactions.

Movement

A Spearman's rank-order correlation test (r_s) was used to determine whether bloater size and emigration date were correlated, with bloater total length and emigration day (i.e., hour since stocking) as model variables. Spearman's rank-order correlation test was used as the data did not meet assumptions (normality of residuals) for a parametric correlation test (e.g., Pearson's product moment test).

The total distance travelled and movement for each fish was measured for the entire study period post-stocking using a center of activity (COA) approach (Simpfendorfer et al. 2002). Location was approximated from the acoustic tag detections of each individual using COAs at a 10 min interval (i.e., the "average" position based on all receiver detections within each 10 min period). After consideration of a range of COAs based on past research on fish (Simpfendorfer et al. 2002; Klinard et al. 2020*b*; Gatch et al. 2022), the 10 min timestep was considered the best, based on generating total distance travelled and relative movement rates of bloater compared to other *Coregonus* spp. (Rudstam et al. 1984; Gjelland et al. 2004). For the 10 min timestep, COAs were calculated in two ways, utilizing all HR and PPM detections separately. Due to the greater number of detections for HR than PPM, COAs were calculated separately to avoid HR detections biasing position estimates as HR receivers were centralized within the array. The total distance travelled within a timestep was calculated by summing all distance measurements on receivers (VR2W and HR2 separately) within the determined timestep for an individual bloater. Notably, the distance travelled is not the distance from the stocking site, rather the distance between two COAs. Relative movement rates were calculated based on the COAs by summing the total distance travelled (km) for each bloater detected in the array over time (hours) for each individual on both PPM and HR array and were compared across depths. Direction of movement following stocking was evaluated by calculating the proportion of time (based on the COAs) each individual spent moving in a specific direction. Directions were assigned every 45° increments with north determined to be 337.5°–22.5°; north-east as 22.5°–67.5°, east as 67.5°–112.5°, south-east as 112.5°–157.5°, south as 157.5°–202.5°, south-west as 202.5°–247.5°, west as 247.5°–292.5°, and north-west as 292.5°–337.5°.

Predator presence in the acoustic array

Each 180 kHz receivers was paired with a 69 kHz receiver to detect acoustically tagged predator presence within the array. No predators were tagged for this project, but a number of separate projects have tagged predators of numerous species in Lake Ontario (e.g., Chinook salmon (*Oncorhynchus tshawytscha*), Coho salmon (*Oncorhynchus kisutch*), Rainbow trout *(Oncorhynchus mykiss)*, Walleye (*Sander vitreus*)), information on these projects is available through the GLATOS (glatos.glos.us) database. Unknown predator refers to confirmed bloater tags that had predation tags appear with their predated ID, inferring a predator (of unknown species) consumed them, (i.e., a predator swimming around with the initially tagged bloater tag in its gut). No statistical analysis was carried out on these detections, and they were reported to provide some context of predators present in the array.

Results

Fish size and detection summary

Across both years, total length of the tagged yearling bloater was 125.5 ± 0.5 mm (mean ± 1 S.E.; range 108–155 mm TL), wet mass was 14.7 ± 0.5 g, and the tag mass:fish mass ratio was 2.67% ± 0.47 (Table 1). None of these variables were significantly different between stocking depths across years (length: $\chi^2 = 0.96$, df = 2, $p = 0.62$; mass: $\chi^2 = 0.20$, df = 2, $p = 0.90$; and tag:fish ratio: $\chi^2 = 3.34$, df = 2, $p = 0.19$). Of the 240 bloater that were released in Lake Ontario, 224 were included in analysis, and produced a total of 568 654 detections (HR and PPM) from 10 May–6 June 2022, and 735 797 from 18 May–1 August 2023 (Table 1).

Survival analysis

For 2022, a total of 50 individuals were censored (left the array) and the remaining 57 individuals were considered dead over the 31-day study period, with both fates varying by depth and year (Table 1 and Fig. 2*a*). These 50 censored individuals did not signal predation and are presumed to have emigrated from the array alive, although they could have been predated with insufficient time for the tag to identify the consumption. In 2023, 74 individuals were censored and 43 were interpreted to have died over the 75-day study period (Table 1 and Fig. 2*b*). The maximum number of bloater at risk of death occurred at the beginning of each study (i.e., 2022: $n = 107$; 2023: $n = 117$), after which the number of bloater included in the studies declined as fish emigrated or mortality occurred (Fig. 3).

Data for both years were combined to assess survival differences in year across treatment depths, with a 3-week post-stocking survival rate of 0.38 (0.31–0.46). The Cox proportional hazards model indicated that there was a significant difference in survival between years and between treatment depths (Table 2); thus, Kaplan–Meier survivorship functions were then estimated for year and treatment depth separately. Survival was higher overall in 2023 compared to 2022, with the highest estimated survival at the deepest stocking depth (100 m) and lowest at the 50 m stocking depth (Table 2). Year and movement rates were the only covariates that significantly influenced survival when analyzed separately (Tables 2 and 3).

Sources of mortality differed between years. In 2022, all three determined sources were consistent across all depths combined (totals across depths: fish predation $n = 19$; barotrauma $n = 20$, avian predation $n = 18$), but in 2023, avian predation accounted for nearly half of all mortality events (totals across depths: fish predation $n = 11$; barotrauma $n = 11$, avian predation $n = 21$).

Movement

Following both stocking events, emigration out of the array began within the first hour and by 72 h post-stocking 45% of the bloater (2022: $n = 47/107$; 2023: $n = 53/117$) had emigrated. Of the 47 bloater that emigrated the array in 2022, 66% ($n = 31/47$) re-entered and exited the array before the end of the 31-day study period, the majority of which returned within the first 48 h following stocking. Similarly in 2023, 56% ($n = 30/53$) of bloater returned to the array after initial emigration. There was no correlation between bloater size and timing of emigration (2022: $r_s = -0.092$, $p = 0.342$; 2023: $r_s = -0.092$, $p = 0.342$). The proportion of time spent trav-

Table 1. Size, number and fate of bloater acoustically tagged and released into southeastern Lake Ontario over three depth treatments in May 2022 and April 2023.

