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Post-stocking movement and survival of hatchery-reared bloater (*Coregonus hoyi*) reintroduced to Lake Ontario

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Abstract

1. Determining the movement and fate of fishes post-stocking is challenging due to the difficulty in monitoring them, particularly immediately after release. Bloater (*Coregonus hoyi*; *Salmonidae*) is a deepwater cisco that has been extirpated from Lake Ontario for several decades and is presently the focus of binational restoration stocking efforts; however, there is limited information to evaluate the efficacy of these efforts. The aim of this study was to examine the initial post-release survival, 3D movement, and behaviour of hatchery-reared bloater stocked in Lake Ontario to expand knowledge of post-stocking ecology of fish and inform stocking practices for deepwater ciscoes.
2. In total, 74 hatchery-reared bloater were tagged with acoustic transmitters with depth and temperature sensors in 2016, 2017, and 2018 and passively monitored on an array of 105 69-kHz acoustic receivers deployed in north-eastern Lake Ontario. Several spatial metrics analysed movements after release to investigate immediate post-stocking survival and behaviour for the first time in a pelagic freshwater forage fish.
3. Estimated survival for tagged bloater was low (≤42%) and detection periods of live bloater ranged from 0.2 to 12.1 days (mean ± *SD*: 2.9 ± 2.9 days). Following release, tagged bloater dispersed quickly and exhibited an association with deeper water (>40 m). Despite overlap in space use for some bloater, there was no evidence of schooling behaviour. Bloater underwent extensive diel vertical migration from near bottom to within metres of the surface. These results demonstrated that, despite high initial mortality, some hatchery-reared bloater survived the initial stress of release and displayed characteristic behaviour of the species.
4. This study demonstrated the value of acoustic telemetry in restoration efforts and revealed survival and behaviour of bloater that has never been observed at this resolution, providing novel information for the management of reintroduced species. Establishment of a self-sustaining population of bloater will help restore fish native to Lake Ontario thus increasing prey fish diversity, improving ecological integrity and resilience, and serving as a model for the reintroduction and management of other native species throughout the Great Lakes.

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KEYWORDS
acoustic telemetry, cisco, diel vertical migration, reintroduction, stocking

1 | INTRODUCTION

Fish stocking is a common practice in freshwater and marine systems worldwide aimed to supplement naturally occurring wild populations, re-establish extirpated species, or introduce non-native species for recreation or management (Cowx, 1994; Worm et al., 2009). The Laurentian Great Lakes, hereafter Great Lakes, consist of five large post-glacial lakes (Lakes Superior, Michigan, Huron, Erie, Ontario) in North America that are connected by a series of natural channels to form the world's largest freshwater ecosystem. More than 20 million fish have been stocked into the Great Lakes annually since the late 20th century to supplement valuable non-native fisheries (e.g. Pacific salmon *Oncorhynchus tshawytscha*; *Salmonidae*) and to mitigate ongoing ecological changes often related to proliferation of introduced non-native species (e.g. alewife *Alosa pseudoharengus*; *Clupeidae*, sea lamprey *Petromyzon marinus*; *Petromyzontidae*) that have negatively impacted the native fish community (Bunnell et al., 2014; Zimmerman & Krueger, 2009). Despite the long history of fish stocking and its prevalence today, the ecology and fate of fishes post-release are largely unknown primarily due to difficulty monitoring them, especially forage fishes at lower trophic levels.

Deepwater ciscoes (*Coregonus* spp.; *Salmonidae*) are a diverse group that once comprised an integral part of the native fish community of the Great Lakes (Eshenroder et al., 2016). As forage fishes that inhabit deep water and migrate vertically in the water column, deepwater ciscoes link deep benthic production and higher trophic level piscivores, serving as an important connection and source of energy within food webs (Favé & Turgeon, 2008; Zimmerman & Krueger, 2009). Presently, most deepwater ciscoes are extinct or have suffered local extirpations that restrict them to Lakes Superior and Huron. An exception is bloater (*Coregonus hoyi*), a deepwater cisco that is extant in Lakes Huron, Michigan, and Superior (Eshenroder et al., 2016; Favé & Turgeon, 2008). Until the mid-1950s, bloater were an abundant forage fish in Lake Ontario but underwent a dramatic population decline as a result of overharvesting and the introduction of the non-native species rainbow smelt (*Osmerus mordax*; *Osmeridae*) and alewife (Mills et al., 2003; Wells, 1969). Despite bloater persisting longer in Lake Ontario than the other two deepwater ciscoes (*Coregonus reighardi*, *Coregonus kiyi*), the last documented catch was in 1983 (Eshenroder et al., 2016; Owens, O'Gorman, Eckert, & Lantry, 2003).

Current knowledge of bloater ecology in the Great Lakes is based on observations from Lakes Huron, Michigan, and Superior and is limited seasonally to autumn and summer (Clemens & Crawford, 2009). A large proportion of studies on bloater have used hydroacoustic and trawl surveys to focus on their depth distribution and physiological ability to exploit deep sections of large lakes (e.g. Clemens & Crawford, 2009; Gorman, Yule, & Stockwell, 2012a; Hrabik, Jensen, Martell, Walters, & Kitchell, 2006). It has been suggested in recent decades that bloater and other deepwater ciscoes undergo diel vertical migration (DVM) in which they ascend through the water column at night to facilitate planktivory on epibenthic mysids (*Mysis relicta*; *Mysidae*; Eshenroder, Argyle, & TeWinkel, 1998; TeWinkel & Fleischer, 1999). However, the inability to track individually identifiable bloater across depths has resulted in limited knowledge regarding the extent, frequency, and amplitude of DVM. Not only is our knowledge of bloater ecology mainly limited to data from extant populations and a few techniques, but the resolution and quality of data are restricted by gear selectivity (Clemens & Crawford, 2009).

The extirpation of bloater in Lake Ontario has left alewife as the dominant offshore prey fish, which constitutes a greater proportion of piscivore diets (Brandt, 1986; Mumby et al., 2018), and has led to decreased energy transfer from the benthic to pelagic food web and, through a number of mechanisms, reduced recruitment of piscivores (Honeyfield et al., 2005). Forage fishes such as alewife that do not undergo DVM offer less potential than bloater for habitat coupling, which facilitates energy and nutrient flow through an ecosystem and is especially valuable in Lake Ontario where the benthic and pelagic habitats are well separated (Gorman, Yule, & Stockwell, 2012b). To address the issues caused by the loss of bloater in Lake Ontario, Canadian and American agencies have developed a binational restoration plan including captive rearing and stocking with the goal of re-establishing a self-sustaining population of bloater in the lake (OMNRF, 2015). A healthy population of bloater will increase prey fish diversity, improve ecological integrity and resilience, and serve as a model for the reintroduction and management of other native species throughout the Great Lakes. Lake Ontario has changed substantially in the 4 decades since bloater were last present (Mills et al., 2003) and there is limited experience culturing and rearing small-bodied coregonids. As a result, it is difficult to predict and assess the post-release behaviour and survival of bloater which is needed to inform future restoration efforts.

Acoustic telemetry is a useful tool for addressing questions about bloater ecology and the viability of stocking as a method to re-establish a self-sustaining population of deepwater ciscoes. An electronic transmitter is fitted to an organism and emits ultrasonic sounds that are detected, decoded, and recorded by submerged acoustic receivers at fixed locations, providing near-continuous spatial and temporal monitoring. In this study, we quantified the initial post-release survival (2 weeks), 3D movement, and behaviour of hatchery-reared bloater stocked in Lake Ontario using acoustic transmitters with pressure (depth) sensors. Our specific objectives were to: (1) conduct a short-term assessment of survival; (2) quantify immediate patterns in movement following release; (3) evaluate horizontal and vertical space use; and (4) assess if bloater displayed schooling behaviour.

2 | METHODS

2.1 | Study site and acoustic receiver array

The study was conducted in the St. Lawrence Channel straddling the Canada–U.S.A. border of eastern Lake Ontario (43°55.307′N, 76°31.715′W; Figure 1). An array of 85 acoustic receivers (69-kHz VR2W receivers, Vemco Inc.) was initially deployed in October 2015 and expanded to 105 receivers by May 2017 (Figure 1). The location of the receiver array was selected because it offers habitats that we anticipated bloater would favour (i.e. deeper channel areas >50 m) while also constraining movements for observations in the otherwise vast expanse (>19,000 km^2) of Lake Ontario. The receiver array was specifically designed to ensure a high certainty of detecting the initial stocking and movements of bloater post-release as well as to detect movement into shallower or deeper water should the bloater move beyond the detectable extent of the array. Receivers were spaced *c.* 1 km apart based on the expected detection efficiency of 80% at 600 m (Klinard, Halfyard, Matley, Fisk, & Johnson, 2019). The primary stocking site was in the centre of the array, which was encircled by an inner ring of 10 receivers to detect initial movement of bloater and a larger ellipse of 40 receivers that defined the limits of our core study area (*c.* 85 km^2, 17.2 linear km of channel). Additional receivers spanned the width of the larger ellipse to detect directional movement of bloater following the contours of the channel. A horseshoe-shaped north gate that extends approximately 5 km from the outer bounds of the core array allowed description of the trajectory of movement should bloater emigrate from the study site into shallower water (<20 m) north and east of the core area. A southern gate consisting of a double line of receivers was situated along the sill separating the shallower eastern basin from the main lake to detect movement of bloater exiting the array into deeper water (>50 m). Receiver moorings were constructed following the methods described by Klinard, Halfyard, et al. (2019) with the receiver hydrophone pointing upwards suspended *c.* 2 m above the lake bottom.

2.2 | Bloater tagging and stocking

Bloater were reared at the Ontario Ministry of Natural Resources and Forestry White Lake Fish Culture Station from fertilised bloater eggs collected from northern Lake Michigan by the U.S. Fish and Wildlife Service. A total of 74 bloater were tagged across four periods: autumn 2016 (*n* = 6), spring 2017 (*n* = 8), autumn 2017 (*n* = 28), and autumn 2018 (*n* = 28; Table 1). Fish were placed in an anaesthetic solution of buffered tricaine methanesulfonate (MS-222; 400 mg/L) and fork length (FL) and wet mass were measured to the nearest 1 mm and 1 g, respectively. An incision of approximately 20 mm in length was made adjacent to the linea alba and a V9TP-2x 69-kHz transmitter (9 × 31 mm, 4.9 g weight in air, nominal delay 120 s, estimated battery life 582 days; Vemco Inc.) equipped with temperature and pressure sensors or V9P-2x 69-kHz transmitter (9 × 29 mm, 4.6 g weight in air, nominal delay 300 s, estimated battery life 912 days) equipped with a pressure sensor was implanted following methods described in Klinard, Halfyard, Fisk, Stewart, and Johnson (2018). Surgeries lasted approximately 120–180 s.

Fish were monitored daily for *c.* 2 weeks following surgery. Tagging resulted in negligible mortality and no tag loss consistent with the

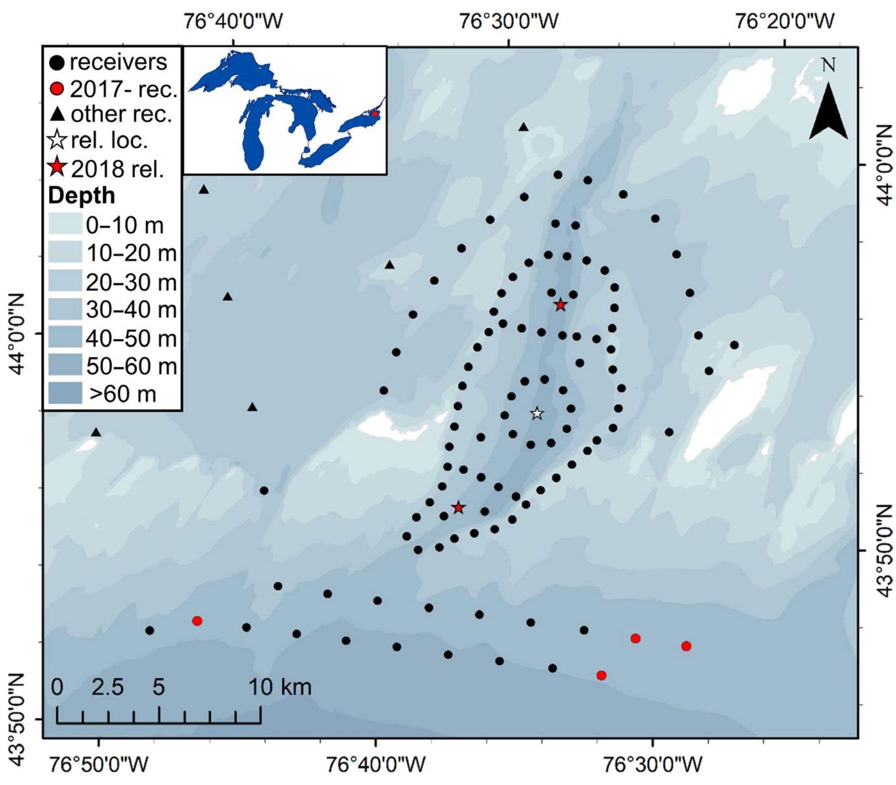

FIGURE 1 Bathymetry and location of receiver moorings in north-eastern Lake Ontario. Red circle in map inset illustrates location of the study site within the Laurentian Great Lakes. Black and red circles signify receivers deployed throughout the entire study period and from June 2017 onwards, respectively. Black triangles signify receivers deployed as part of a separate telemetry project during the study period. The white star indicates the release location of all stocked bloater from 2016 to 2017 and the red stars indicate the release locations in 2018 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Summary of bloater tagged and released into eastern Lake Ontario over four periods in autumn 2016, spring 2017, autumn 2017, and autumn 2018