Year	Depth (m)	n	Mass (g)	Total length (mm)	Total alive detections* (pulse position modulation)	Total alive detections* (high-resolution)	Fish predation	Stress	Avian predation	Censored†
2022	5	35	15.2 ± 0.5	128.7 ± 1.3	2730	100 488	10	1	5	19
	50	36	14.7 ± 0.4	126.7 ± 1.2	2133	139 828	8	7	6	15
	100	36	14.2 ± 0.3	125.5 ± 0.9	4851	318 624	1	12	7	16
	Total	**107**	**14.7 ± 0.2**	**126.9 ± 0.7**	**9714**	**558 940**	**19**	**20**	**18**	**50**
2023	5	40	14.5 ± 0.5	123.7 ± 1.3	4260	13 345	2	1	10	28
	50	40	14.7 ± 0.5	123.3 ± 1.3	44 509	48 709	7	7	5	20
	100	37	15.0 ± 0.5	124.8 ± 1.3	10 311	46 009	2	3	6	26
	Total	**117**	**14.8 ± 0.3**	**123.9 ± 0.7**	**59 080**	**108 063**	**11**	**11**	**21**	**74**
Combined		**224**	**14.7 ± 0.5**	**125.5 ± 0.5**	**68 794**	**667 003**	**30**	**31**	**39**	**124**

Note: Mean ± 1 SE are shown for mass (g) and total length (mm). 2022: one individual removed from 5 m group due to morality during transport. 12 tags removed for early pred switch. 63 of 66 VR2W180s had detections. All 42 HR2s had detections. 2023: 41 of 42 HR2s VR2W180s had detections. All 66 VR2W180s had detections.
*Total alive detections refers only detections of individuals that were considered alive at the time of detection.
†Censored refers to an individual that is considered alive at the time of emigration from the array.

eling in each direction was not significantly different across depths (2022: $F_{(2,21)} = 1.63e^{-3}$, $p > 0.9$; 2023: $F_{(2,21)} = 1.97e^{-32}$, $p > 0.9$) with relatively little variation in the directions in 2023, compared to 2022 (Fig. 4).

In 2022, the total distance travelled by bloater following release varied by individual; however, there were no significant differences from depth treatment for either the PPM ($\chi^2 = 0.23$, df = 1, $p = 0.77$) or the HR data ($\chi^2 = 0.51$, df = 1, p value = 0.66) (Table 3). Conversely, in 2023, there were significant differences in the total distance travelled by depth for both the HR ($\chi^2 = 14.7$, df = 1, p value < 0.001) and PPM data ($\chi^2 = 36.2$, df = 1, p value < 0.001).

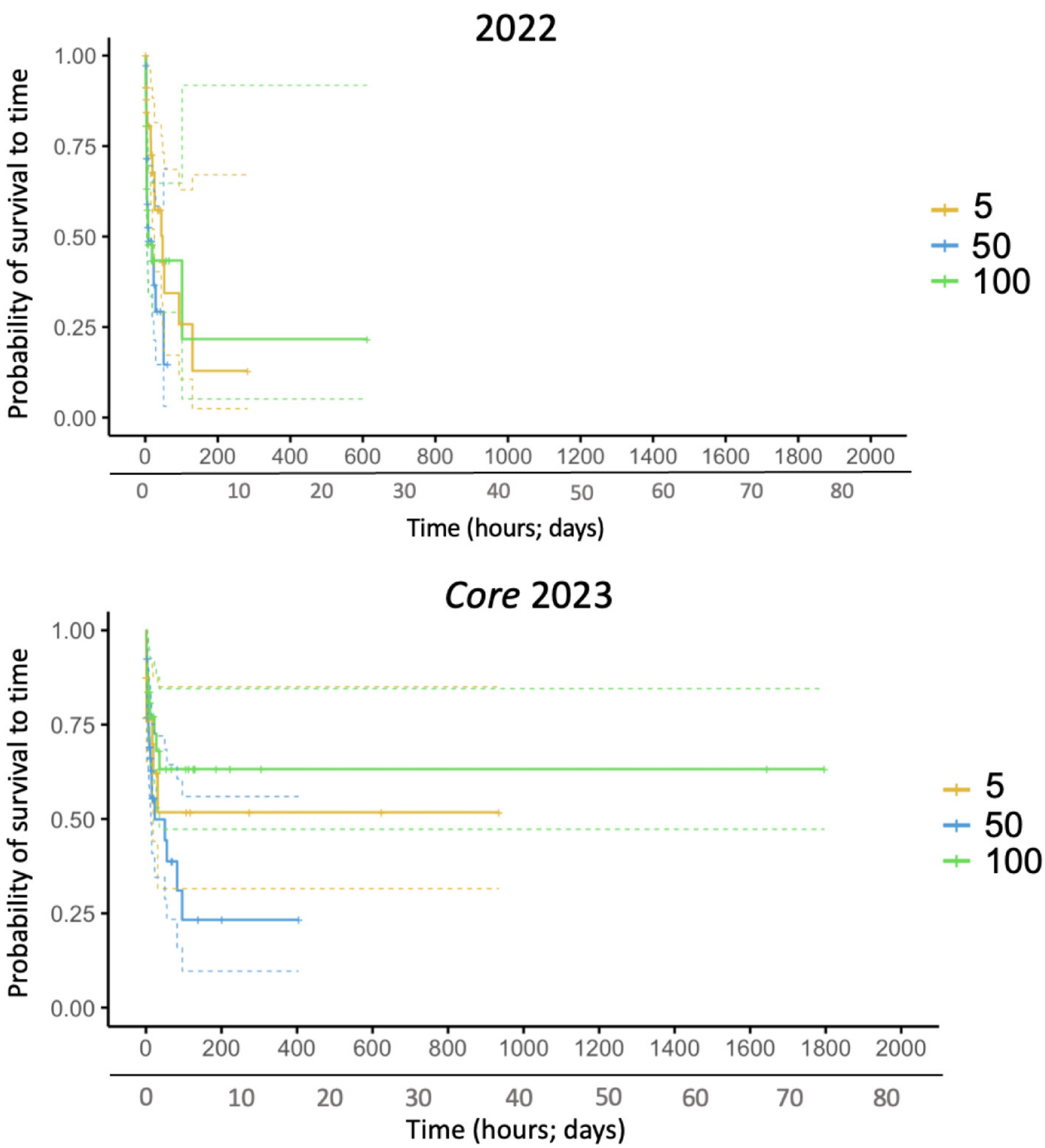
Predator presence

Tagged predator presence within the array was observed in both years during the study and included Chinook salmon, walleye, and lake trout. Fewer tagged predators were present around the stocking sites in 2022 (5 m: $n = 1$ (lake trout), 50 m: $n = 1$ (walleye); 100 m: $n = 1$ (lake trout) than 2023 (5 m: $n = 1$ (lake trout), 50 m: $n = 12$ (unknown adult bloater predators); 100 m: $n = 7$ (unknown = 5, 1 = lake trout, 1 = chinook salmon)).