Release group	Tagging date	Release date	*n* stocked	*n* tagged	Mass (g)	Fork length (mm)
Autumn 2016	2016–10–27	2016–11–08	36,092	6	285 ± 63 (179–362)	269 ± 14 (245–285)
Spring 2017	2017–03–20	2017–04–10	990	8	336 ± 46 (267–402)	306 ± 8 (297–320)
Autumn 2017	2017–10–23	2017–11–07	12,490	28	284 ± 44 (210–409)	262 ± 13 (235–285)
Autumn 2018	2018–11–06	2018–11–19	9,023	32	109 ± 23 (50–173)	199 ± 9 (181–223)

Mean ± *SD* (range) are shown for mass (g) and fork length (mm) and refers to tagged individuals.

findings of Klinard et al. (2018). Tagged fish were hand netted into a stocking truck equipped with an oxygenated tank along with *c.* 10,000–30,000 untagged individuals for transport to Lake Ontario. Fish were hand netted off the stocking truck to aerated holding tanks supplied with a continuous flow of lake water on the vessel, which transported the fish to the release location where tagged bloater were hand netted for release. The release location was in the centre of the receiver array where depth was *c.* 50 m (Figure 1). Stocking occurred on 8 November 2016, 10 April 2017, 7 November 2017, and 19 November 2018 and all fish were released in surface waters between 11:00 and 16:00 (Table 1). Underwater videography during transport and release showed that all tagged fish appeared to be healthy and active and exhibited no signs of stress. The lake was isothermal during all release periods and the water temperature at release was 11, 2, 12, and 8°C for the autumn 2016, spring 2017, autumn 2017, and autumn 2018 stocking periods, respectively.

2.3 | Data analysis

To examine initial post-release movement and space use and reduce the likelihood that data collected represented movements of a predator that had consumed a tagged bloater, suspect detections that appeared to have originated from a predator were removed. Suspect detections were identified based on visual comparison of spatial and temporal patterns in location and depth use of acoustically tagged predators in Lake Ontario. Tagged predators included *Salmonidae* Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), lake trout (*Salvelinus namaycush*), and rainbow trout (*Oncorhynchus mykiss*) that are part of ongoing telemetry projects in Lake Ontario through GLATOS (unpublished data). We cannot be certain that all predator data were excluded and all bloater data were included since it is difficult to predict the behaviour of stocked bloater. Individuals with insufficient detection data (i.e. ≤10 detections) were removed from further analyses. We believe that this filtering step increased the probability that only bloater detections were analysed. Instances of mortality in the remaining data were identified by visual assessment of depth sensor data with the portion of data that was assessed as dead (constant depth consistent with bottom depth and detections at a single location) removed. Statistical significance was assumed at $p \le 0.05$ and all analyses were completed in R version 3.6.1 (R Development Core Team, 2019).

2.4 | Twenty-four-hour post-stocking movement

To account for the uncertainty associated with the actual location of tagged individuals due to the detection range of the receivers, each bloater detection was assigned a location that was randomly estimated within 600 m (expected detection range) of the receiver. Location estimates were then calculated using a 30-min mean position algorithm to derive centres of activity (COAs) following the methods described in Simpfendorfer, Heupel, and Hueter (2002). A 30-min time interval ensured a sufficient amount of detection data was incorporated into each location estimate to produce more accurate positions while maximising the number of positions within a day (i.e. possible 48 positions per day). To assess initial direction and distance of movement, we selected the last COA in the 24-hr post-release period for each live individual and plotted the angle and distance from release.

2.5 | Horizontal space use

Horizontal autocorrelated kernel density estimates (AKDE) representing the core activity space (50%) and activity space extent (95%) of individuals were calculated from the COAs of live bloater using the *akde* function in the R package *ctmm* (Fleming et al., 2015). We chose to use AKDEs as opposed to conventional kernel density estimation (KDE), which explicitly assumes that location data are independent and identically distributed and often results in KDEs that underestimate activity space areas (Fleming & Calabrese, 2017; Fleming et al., 2015; Noonan et al., 2019). AKDE estimates the correlation structure in the data by fitting continuous-time movement models and selecting the best fitting model based on the approximate small sample size corrected Akaike information criterion to address the stronger autocorrelation that is associated with the ever-finer sampling of movement paths (Kays, Crofoot, Jetz, & Wikelski, 2015; Noonan et al., 2019).

Patterns in horizontal space use were determined by examining the areas of overlap of the 95% AKDEs of all individuals within each release group. To evaluate possible drivers of horizontal space use among individuals, we modelled the 95% AKDE size (km^2) as a function of covariates using a γ generalised linear model (GLM) with a log link function. Fixed covariates were release period (categorical with four levels), FL (continuous), number of days detected (continuous), and number of COAs (continuous). The number of days detected and the number of COAs were highly collinear (Pearson's pairwise cc = 0.97) and thus, were considered as a single covariate represented by the number of days detected in further analyses. The *glm* function in the R package *stats* was used to fit the GLM (R Core Team, 2013). Model assumptions were verified by plotting residuals versus fitted values, versus each covariate in the model.

To identify schooling behaviour, we conducted a proximity analysis using COAs of bloater from the release group with the largest number of bloater detected (autumn 2017; *n* = 18). The following analyses were performed using both the COAs from the first 24 hr following release as well as the entire detection period. A proximity index was calculated for each pair of individuals using the *Prox* function in the R package *wildlifeDI* (Long, 2014). The *Prox* function determines the proportion of simultaneous fixes that are proximal based on a selected distance threshold to evaluate positions through space and time. We selected a timestep of 30 min to complement the 30-min interval of the COAs and conducted a sensitivity analysis to select an appropriate distance threshold at which fish would be considered proximal. Because COAs were derived from detections with positions randomly assigned within a 600-m radius of the receiver they were recorded on, we ran 10 iterations of COA calculations each for select individuals using new randomised detection positions each time. We compared interactions of COAs within an individual by calculating the proximity index among iterations at a select distance threshold. The process was repeated for several distance thresholds and individuals to determine the minimum distance that provided a >0.95 proximity index among all iterations of each individual. Sensitivity analysis revealed 800 m as the most appropriate distance threshold at which to calculate proximity index for every pair of individuals. This method of analysis includes only comparable timesteps (i.e. timesteps in which both fish in a pairing were detected) as a conservative approach to evaluate schooling behaviour of fish as absence of a detection does not guarantee absence from the study site.

2.6 | Vertical space use

Depth values associated with each detection were averaged into 30-min intervals for each individual during COA calculation. To evaluate possible drivers of horizontal space use among individuals, we modelled the averaged depth values as a function of covariates using a γ generalised linear mixed model (GLMM) with an inverse link function. Fixed covariates were release period (categorical with four levels), number of days detected (continuous), FL (continuous), and time of day to account for DVM (categorical with four levels: late night 0–6 hr, morning 6–12 hr, midday 12–18 hr, early night 18–24 hr) and tag ID was included as a random effect. The *glmer* function in the R package *lme4* was used to fit the GLMM (Bates, Maechler, Boker, & Walker, 2015). Model assumptions were verified by plotting residuals versus fitted values, versus each covariate in the model. A post hoc Tukey's test determined which time periods and release periods differed when they significantly influenced depth use.

2.7 | Diel patterns in horizontal space use

To further explore diel patterns in space use, we compared overall horizontal space use between day and night. For each individual, all of the COAs that occurred during the day and night were pooled, respectively. Day and night were designated based on sunrise and sunset times throughout the study duration determined using the *sunrise* function in the R package *maptools* (Bivand & Lewin-Koh, 2019). The *kernelUD* function in the R package *adehabitatHR* was used to calculate an overall day kernel utilisation distribution (KUD) and overall night KUD for each individual representing the core (50%) and extent (95%) of activity space (*h* = 600; Calenge, 2006). Individuals with fewer than five total COAs during either the day or night period were removed from KUD calculations as a minimum of five relocations are required to calculate a kernel using the *kernelUD* function. A paired *t*-test was performed to compare day/night differences in horizontal space use within individuals.

2.8 | Fate of tagged bloater

The fate of all tagged bloater that were considered not predated and had sufficient detection data (*n* = 51) was assessed to determine if spatial and temporal patterns of space use were related to survival among individuals. Inferring fate from acoustic telemetry studies is challenging because death, undetected fish, and tag expulsion are often represented by similar detection histories. Here, we consider the final detections of fish as a death event or representative of a final detection prior to death or emigration. For tags that show continuous detections at a single or neighbouring receiver, we assume death at the start of the period of continuous detections. For fish that were assessed as dead, the location of their death was examined in relation to the number of days with detections of the live fish prior to assumed mortality. Fish with active and mobile detection histories were considered still alive at the time of their last detection and their last known COA was examined in relation to the number of days they had been detected in total.

3 | RESULTS

3.1 | Detection summary

Of the 74 bloater that were tagged and released in north-eastern Lake Ontario from November 2016 to November 2018, 70 fish were detected. The four tags that were never detected were part of the autumn 2017 release group; the fate of these fish is unknown. These tags were confirmed to be transmitting prior to release. Of the 70 individuals that were detected, six had insufficient detection data (i.e. ≤10 detections total) and were removed from the dataset. An additional 16 (22% of all tagged) individuals were removed as their depth data suggested rapid mortality (<1 hr). Of the remaining 48 individuals, 13 were identified as suspected predators (*n* = 3 spring

2017, n = 3 autumn 2017, n = 7 autumn 2018) with minimal (<1 hr) or no bloater detections and were removed from the dataset. Of the 13 fish identified as suspected predators, five had detections that indicated eventual death or tag expulsion following predation. One individual had ≤10 detections as a live bloater and was removed. The final detection dataset included 34 fish that exhibited detection data assessed as a live bloater (Table 2). Of the 34 final bloater, one had depth data that suggested predation followed by tag expulsion and 12 had depth data that indicated eventual death (n = 1 autumn 2016, n = 1 spring 2017, n = 8 autumn 2017, n = 2 autumn 2018). All detections that were not representative of a live bloater (i.e. predator or mortality) were removed and only detection data of living bloater were used for all analyses (Table 2). Overall, 35 fish (47% of all tagged) had confirmed death at some point during their detection duration. Including the fish that were suspected to be predated (n = 8), a total of 43 fish (58% of all tagged) were considered to have died as a result of natural mortality or predation. The number of days detected alive for the 34 bloater that were used in analyses ranged from 0.2 to 12.1 with a mean ± SD of 4 days (n = 1), 3.8 ± 1.4, 3.9 ± 3.5, and 1.4 ± 1.4 days for the autumn 2016, spring 2017, autumn 2017, and autumn 2018 release groups, respectively (Table 2).

3.2 | Twenty-four-hour post-stocking movement

Position estimates 24 hr post-release revealed strong preference for the northeast quadrant of the array across all release locations (Figure 2). A total of 24 fish (71%) were detected in the northeast quadrant at distances of 1,000–7,000 m from release. The northeast direction of fish movement corresponds to the deeper waters (40–60 m) of the channel (Figure 1). Within the 24-hr period, several individuals moved away from the release location with 59% (n = 20) of fish positioned beyond 2,000 m. There were no strong patterns in the distance or direction of movement across release groups; however, bloater released at the northern location were slightly further from release than bloater released at the central and southern locations.

3.3 | Horizontal space use

The core activity space (50% AKDE) of individual bloater ranged from 0.8 to 164.7 km^2 while the activity space extent (95% AKDE) ranged from 2.9 to 640.0 km^2 (Table 2). The highest degree of overlap in horizontal space use occurred around the release location for each release group (Figure 3). The autumn 2016 and spring 2017 release groups had small sample sizes of one and two, respectively, but all individuals exhibited similar size and location of AKDEs (Figure 3a,b). The autumn 2017 release group had the largest sample size of 18, although few individuals had AKDEs that extended beyond the main array (Figure 3c). One individual was detected on receivers west of our array, resulting in the largest AKDE among all tagged bloater. The autumn 2018 bloater had more dispersed activity spaces with lower overlap as a result of being released at two locations in the north and south sections of the array (Figure 3d). Space use was focused in the

TABLE 2 Summary of detection metrics for live detections of the 34 tagged bloater that were used in analyses

Release group	n tagged	n analysed	Days detected	50% AKDE (km^2)	95% AKDE (km^2)	n detections
Autumn 2016	6	1	4	33.5	124.3	784
Spring 2017	8	2	3.8 ± 1.4 (2.8–4.8)	27.1 ± 0.3 (26.9–27.3)	105.2 ± 2.8 (103.2–107.2)	821 ± 245 (648–994)
Autumn 2017	28	18	3.9 ± 3.5 (0.6–12.1)	21.0 ± 37.0 (3.4–164.7)	87.1 ± 141.9 (14.0–640.0)	550 ± 687 (23–2,380)
Autumn 2018	32	13	1.4 ± 1.4 (0.2–4.3)	23.9 ± 35.8 (0.8–124.5)	91.5 ± 134.7 (2.9–469.2)	147 ± 101 (15–370)

Note: Mean ± SD is shown for days detected, 50% AKDE (km^2), 95% AKDE (km^2), and number of detections and refers to analysed individuals

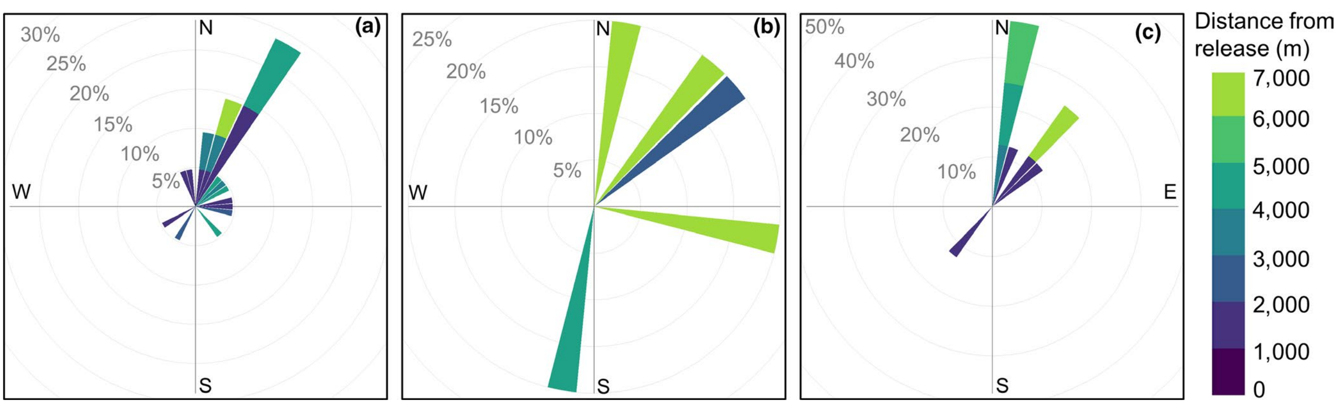

FIGURE 2 Distance and direction of the last centre of activity in the 24 hr following release for all live tagged bloater (n = 34). Bloater are shown by release location: (a) centre release site (n = 21); (b) northern release site (n = 5); and (c) southern release site (n = 8). Length of wedge corresponds to the number of individuals represented as a percentage and colour indicates the distance from the release site [Colour figure can be viewed at wileyonlinelibrary.com]