Discussion

The fate of stocked fish, particularly the factors that influence survival upon release, is a significant unknown in the Great Lakes and potentially limiting the success of restoration efforts of extirpated or compromised populations. Here, we quantified the behaviour and fate of individual bloater, a prey fish, using passive acoustic telemetry at different stocking depth treatments to better understand which factors most strongly influence survival of hatchery-raised prey fish in Lake Ontario. Short-term, 3-week post-stocking survival was 0.38 (0.31–0.46) and was higher in 2023 (0.48) than in 2022 (0.12) despite these fish having experienced the same tagging and stocking treatments. Survival was highest (0.54) for fish stocked at the deepest depth (100 m), and lowest (0.23) for the middle stocking depth (50 m), likely a result of both stressors at play (i.e., moderate predation and moderate barotrauma). Avian predation accounted for the greatest number of moralities (35%) and was consistent across stocking depths. Fish predation and stress were responsible for similar number of deaths (31% and 30%, respectively), with fish predation decreasing but stress increasing with stocking depth. Following both stocking events, nearly half of the tagged bloater emigrated from the array within 72 h. Directional movement showed no significant variation across depths, although more consistent directionality was observed in 2023 compared to 2022. In 2022, there were no significant differences in total distance travelled among different depths but 2023, travel distances varied significantly by depth. Relative movement rates increased in 2023 compared to 2022, but did not significantly differ across depths in either year. This study found that post-stocking survival is variable year to year, higher in the deepest (100 m) stocking site, with fish, bird, and environmental stress as sources of mortality. These results demonstrate that stocking methods, in this case stocking depth, can

Fig. 2. Kaplan–Meier survivorship estimates for bloater released across three bathymetric depths in southeastern Lake Ontario in 2022 and 2023 for the same array coverage. Depth treatments are coded by colour, orange indicates 5 m treatment, blue indicates 50 m treatment, and green indicates 100 m treatment. The dashed lines represent 95% confidence intervals.



produce a gradient in the rate and sources of mortality for stocked prey fish in the Great Lakes.

The higher survival of the hatchery-raised bloater in the second year of stocking could be related to environmental conditions. Although reduced survival from handling, transport, and stocking of hatchery-reared fish is well documented (Brown and Day 2002) and could have contributed to higher overall mortality of bloater in this study, the procedures used in transporting and releasing the fish were very consistent between years. Variations in weather conditions between the two years may have contributed to the observed differences in survival. Water temperature was lower in the first year (7 °C) compared to the second year (11 °C), but air temperatures during the stocking were colder in year two. Year two also had a mix of sun and cloud compared with sunny conditions in year one. Overcast weather can reduce temperature fluctuations between the air and water, potentially decreasing the thermal shock as fish move from transport tanks into the lake. The cooler, stable conditions may also reduce physiological stress, helping the fish maintain energy reserves critical for adjusting to their new environment. These conditions may explain the lower incidence of stress-related mortality

Fig. 3. Ratio of distribution of mortality (black) or censoring events (grey) over the duration of the study for bloater released in southeastern Lake Ontario (A) 10 May–6 June 2022 and (B) 18 May–1 August 2023.

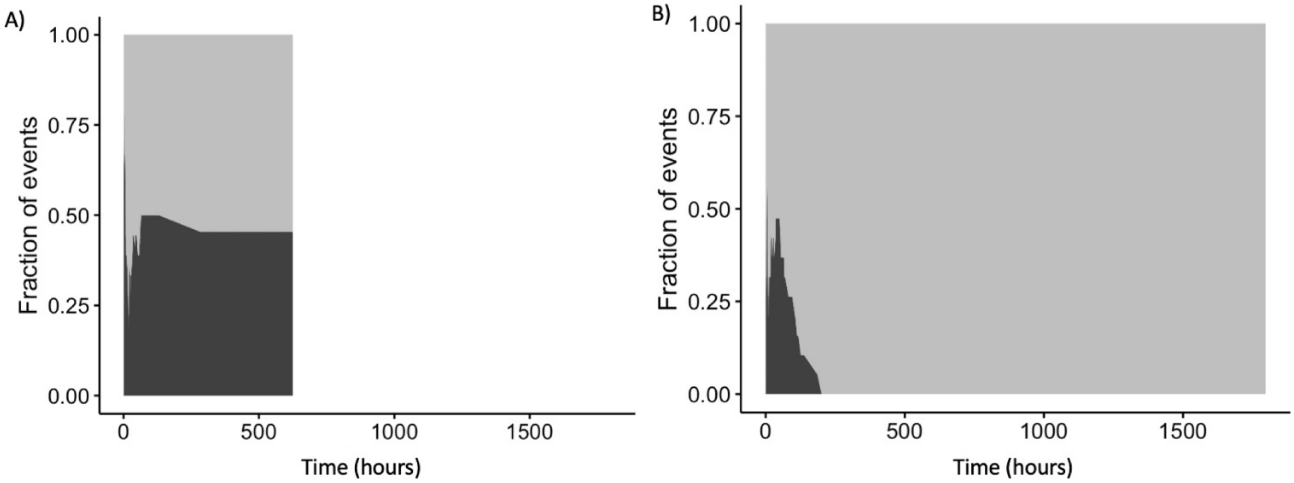


Table 2. Survival (95% confidence intervals) of stocked bloater combined across years (in 2022 (10 May–6 June) and 2023 (18 May–1 August)) and stocking depth in southeastern Lake Ontario.