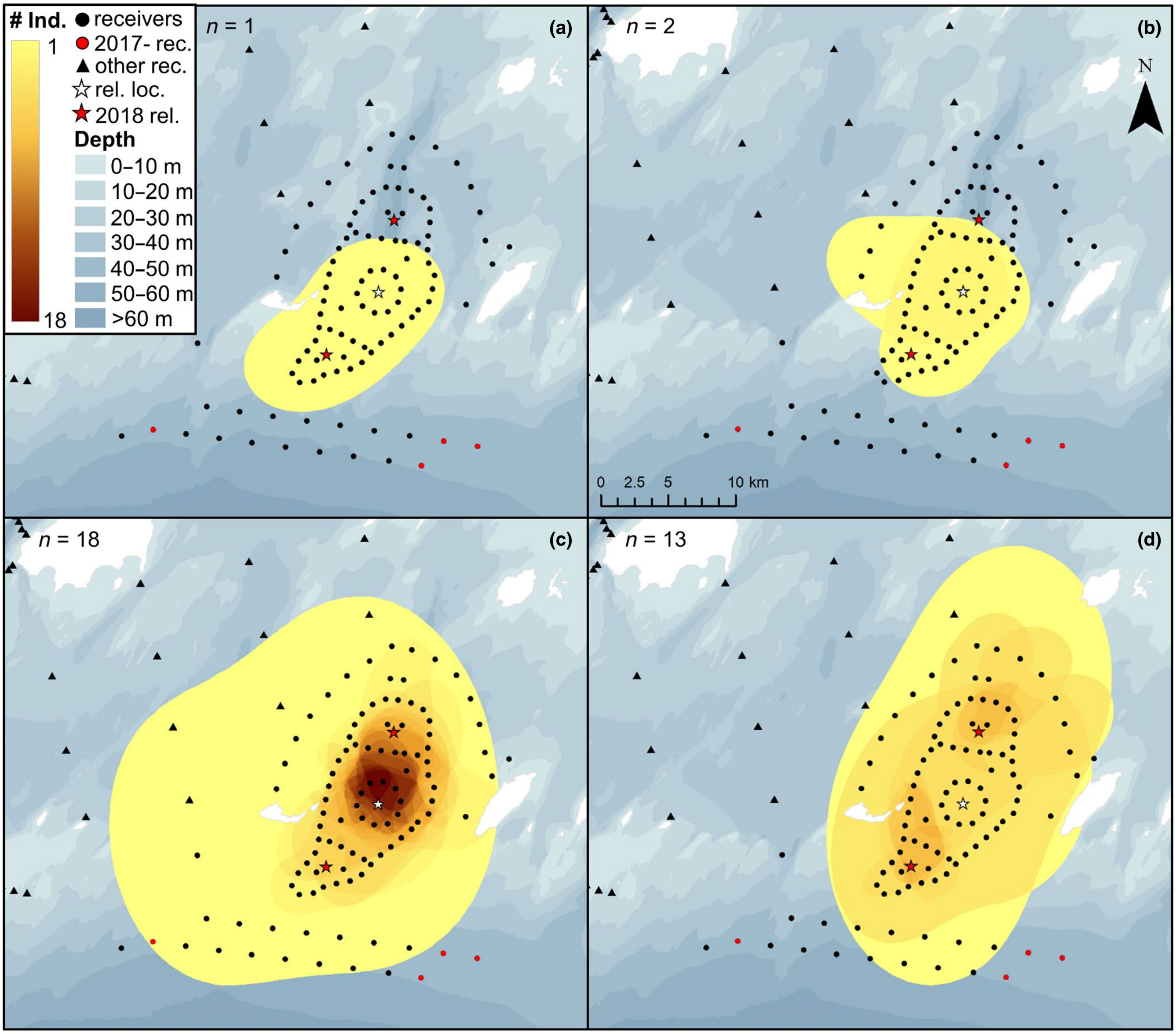

FIGURE 3 Overlapping autocorrelated kernel density estimates representing the activity space extent (95%) for each tagged bloater. Colour gradient signifies the number of individuals with overlapping activity space in a location. Habitat use extent estimates are shown by release group: (a) autumn 2016 (*n* = 1); (b) spring 2017 (*n* = 2); (c) autumn 2017 (*n* = 18); and (d) autumn 2018 (*n* = 13) [Colour figure can be viewed at wileyonlinelibrary.com]

main array with no individuals detected moving into surrounding waters where receivers were located. The number of days detected was the only explanatory variable that had a significant impact on overall 95% AKDE size of tagged bloater (β = 0.305, t = 3.904, p = 0.001). An increase in the number of days that an individual was detected was associated with an increase in the size of their activity space extent. Model validation indicated no problems.

Proximity analysis revealed few individuals that would be considered schooling on the basis of a proximity index ≥0.5 denoting attraction (Long, 2014). A total of six pairs (out of 153) had a proximity index ≥0.5 within the first 24 hr following release but this decreased to two pairs over the entire detection period (Figure 4). Proximity indexes during the first 24 hr ranged from 0.50 to 0.56 (Figure 4a). The two pairs that had indexes ≥0.5 across the entire detection duration were also low (0.55 and 0.65) and were two of the same pairs from the 24-hr period (Figure 4b).

3.4 | Vertical space use

Time of day and release period had a significant effect on the depth use of bloater. A post hoc Tukey's test revealed that all time periods except for morning (6–12 hr) and midday (12–18 hr) differed significantly and that only the autumn 2016 and spring 2017 as well as spring 2017 and autumn 2017 release groups were significantly different. Bloater exhibited the shallowest depth use during early night (18–24 hr) and the largest change in depth use between the 12–18 and 18–24 hr periods (Figure 5). Depth use was deepest and remained relatively

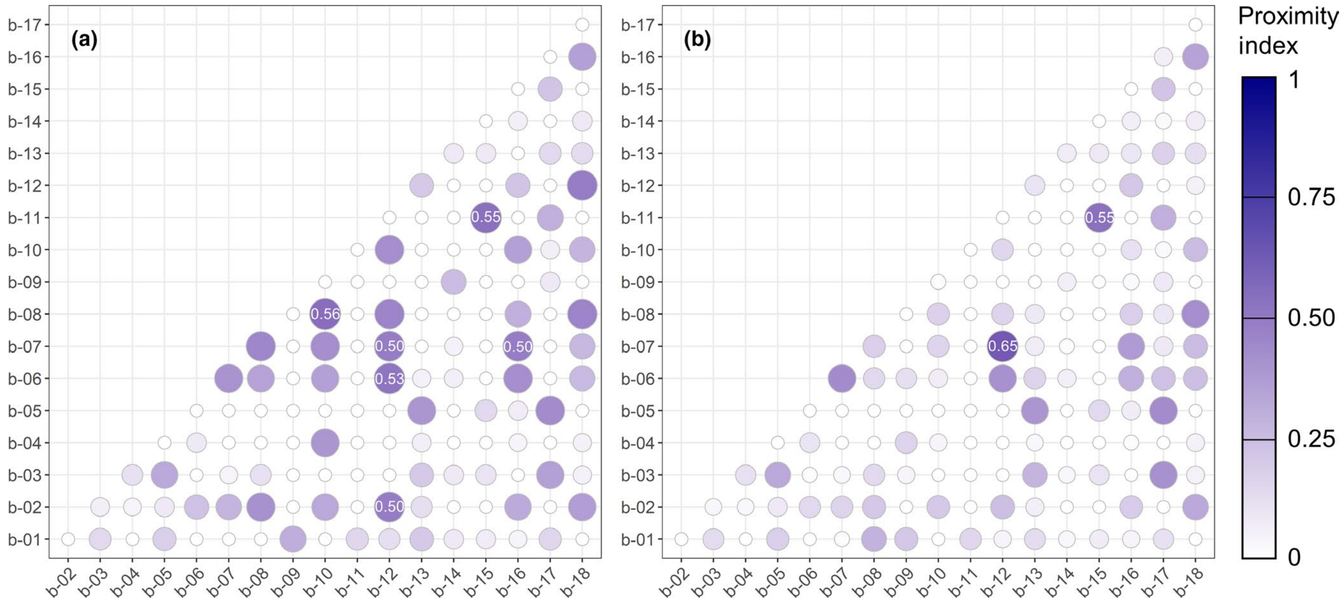

FIGURE 4 Correlograms illustrating the proximity index between each pair of tagged bloater from the autumn 2017 release group (n = 18) for: (a) the first 24 hr following release and (b) the entire detection period of each fish. Individual fish IDs are listed along the axes. Circle colour and size correspond to proximity index and are written for pairs where proximity index ≥0.05 [Colour figure can be viewed at wileyonlinelibrary.com]

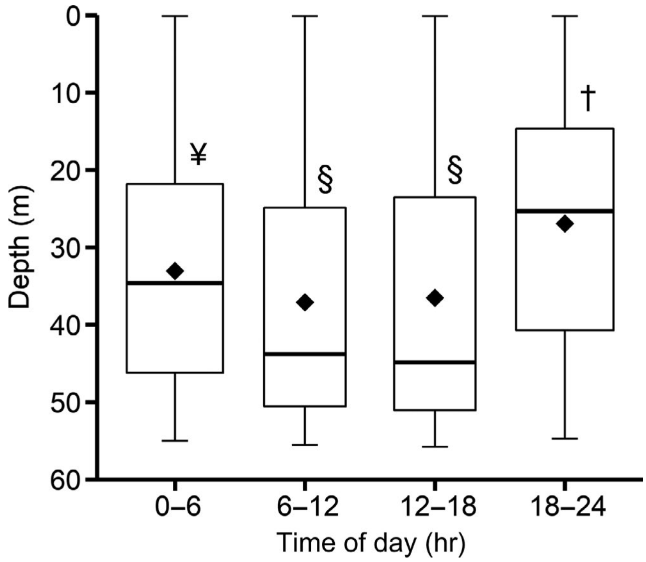

FIGURE 5 Effect of time of day on depth use of tagged bloater. Time of day is shown in four periods: 0–6 hr (late night), 6–12 hr (morning), 12–18 hr (midday), and 18–24 hr (early night). Boxes are the 25th and 75th percentiles, whiskers represent 10th and 90th percentiles, solid midline indicates the median, and the diamond signifies the mean. Box widths are proportional to the square-roots of the number of observations in the time periods and symbols above each box represent statistically different time periods based on contrasts following the mixed effects model

consistent during the 6–12 and 12–18 hr periods. Further examination of individual depth use revealed strong DVM during which bloater remained at depth near the lake bottom during the day, ascended to within metres of the surface shortly after sunset, and descended back down to depth before sunrise (Figure 6).

3.5 | Diel patterns in horizontal space use

Of the 34 fish that had live detections, 26 had a sufficient number (five or more) of detections during both the day and night periods to calculate a KUD. Comparing day and night 95% KUD revealed a significant difference (t-test: $t_{25} = -2.52$, $p = 0.019$) in overall day/night horizontal space use within each individual.

3.6 | Fate of tagged bloater

Bloater were detected for a range of <1 to 12 days (Figure 7). Of the 51 fish with known fate, 21 (41%) were alive at the time of their last detection and 30 (59%) were confirmed or presumed dead at some point during their detection history. The bloater that were considered dead often had their location of death in the deeper waters of the main array with only one fish detected on the gate receivers (Figure 7b). In general, bloater that died further from the release point were often detected for a longer period than those that died in the centre of the array. A total of 18 bloater (60% of 30 fish confirmed or presumed dead) that were confirmed or presumed dead had died on the day of release. However, several individuals were detected upwards of 5 days with one fish detected for 12 days making strong DVM prior to death. The 21 bloater that were last detected alive had final positions that were more dispersed throughout the array including six individuals on gate receivers (Figure 7a). The longest detection period for the live bloater was 12 days with the individual exhibiting strong DVM prior to its final position on the northern gate of receivers. Ten individuals had approximately 1 day of detections with many of their last positions around or inside of the main array.

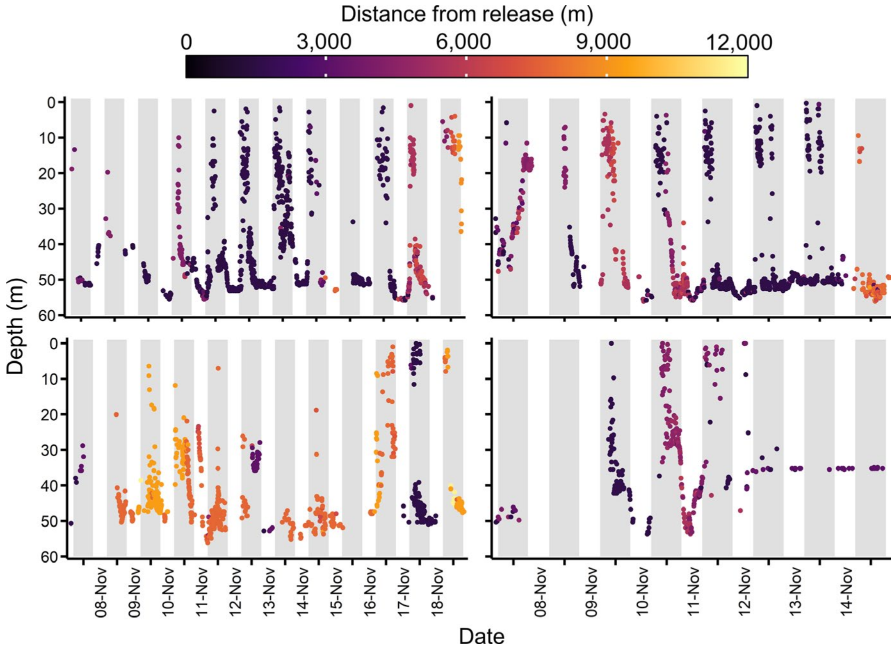

FIGURE 6 Depth profiles of four bloater displaying diel vertical migration. Each circle represents a single detection and the colour of the circle corresponds to the distance from the release site (m) at time of detection. Grey shaded areas indicate night periods based on daily sunrise and sunset times from the R package *maptools* [Colour figure can be viewed at wileyonlinelibrary.com]