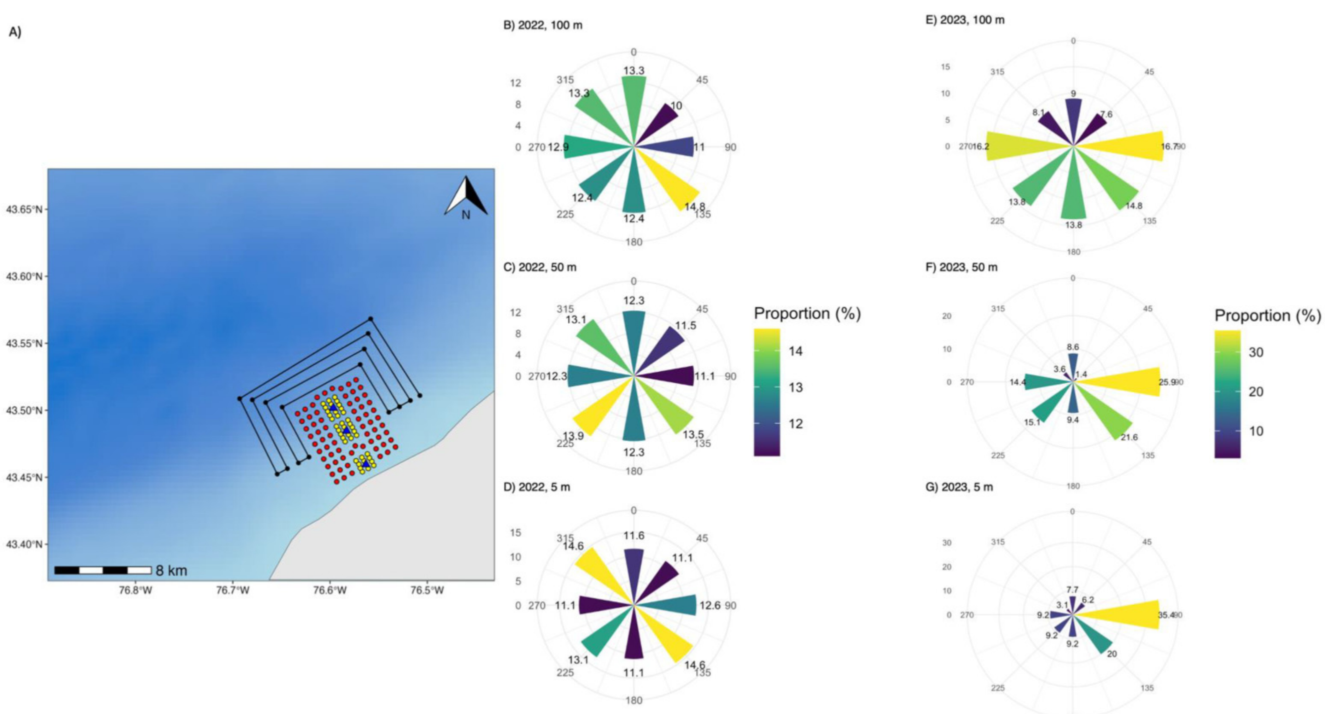
Treatment depth	Year	*N* of individuals	Overall survival	Covariate	χ^2	*p* value
All	All	224	0.38 (0.31–0.46)	Year (all)	8.3	0.02
				Treatment depth (all)	5.98	0.05
				Weight	2.9	0.09
All	2022	107	0.12 (0.03–0.38)	Treatment depth (all)	2.99	0.2
				Weight	0.46	0.5
				PPM Movement rate	20.98	0.0005
				HR Movement rate	6.63	0.01
All	2023	116	0.48 (0.37–0.62)	Treatment depth (all)	3.73	0.2
				Weight	0.85	0.4
				PPM Movement rate	2.28	0.1
				HR Movement rate	4.2	0.04
All	*Core* 2023	110	0.44 (0.33–0.59)	Treatment depth (all)	4.39	0.1
				Weight	1.28	0.3
				PPM Movement rate	2.0	0.2
				HR Movement rate	0.13	0.7
5	All	75	0.37 (0.24–0.56)	Year (All)	0.06	1.0
				Weight	2.67	0.1
				PPM Movement rate	0.48	0.5
				HR Movement rate	2.63	0.1
50	All	76	0.23 (0.13–0.39)	Year (All)	4.77	0.09
				Weight	3.03	0.08
				PPM Movement rate	1.71	0.2
				HR Movement rate	2.19	0.1
100	All	73	0.54 (0.44–0.66)	Year (All)	12.07	0.002
				Weight	3.05	0.08
				PPM Movement rate	17.1	0.00004
				HR Movement rate	1.48	0.2

Table 3. Total distance travelled and relative movement rates (both mean ± SE) of acoustically tagged bloater on the high residence (HR) and pulse position modulation (PPM) array released over three depth treatments in Lake Ontario May 2022 and 2023.

Year	Array	Depth	Total distance travelled (km)	*p* value (for total distance travelled)	Movement rates (body lengths/s)
2022	HR	5	6.4 ± 1.4^{A}	0.66	1.47 ± 0.13
		50	5.4 ± 1.2^{A}		1.54 ± 0.13
		100	5.1 ± 1.3^{A}		1.14 ± 0.09
	PPM	5	5.4 ± 0.9^{A}	0.77	1.63 ± 0.16
		50	5.3 ± 0.9^{A}		2.24 ± 0.22
		100	7.7 ± 2.9^{A}		2.09 ± 0.19
Core 2023	HR	5	4.5 ± 1.8^{A}	<0.0001	2.25 ± 0.03
		50	5.6 ± 0.7^{A}		2.26 ± 0.02
		100	8.1 ± 1.6^{B}		2.23 ± 0.02
	PPM	5	17.9 ± 8.4^{A}	<0.0001	2.17 ± 0.07
		50	6.3 ± 8.9^{B}		2.28 ± 0.02
		100	11.8 ± 2.0^{A}		2.22 ± 0.02
Large 2023	HR	5	5.3 ± 1.9^{A}	<0.0001	2.25 ± 0.03
		50	7.8 ± 0.8^{A}		2.26 ± 0.02
		100	11.2 ± 1.7^{B}		2.23 ± 0.02
	PPM	5	26.1 ± 10.6^{A}	<0.0001	2.17 ± 0.07
		50	8.9 ± 1.4^{B}		2.28 ± 0.02
		100	19.1 ± 3.7^{A}		2.22 ± 0.02

Note: Groups denoted with different letters indicate which groups significantly differed from each other.

Fig. 4. Map of the array in 2022 (A). Proportion of direction of dispersal following stocking in 2022 and 2023. Dispersal in 2022 (B–D) and 2023 (E–G) across stocking depths. Directions were assigned every 45° increments with north determined to be 337.5°–22.5°; north-east as 22.5°–67.5°, east as 67.5°–112.5°, south-east as 112.5°–157.5°, south as 157.5°–202.5°, south-west as 202.5°–247.5°, west as 247.5°–292.5°, and north-west as 292.5°–337.5°.



observed in year two, as bloater stocked under reduced light levels on overcast days could experience less stress compared to those released under high light intensity on sunny days, and the thermal change as fish move from transport tanks into the lake could be reduced. Clearly, details during the transport and release of fish, and the conditions experienced needs additional research.

There are comparable studies within Lake Ontario and the Great Lakes region that estimate low survival rates of stocked bloater and other coregonine species, such as cisco (*Coregonus artedi*). For example, in the Canadian waters of Lake Ontario, apparent survival estimates for tagged age-1 juvenile bloater stocked over 50 m of water were low (≤42%), with mortalities occurring in similar numbers from fish and avian predation and physiological stress at depth (Klinard et al. 2020*b*). Similarly, whole-lake acoustic telemetry revealed low estimated survival for stocked age-1 cisco (15% at 6 months) with 30% of mortalities occurring on the day of release in Keuka Lake with related sources of mortality (Koeberle et al. 2023).

This low initial survival would likely result in few bloater recruiting into the population. Bloater recaptured in bottom-trawl surveys in Lake Ontario revealed that stocked fish use similar habitats and food resources as historical populations, but the low number of recaptures ($n = 13$) over the past decade (2012–2023) indicates low survival of stocked fish (Weidel et al. 2022, 2023). Low survival of a stocked prey species might not be surprising given that over 48 million predatory individuals were stocked into Lake Ontario over the same period that one million bloater were stocked (Lake 2018; Klinard et al. 2019; Connerton 2020; Weidel et al. 2022). These low returns of stocked bloater in surveys and high initial mortality demonstrate that too few fish are being stocked to generate sufficient returns. However, the production and release of more hatchery-raised bloater is not financially or logistically feasible and thus consideration of different methods of stocking, such as nighttime stocking, that would increase survival, need to be considered.

The fate of bloater that emigrated beyond the acoustic array, and censored for survival analysis, remains largely unknown aside for few individuals ($n = 4$ in 2022 and $n = 5$ in 2023) detected by an autonomous glider operating outside the array. Expanding the acoustic array to include deeper regions of the lake where bloater are believed to naturally reside (typically >40 m; Eshenroder et al. 2016) could improve the ecological relevance of future studies on stocked bloater survival. However, implementing such expansions in large ecosystems like Lake Ontario is both financially and logistically challenging. The use of a glider equipped with acoustic receivers provides an efficient alternative for tracking bloater and other tagged species in near real time over an extended study area, requiring relatively few resources. However, the glider is slow moving and can only cover a small area at a time, the chance of detecting numerous bloater outside the array was likely low, especially given the detection range of 180 kHz VR2C-mobile receivers forward mounted on the glider have a limited estimated detection range (~80 m, T. Hayden, unpublished data). Regardless, these detections provide valuable information on bloater fate, supporting the assumption that fish censored upon emigration did indeed survive beyond the array coverage. It is important to note here that glider-mounted telemetry receivers are increasingly being used in the Great Lakes, but work needs to be done to evaluate their performance (e.g., detection range and efficiency) in fish tracking studies (Cypher et al. 2023).

The high mortality upon release of juvenile bloater stem from three likely sources, avian predation (39%), fish predation (30%), and physiological stress (i.e., barotrauma, 31%). The direct observation of gulls feeding on the bloater immediately after stocking strengthens our suspicions that avian predation is the associated fate of those suspected bloater deaths.

The stress-related mortality has been observed in experimental trials by USGS involving a hyperbaric apparatus, which demonstrated significant behavioural impairment from compression barotrauma at pressures as low as 0.5 atm (5 m depth) and mortality exceeding 20% at 5 atm (50 m depth) (O. Gorman, U.S. Geological Survey, unpublished data). The laboratory results are supported by field observations of bloater rapidly descending upon release and failed to move again. Stocking depth influenced the survival and sources of mortality of hatchery-raised bloater, although this varied between the 2 years. Survival increased from shallow to deep in both years. Fish predation accounted for 30% of the bloater mortalities and was greater at shallower depths. This rate is consistent with an estimate of 22.8% from a similar acoustic telemetry study in northern Lake Ontario that stocked at a depth of ~50 m (Klinard et al. 2020*b*). There are limited studies on the rate of fish predation on stocked prey fish to put these results in better context, and few small wild fish prey predation studies (e.g., Klinard et al. 2020*b*; Kraus et al. 2024). Given the size of the juvenile bloater stocked, there are a number of potential fish predators, including lake trout and other salmonids (e.g., Chinook salmon), which were present in the array at the time of stocking. Using machine learning techniques and retention of predated tags in the stomach of the predator, Klinard et al. (2021) estimated that these species, along with brown trout (*Salmo trutta*), coho salmon (*Oncorhynchus kisutch*), and rainbow trout (*Oncorhynchus mykiss*), consumed stocked bloater. The higher predation at the 5 and 50 m depths is consistent with the depths these species occupy in May during the stocking events. For example, Raby et al. (2020) found that Chinook salmon occupy depths of 14.4 ± 2.5 (mean ± 1 SD) m, while Atlantic salmon were reported occupying depths of 22.0 ± 4.6 m during the spring period (Larocque et al. 2022). Similarly, brown trout tend to stay nearshore (<2 km) year-round and spend the spring and summer near the thermocline (14.6 ± 6.7 m) at warmer temperatures (13.4 ± 3.7 °C; Nettles et al. 1987; Olson et al. 1988).

Avian predators, gulls and cormorants, accounted for the greatest number of bloater mortalities across both years, which was consistent across the depths for both years except for the 100 m site in 2023. The total number consumed by birds was consistent between years, whereas fish predation and stress were lower in year 2 than 1. These mortalities occurred quickly after stocking, between midday and dusk hours (12:00–21:00), suggesting that the stocked bloater were most vulnerable near the surface immediately after stocking. Avian predation was likely less important as the bloater acclimated to the lake and descend to depth during the day, as demonstrated in surviving stocked bloater in the north of Lake Ontario (Klinard et al. 2020*b*). Comparably, Jensen et al. (2009) found up to 12% of the tags from hatchery-reared Atlantic salmon smolts in the River Eira (Norway) were found immediately after release in sea gull *Larus* spp. pellets. Similarly, Fielder et al. (2023) assessed the spatial and temporal extent of predator movements in Lake Huron and found that double-crested cormorants were the first potential predator to arrive at a stocking site, outcompeting two top predators, walleye and lake trout.

A total of 31 bloater died from non-predation causes within 4–12 h of release, most of these (94%) were from the 50 and 100 m stocking depths. The cause of these deaths cannot be confirmed and could be related to stress of transport and stocking, the differences in mortality between depths suggest an additional mechanism was response for the deaths. For hatchery-reared fish that have not experienced changes in water pressure prior to release, rapid compression barotrauma could cause a significant stress. Current stocking protocols for bloater involve releasing fish at depths > 50 m, where they descend rapidly immediately upon release (Klinard et al. 2020*b*). In hatchery settings, tanks are typically less than 2 m deep and the bloater's innate response when stressed is to dive; however, in the wild, they are not restricted to a shallow tank. Upon release, they exhibit similar behavioural responses by descending rapidly, exposing themselves to one atmosphere of pressure for every 10 m depth. Such rapid compression could be a source of stress and physical trauma for fish, which have only experienced ~0 atm of pressure (relative to sea level) in the hatchery. Similar behaviour was observed by Klinard et al. (2020*b*) where 16 tagged individuals (equipped with acoustic depth tags) released over depths of *c.* 50 m were removed from analysis as their depth data suggested rapid mortality (<1 h). Laboratory experimentation with hatchery-raised bloater using a specially designed hyperbaric apparatus to study the effects of pressure on fish, demonstrated significant negative impacts of barotrauma on bloater behaviour at 0.5 atm (5 m depth) and >20% mortality at 5 atm (50 m depth) (Owen Gorman, U.S. Geological Service, unpublished data). Mortality due to suspected compression barotrauma was minor at the 5 m depth compared to the deeper 50 and 100 m depths. Less stress observed, and presumably barotrauma induced mortalities at the 100 m in 2023 could be due to factors, such as weather conditions, time of stocking, or water clarity, that might have caused bloater to descend more gradually. Knowledge of possible effects of barotrauma on juvenile hatchery-reared fish could refine objectives for restoration stocking strategies or provide suggestions for alternative stocking practices (i.e., offshore versus nearshore).