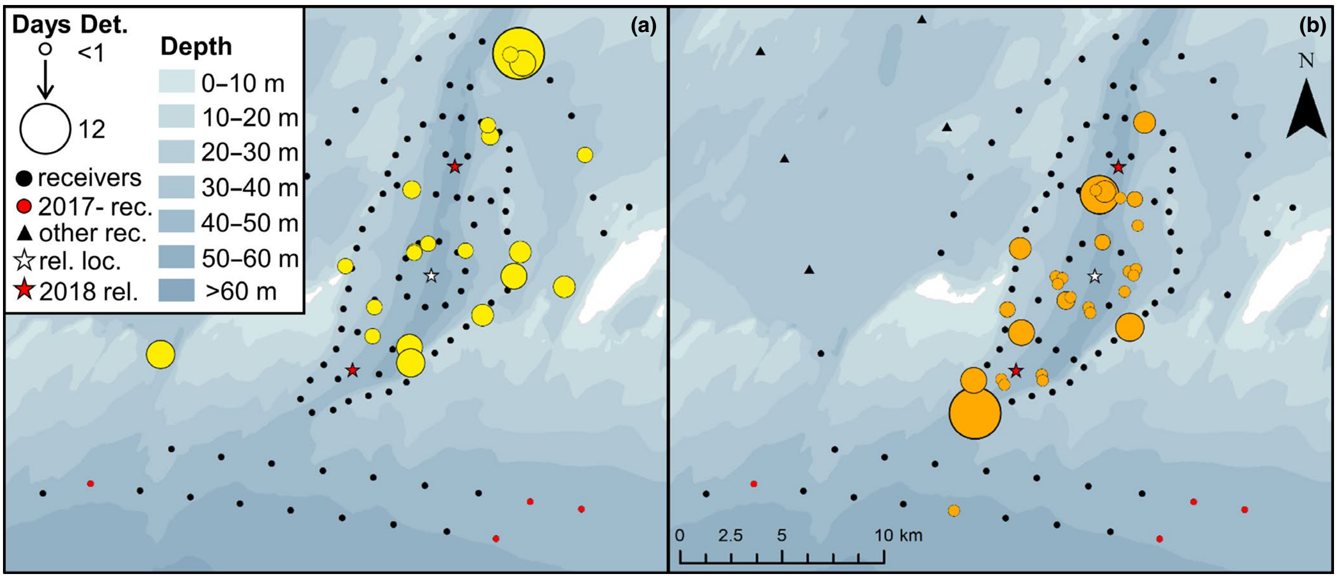

FIGURE 7 Fate of all tagged bloater stocked that were not assessed as suspected predators and had sufficient detection data (>10 detections) to assign fate (n = 51). Yellow circles in (a) signify the last centre of activity for fish that were last detected alive (n = 21) whereas orange circles in (b) signify the location of death for fish that died based on depth data (n = 30). Symbol size corresponds to the number of days detected prior to the last detection for live fish (a) or prior to death (b) with <1 day indicating rapid mortality (<1 hr) [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Understanding the movement and behaviour of bloater in Lake Ontario broadens our limited existing knowledge of bloater ecology while also providing findings that can be applied to the adaptive management of reintroduction efforts for bloater and other deepwater fishes. Passive acoustic telemetry allows for the monitoring of bloater movements at spatial and temporal scales that have never before been observed for this species. This study demonstrated that following release, there was a minimum mortality of 58% of all tagged bloater as a result of natural mortality or predation. Filtered detection periods of bloater were variable, with most fish detected for <1 day in the array and few detected for up to 12 days. Bloater dispersed quickly from the release site towards deeper waters (>40 m) and they underwent extensive DVM from lake bottom (*c.* 50 m) to within metres of the surface during autumn and spring when the lake was isothermal. Despite overlap in the activity space of many individuals, there was no evidence of schooling behaviour. While initial apparent survival was low (≤42%), some bloater (n = 10) were last detected alive on the outskirts of the array and may have exited the array and survived elsewhere in the lake.

Bloater underwent strong DVM, from lake bottom to within metres of the surface, which has not been observed before at this frequency and amplitude. Gear selectivity has previously played a large role in restricting the ability to examine the depth distribution and vertical migration of bloater (Clemens & Crawford, 2009). As a result, existing research suggests that adult bloater frequently occupy depths ranging from 36 to 100 m and are rarely <10 m deep (Gorman et al., 2012a; Jobes, 1949; Koelz, 1929; Wells, 1968). Night-time midwater trawls in Lake Superior showed peak abundance around 30 m with few bloater captured >50 m (Hrabik et al., 2006). Using acoustic telemetry allowed us to observe extensive DVM of bloater that supported previous findings and also showed that bloater exhibit shallower depth use at night than previously known. The extent of DVM observed in this study might have been possible due to the lake being isothermal and not presenting a thermal constraint. Ahrenstorff, Hrabik, Stockwell, Yule, and Sass (2011) found that *Coregonus kiyi*, another deepwater cisco, demonstrated DVM in Lake Superior across spring, summer, and autumn with the depth extent largest in the autumn and the duration longest in the spring. Similarly, Mehner, Kasprzak, and Hölker (2007) witnessed a consistent DVM in two coregonid species (*Coregonus albula* and *Coregonus fontanae*) throughout the entire year in a lake in Germany regardless of season.

It has been suggested that vertically migrating fishes undergo DVM to stay within light levels that maximise foraging while minimising predation risk (Ahrenstorff et al., 2011; Clemens & Crawford, 2009). Hrabik et al. (2006) concluded that data from hydroacoustic surveys in Lake Superior suggests that ambient light levels and siscowet lake trout (*Salvelinus namaycush siscowet*) controlled DVM in deepwater ciscoes including bloater. It is possible that the vertical distribution of *Mysis*, position of the thermocline during stratified conditions, and predator distributions influence bloater DVM in Lake Ontario.