The distance and direction of movement of bloater following release showed variation in dispersal from the three release sites with no definitive trend in any direction. A large proportion of individual bloater had COA estimates along the deeper northeast and northwest edges of the array within 12–24 h following release, particularly those released at the 100 m treatment, suggest a preference to move to deeper areas. In year 1, stocked bloater had nondefinitive movement in the first 24 h, then dispersed from the stocking sites suggesting high stress in the first year. Whereas in the second year, stocked bloater moved more definitively immediately following release indicating lower stress. After dispersing laterally from the 50 and 100 m array bloater returned periodically throughout the study, specifically in 2023, suggesting a preference for this depth range, consistent with findings from previous studies that have observed bloater at depths greater than 35 m (Wells 1968; Gorman et al. 2012; Klinard et al. 2020*b*). The 100 m individuals had the shortest distance to travel to emigrate from the array northward and were detected by the glider, alive outside the array. In contrast, a number of individuals released at the 5 m site in 2023 migrated east, southeast (i.e., towards shallower water) and were not detected following initial release; thus, the 5 m COAs for this site were limited in number. The individuals released at the 5 m depth could be under stress from heavier predator presence and driven out to depth or towards shore faster than individuals released at the deeper depths.

The average movement rate of bloater across all depths for the PPM and HR remained consistent throughout the first few days following stocking, although were higher overall for the 2023 individuals highlighting the variability in post-stocking behavioural responses. These movement rates are relative estimates of movement rates rather than absolute swim speeds since we are estimating linear distances moved per unit time, as opposed to more natural meandering paths, although they are similar to past studies on coregonids. Gjellard et al. (2004) used hydroacoustics to determine the influence of light on swim speeds of pelagic whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) in subarctic lakes in northern Norway. They determined average swimming speed was highest in periods with low incident light or crepuscular light (0.16–0.18 m/s) and lowest in darkness (0.08–0.10 m/s). Similarly, Rudstam et al. (1984) reported routine swimming speed for 15 cm bloater swimming at a mean speed of 0.186 m/s in tanks around 09:00 in June. This is similar to our estimates for relatively the same size fish in crepuscular or daylight, with values typically around 0.25 m/s. Although the short-term tracking of bloater movements in this study may not be representative of long-term behaviour, there are limited data for hatchery-reared juvenile bloater of this size class to compare to within the Great Lakes.

The survival rate of the bloater could have been impacted by carrying the acoustic telemetry tag, but these tags were not expected to cause high mortality as studies have shown no or little negative effects of similar surgical implants (Jepsen et al. 2008; Klinard et al. 2018). Moore (2000) recommended that tags be <5% of the fish's mass to minimise effects on behaviour and survival of Atlantic salmon post-smolts. Similarly, Darcy et al. (2019) compared a variety of response metrics relative to tag burden in juvenile lake trout and rainbow trout and found no statistically significant effects of tag burden. In the present study, tag burden (2.67% ± 0.47; mean ± 1 S.D.) was well below both mentioned studies tag effect means. Further, there was low variability in hatchery bloater size in our study and there was no statistical difference in tag:fish ratios between the fish that were interpreted as dead and those that were interpreted to have survived, suggesting that tag weight did not affect survival. Tag failure is an unlikely explanation for the differences in sources mortality among groups, as these tags have proven to be extremely reliable with a fail rate of 5%–6% (Halfyard et al. 2017).

The high mortality upon initial stocking and several days after release due to predation and stress (i.e., barotrauma) indicates that there are significant barriers to the survival of stocked prey fish that results in over half of them dying within the first month. Modifying stocking practices (i.e., nearshore stocking, soft release, day vs. night stocking) to increase the survival of stocked bloater are crucial next steps to explore. For example, given the diel vertical movement of bloater and their shallow depth use at night (Klinard et al. 2020*b*), stocking offshore at night may improve their overall survival as it would provide reduced light and predator foraging efficiency and provide a longer acclimation period before descending to depth. Weidel et al. (2022) noted that bloater restoration in Lake Ontario could benefit from identifying the environmental conditions that contribute to successful bloater reproduction in the upper Great Lakes as well as seeking to improve post-stocking survival through predator and food acclimation in the hatchery or acclimating stocked fish in the lake prior to release. Given that salmonids occupy a large portion of the Lake Ontario water column during the spring when stocking occurs (Ivanova et al. 2021, 2022), and avian predators are largely limited to surface waters, it could be beneficial to expose juvenile hatchery-reared bloater to predators prior to release in a "soft release" fashion. Since bloater are reared in a hatchery setting, they may not develop the appropriate predator avoidance cues that wild conspecifics have. A soft release would hold the fish in underwater pens for several days to weeks to acclimate to their new environment and provide the opportunity to get accustomed to predators without direct exposure, which could in turn reduce initial predation rates. Brown and Day (2002) reviewed stocking practices and suggested that predator and food acclimation as well as soft release procedures have potential to improve released fish survival. Such practices have doubled survival rate of stocked salmonines in Lake Ontario (Connerton 2021); these practices could be applied to bloater restoration to potentially improve the survival of bloater. Although such practices may improve individual survival, they would also likely limit the total number of fish that could be produced and stocked. Any gains in survival will need to be weighed against any decreases in the total number stocked to maximize the population benefits of stocking.

Acknowledgements

We thank Steve Davis (USFWS) and all Northeast Fishery Center staff for providing the bloater for this study. Special thanks to the vessel crews of the USFWS and USGS-LOBS. This paper is contribution 143 of the Great Lakes Acoustic Telemetry Observation System (GLATOS). The finding and conclusions of this article are those of the author and do not represent the views of the U.S. Fish and Wildlife Service.

Article information

History dates

Received: 14 November 2024
Accepted: 20 February 2025
Accepted manuscript online: 14 March 2025
Version of record online: 10 April 2025

Copyright

Data availability

Data and code are available on Borealis (https://doi.org/10.5683/SP3/QICSOT).

Author information

Author ORCIDs

Lydia L. Paulic https://orcid.org/0009-0008-0011-942X
Silviya V. Ivanova https://orcid.org/0000-0003-2886-8533
Collin Farrell https://orcid.org/0000-0001-7591-6775
Aaron T. Fisk https://orcid.org/0000-0002-4208-4068

Author contributions

Conceptualization: LLP, SVI, DG, JS, TBJ, ATF
Methodology: LLP, SVI, DG, JS, TBJ, ATF
Writing – original draft: LLP
Writing – review & editing: LLP, SVI, KM, RJJ, DG, CF, JS, TBJ, ATF

Competing interests

The authors declare there are no competing interests.

Funding information

Funding for this project was provided by the U.S. Fish and Wildlife Service to ATF, TBJ, DG, and JS (project #F21AP03530).

References

Brown, C., and Day, R.L. 2002. The future of stock enhancements: lessons for hatchery practice from conservation biology. Fish Fish. **3**(2): 79–94. doi:10.1046/j.1467-2979.2002.00077.x.

Bunnell, D.B., Anneville, O., Baer, J., Bean, C.W., Kahilainen, K.K., Sandström, A., et al. 2024. How diverse is the toolbox? A review of management actions to conserve or restore coregonines. Int. J. Limnol. **60**: 5. doi:10.1051/limn/2024002.

Christie, W.J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fishery Commission Technical Report No. 23, Great Lakes Fishery Commission, Ann Arbor, MI.

Connerton, M. 2021. Natural reproduction, survival, homing and straying of Chinook Salmon in Lake Ontario. SUNY Environmental Science and Forestry. Ph.D. thesis.

Connerton, M.J. 2020. New York Lake Ontario and Upper St. Lawrence River Stocking Program 2019. NYSDEC 2019 Annual Report, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee. Albany, NY. pp. 1.1–1.14.

Cox, D.R. 1972. Regression models and life tables (with discussion). J. R. Stat. Soc. Ser. B Stat. Methodol. **34**: 187–220. doi:10.1111/j.2517-6161.1972.tb00899.x.

Cypher, A.D., Statscewich, H., Campbell, R., Danielson, S.L., Eiler, J., and Bishop, M.A. 2023. Detection efficiency of an autonomous underwater glider carrying an integrated acoustic receiver for acoustically tagged Pacific herring. ICES J. Mar. Sci. **80**(2): 329–341. doi:10.1093/icesjms/fsac241.

Darcy, A.P., Raby, G.D., Johnson, T.B., Pitcher, T.E., and Fisk, A.T. 2019. DEffects of intracoelomic transmitter implantation on metabolic rate, swimming performance, growth and survival in juveniles of two salmonids. J. Fish Biol. **95**(4): 1094–1106. doi:10.1111/jfb.14102.

Eshenroder, R.L., Vecsei, P., Gorman, O.T., Yule, D.L., Pratt, T.C., Mandrak, N.E., et al. 2016. Ciscoes (*Coregonus*, Subgenus *Leucichthys*) of the Laurentian Great Lakes and Lake Nipigon. Great Lakes Fishery Commission Miscellaneous Publication 216-01, Great Lakes Fishery Commission, Ann Arbor, M.I.

Fielder, D.G., Hayden, T.A., Binder, T.R., Dorr, B.S., and Currier, H.A. 2023. Predator telemetry informs temporal and spatial overlap with stocked salmonids in Lake Huron. Anim. Biotelemet. **11**(1): 1–13. doi:10.1186/s40317-023-00336-z.

Futia, M.H., Connerton, M.J., Weidel, B.C., and Rinchard, J. 2019. Diet predictions of Lake Ontario salmonines based on fatty acids and correlations between their fat content and thiamine concentrations. J. Great Lakes Res. **45**(5): 934–948. doi:10.1016/j.jglr.2019.08.005.

Gatch, A.J., Furgal, S.L., Gorsky, D., Marsden, J.E., Biesinger, Z.F., and Lantry, B.F. 2022. Evaluation of post-stocking dispersal and mortality of juvenile lake trout *Salvelinus namaycush* in Lake Ontario using acoustic telemetry. J. Great Lakes Res. **48**(2): 572–580. doi:10.1016/j.jglr.2022.01.014.

Gjelland, K.Ø., Bøhn, T., Knudsen, F.R., and Amundsen, P.A. 2004. Influence of light on the swimming speed of coregonids in subarctic lakes. Ann. Zool. Fenn. 137–146.

Gorman, O.T., Yule, D.L., and Stockwell, J.D. 2012. Habitat use by fishes of Lake Superior. I. Diel patterns of habitat use in nearshore and offshore waters of the Apostle Islands region. Aquat. Ecosyst. Health Manage. **15**(3): 333–354. doi:10.1080/14634988.2012.715972.

Halfyard, E.A., Webber, D., Del Papa, J., Leadley, T., Kessel, S.T., Colborne, S.F., and Fisk, A.T. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. Methods Ecol. Evol. **8**(9): 1063–1071. doi:10.1111/2041-210X.12726.

Ivanova, S.V., Johnson, T.B., Metcalfe, B., and Fisk, A.T. 2021. Spatial distribution of lake trout (*Salvelinus namaycush*) across seasonal thermal cycles in a large lake. Freshw. Biol. **66**(4): 615–627. doi:10.1111/fwb.13665.

Ivanova, S.V., Raby, G., Johnson, T.B., Larocque, S.M., and Fisk, A.T. 2022. Effects of life stage on the spatial ecology of Chinook salmon (*Oncorhynchus tshawytscha*) during pelagic freshwater foraging. Fish. Res. **254**: 106395. doi:10.1016/j.fishres.2022.106395.

Jensen, A.J., Bremset, G., Finstad, B., Hvidsten, N.A., Jensas, J.G., Johnsen, B.O., and Lund, E. 2009. Fish biology surveys in the Aura watercourse. Annual Report 2008. NINA Report 451, 153(In Norwegian with English translation).

Jepsen, N., Mikkelsen, J.S., and Koed, A. 2008. Effects of tag and suture type on survival and growth of brown trout with surgically implanted telemetry tags in the wild. J. Fish Biol. **72**(3): 594–602. doi:10.1111/j.1095-8649.2007.01724.x.

Kaplan, E.L., and Meier, P. 1958. Nonparametric estimation from incomplete observations. J. Am. Statist. Assoc. **53**(282): 457–481. doi:10.2307/2281868.

Klinard, N.V., and Matley, J.K. 2020a. Living until proven dead: addressing mortality in acoustic telemetry research. Rev. Fish Biol. Fish. **30**(3): 485–499. doi:10.1007/s11160-020-09613-z.

Klinard, N.V., Halfyard, E.A., Fisk, A.T., Stewart, T.J., and Johnson, T.B. 2018. Effects of surgically implanted acoustic tags on body condition, growth, and survival in a small, laterally compressed forage fish. Trans. Am. Fish. Soc. **147**(4): 749–757. doi:10.1002/tafs.10064.

Klinard, N.V., Matley, J.K., Fisk, A.T., and Johnson, T.B. 2019. Long-term retention of acoustic telemetry transmitters in temperate predators revealed by predation tags implanted in wild prey fish. J. Fish Biol. **95**(6): 1512–1516. doi:10.1111/jfb.14156. PMID: 31605542.

Klinard, N.V., Matley, J.K., Halfyard, E.A., Connerton, M., Johnson, T.B., and Fisk, A.T. 2020b. Post-stocking movement and survival of hatchery-reared bloater (*Coregonus hoyi*) reintroduced to Lake Ontario. Freshw. Biol. **65**(6): 1073–1085. doi:10.1111/fwb.13491.

Klinard, N.V., Matley, J.K., Ivanova, S.V., Larocque, S.M., Fisk, A.T., and Johnson, T.B. 2021. Application of machine learning to identify predators of stocked fish in Lake Ontario: using acoustic telemetry predation tags to inform management. J. Fish Biol. **98**(1): 237–250. doi:10.1111/jfb.14574. PMID: 33015862.

Koeberle, A.L., Pearsall, W., Hammers, B.E., Mulhall, D., McKenna, J.E., Jr, Chalupnicki, M., et al. 2023. Whole-lake acoustic telemetry to evaluate survival of stocked juvenile fish. Sci. Rep. **13**(1): 18956. doi:10.1038/s41598-023-46330-6. PMID: 37919328.

Kraus, R.T., Markham, J., Robinson, J., MacDougall, T., Faust, M.D., Schmitt, J.D., et al. 2024. On the survival and habitat use of hatchery-reared cisco (*Coregonus artedi*) in Lake Erie. J. Great Lakes Res. **50**(3): 102343. doi:10.1016/j.jglr.2024.102343.

Krueger, C.C., Holbrook, C.M., Binder, T.R., Vandergoot, C.S., Hayden, T.A., Hondorp, D.W., et al. 2018. Acoustic telemetry observation systems: challenges encountered and overcome in the Laurentian Great Lakes. Can. J. Fish. Aquat.Sci. **75**(10): 1755–1763. doi:10.1139/cjfas-2017-0406.

Lake, C. 2018. Stocking summary (Lake Ontario Fish Communities and Fisheries: 2017 Annual Report of the Lake Ontario Management Unit), Lake Ontario Fish Communities and Fisheries: 2017 Annual Report of the Lake Ontario Management Unit.

Lantry, B.F., O'Gorman, R., Strang, T.G., Lantry, J.R., Connerton, M.J., and Schaner, T. 2011. Evaluation of offshore stocking of lake trout in Lake Ontario. North Am. J. Fish. Manage. **31**(4): 671–682. doi:10.1080/02755947.2011.608613.

Larocque, S.M., Lake, C., Johnson, T.B., and Fisk, A.T. 2022. Patterns in spatial use of land-locked Atlantic salmon (Salmo salar) in a large lake. J. Great Lakes Res. **48**: 381–391. doi:10.1016/j.jglr.2021.12.002.

Moore, A. 2000. Tracking Atlantic salmon post-smolts in the sea. *In* The ocean life of Atlantic Salmon—environmental and biological factors influencing survival.

Mumby, J.A., Larocque, S.M., Johnson, T.B., Stewart, T.J., Fitzsimons, J.D., Weidel, B.C., et al. 2018. Diet and trophic niche space and overlap of Lake Ontario salmonid species using stable isotopes and stomach contents. J. Great Lakes Res. **44**(6): 1383–1392. doi:10.1016/j.jglr.2018.08.009.

Nettles, D.C., Haynes, J.M., Olson, R.A., and Winter, J.D. 1987. Seasonal movements and habitats of brown trout (*Salmo trutta*) in southcentral Lake Ontario. J. Great Lakes Res. **13**(2): 168–177. doi:10.1016/S0380-1330(87)71640-2.

Olson, R.A., Winter, J.D., Nettles, D.C., and Haynes, J.M. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. Trans. Am. Fish. Soc. **117**: 552–559. doi:10.1577/1548-8659(1988)117⟨0552:RPISBS⟩2.3.CO;2.

Pace, M.L., Cole, J.J., Carpenter, S.R., and Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. Trends Ecol. Evol. **14**(12): 483–488. doi:10.1016/S0169-5347(99)01723-1. PMID: 10542455.

Pollock, K.H., Winterstein, S.R., and Conroy, M.J. 1989. Estimation and analysis of survival distributions for radio-tagged animals. Biometrics, **45**: 99–109. doi:10.2307/2532037.

Raby, G.D., Johnson, T.B., Kessel, S.T., Stewart, T.J., and Fisk, A.T. 2020. Pop-off data storage tags reveal niche partitioning between native and non-native predators in a novel ecosystem. J. Appl. Ecol. **57**(1): 181–191. doi:10.1111/1365-2664.13522.

R Core Team. 2013. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0, http://www.R-project.org/.

Rudstam, L.G., Magnuson, J.J., and Tonn, W.M. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can. J. Fish. Aquat.Sci. **41**(8): 1252–1255. doi:10.1139/f84-151.

Simpfendorfer, C.A., Heupel, M.R., and Hueter, R.E. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can. J. Fish. Aquat.Sci. **59**(1): 23–32. doi:10.1139/f01-191.

Stewart, T.J., Todd, A., and LaPan, S.R. 2017. Fish community objectives for Lake Ontario. Ann Arbor, Michigan: Great Lakes Fishery Commission. 2100 Commonwealth Blvd. Suite 209, Ann Arbor, MI 48105.

Summerfelt, R.C., and Smith, L.S. 1990. Anesthesia, surgery, and related techniques. *In* Methods for fish biology. *Edited by* C.B. Schreck and P.B. Moyle. American Fisheries Society, Bethesda, Maryland. pp. 213–272.

Sweka, J.A., Davis, L.A., and Wagner, T. 2017. Fall and winter survival of brook trout and brown trout in a north-central Pennsylvania watershed. Trans. Am. Fish. Soc. **146**(4): 744–752. doi:10.1080/00028487.2017.1305987.

Villegas-Ríos, D., Freitas, C., Moland, E., Thorbjørnsen, S.H., and Olsen, E.M. 2020. Inferring individual fate from aquatic acoustic telemetry data. Methods Ecol. Evol. **11**(10): 1186–1198. doi:10.1111/2041-210X.13446.

Weidel, B.C., Ackiss, A.S., Chalupnicki, M.A., Connerton, M.J., Davis, S., Dettmers, J.M., et al. 2022. Results of the collaborative Lake Ontario bloater restoration stocking and assessment, 2012–2020. J. Great Lakes Res. **48**(2): 371–380. doi:10.1016/j.jglr.2021.11.014.

Weidel, B.C., Goretzke, J., Holden, J.P., and Minihkeim, S. 2023. Lake Ontario April prey fish survey results and alewife assessment, 2023. Lake Ontario April prey fish survey results and Alewife assessment, 2021.

Weidel, B.C., Minihkeim, S., Holden, J.P., Goretzke, J., and Connerton, M.J. 2021. Lake Ontario April prey fish survey results and alewife assessment, 2021. Great Lakes Fishery Commission.

Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. Fish. Bull. **67**(1): 1–15.

Zimmerman, M.S., and Krueger, C.C. 2009. An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. North Am. J. Fish. Manage. **29**(5): 1352–1371. doi:10.1577/M08-194.1.