Direction and movement of bloater 24 hr following release showed dispersal from the release site towards the north-east waters of the St. Lawrence Channel, suggesting preference for deeper waters (>40 m) and bathymetric structure. The directional movement of bloater to deep waters several kilometres from the release point is consistent with findings from other studies that have shown that bloater are generally found at depths of >35 m (Gorman et al., 2012a, 2012b; Jobes, 1949; Wells, 1968). Although similar depths are present to the southwest following the channel into the deeper (>60 m) open lake, the majority of bloater followed the channel to the northeast. Movement of tagged bloater towards the northeast may be the result of bloater actively moving with the current and following bathymetric structure prior to acclimatisation.

Bloater had limited overlap in activity space at locations further from the release point, which is likely to be influenced by a shorter detection period and smaller activity space for the fish that either died or left the array shortly after release. Although the mean extent of activity space (95% AKDE) across all release groups was >80 km^2, space use increased with the number of days detected and varied between years of the study. Increased overall horizontal space use associated with longer survival and detection periods indicates that bloater disperse to new areas rather than staying at the release location. One live bloater in the autumn 2017 release group was detected on receivers *c*. 20 km west of the release site where receivers are deployed in shallower waters (20–30 m). Bloater exhibit preference for a narrow range of cool temperature (4–11°C) that correspond to hypolimnetic waters (Crowder & Crawford, 1984; Eshenroder et al., 1998; Wells, 1968); however, during the winter months, the lake is isothermal, so it is possible that bloater expanded their space use into shallower water within their thermal preference range. The discrepancies in the number of bloater with detection data in the autumn (n = 32) compared to the spring (n = 2) and the short detection periods limited our ability to conduct seasonal comparisons in movement. Space used by bloater may vary with environmental conditions and could be much larger, particularly over longer periods than the current study or with a large receiver array. Research on the movement of bloater is limited seasonally with most studies occurring in the autumn and summer and few during the spring, but studies have previously shown that bloater occupy deep offshore waters in the autumn (Brandt et al., 1991; Koelz, 1929; Wells & Beeton, 1963).

The release groups with the largest sample sizes (autumn 2017 and autumn 2018) had similar core activity space and activity space extent sizes despite the smaller size of the autumn 2018 bloater (mean ± *SD*: 109 ± 23 g) relative to the autumn 2017 bloater (284 ± 44 g), indicating that fish size within the observed range does not influence horizontal space use. Taylor, Laffan, Fairfax, and Payne (2017) compared the movement patterns of hatchery-reared Mulloway (*Argyrosomus japonicus*) to wild Mulloway using acoustic telemetry and found significant differences in space use between wild and hatchery fish as well as a period of acclimatisation following release. Although the short-term tracking of bloater movements in this study may not be representative of long-term behaviour, no such data exist for bloater or other coregonids to compare. Similarly, the results from this study are limited by the spatial extent of our receiver array, which although large (*c*. 375 km^2), only covers a fraction of Lake Ontario (*c*. 19,000 km^2). Nevertheless, the high number of detections within our array and similar short-term space use patterns between size classes suggest no immediate distinction in behavioural response following stocking.

Although bloater within each release group exhibited a high degree of overlap in space use around the release location, they did not appear to aggregate and form schools within the array, even when a conservative approach was used. Other coregonids have exhibited schooling behaviour (Eckmann, 1991), which suggests that bloater may also display schooling. It is possible that due to the short period of time that many fish were detected in the array, the period of acclimatisation, and a relatively low number of tagged fish versus total stocked (*c*. 30 tags per 10,000–30,000 released fish) we did not witness schooling behaviour. Given the limited knowledge of bloater ecology, it may be possible that they school at different times of the year related to spawning and lake conditions (thermal stratification). Studying the movements and aggregations of stocked bloater is an important part of understanding their ecology and would contribute to improving stocking practices based on species-specific behaviour.

The occurrence of 13 suspected predation events supports recent findings in Klinard, Matley, Fisk, and Johnson (2019) that showed high predation (49%) of tagged bloater within *c*. 2 weeks following release. The autumn 2018 release group had more than twice as many suspected predation events (n = 7) than all other release groups. The autumn 2018 bloater were also smaller than other groups and most comparable in size to the tagged bloater in Klinard, Halfyard, et al. (2019), supporting the idea that smaller bloater are more vulnerable to predation. Lake trout are a common predator in Lake Ontario that are frequently present in our study site (unpublished data). While all tagged bloater are within the general prey size range of lake trout (Schoen & Beauchamp, 2010), the smaller bloater are vulnerable to predation by a wider range of lake trout (or other predators). Although it is difficult to assess predation without predation tags or more extensive detection data, we have stringently removed potential detections of predators that consumed tagged bloater. The short detection periods that show DVM characteristic of bloater were used to support cut-offs between bloater and predator movements in the filtered dataset. If it occurred that some predator detections were not removed, the data would probably be minimal and have a negligible impact on the results.

The four bloater that were never detected and the six that had minimal detection data (≤10 detections; most had only one detection) either left the array quickly, remained in the array undetected, or underwent rapid consumption/mortality followed by tags/fish sinking to the lake bottom beyond detection range. Detection efficiency of receivers around the stocking site could have been reduced during stocking because of the influx and density of tags at one location. As fish began to move and disperse, detection efficiency of receivers increased and thus, fish were likely to be detected moving throughout the array or exiting the array. Based on array configuration and known detection efficiency (80% at 600 m), we do not believe bloater or predators could swim out of the array undetected. Since receivers are suspended *c*. 2 m above the lake bottom with the hydrophone pointing upwards, it is possible that a tag remaining stationary on the lake bottom below the receiver could evade detection, especially considering the bathymetrical variation within the study site. Based on the above, we hypothesise that fish that were never detected or only detected in the middle of the array survived for a short period (<1 hr) before sinking to the bottom without further detection.

Excluding predators and fish with minimal or no detection data, tagged bloater displayed short-term (12 days) apparent survival (maximum 53%) following release. Assuming that fish with minimal or no data and those assessed as predated were all dead, 24/74 (32%) bloater survived this initial period. Based on a prior study evaluating tagging effects that showed high survival and no tag loss, we do not believe that surgery or tag presence caused mortality (Klinard et al., 2018). A survival rate of 32% is unsurprising considering the high predation rates observed by Klinard, Halfyard, et al. (2019) and natural stocking mortality. Survival of bloater was low initially with 16 individuals considered dead (constant depth at one location for a prolonged period) within 1 hr after release, which may be due to stress associated with stocking and acclimatising to a new environment. However, there were no evident differences in vertical space use between fish that survived and those that eventually died. Thorstad et al. (2012) used acoustic telemetry to examine post-stocking survival of hatchery-reared Atlantic salmon smolts stocked in a river and found survival over the first few days to be 12%. Similarly, Karam, Kesner, and Marsh (2008) used acoustic telemetry to examine post-stocking mortality of razorback sucker (*Xyrauchen texanus*) stocked in a lake and revealed a 2-week survival of 75% and subsequent 6-month survival of 16% with the main source of mortality believed to be predation. To our knowledge, there are currently no studies that examine the post-release survival of bloater or other deepwater ciscoes.

Of the 21 individuals that were alive at the time of their last detection, 10 were located near the outer receivers in the array, suggesting that they could have left the area and were not detected further due to receiver array extent. Since 2015, seven untagged bloater (of nearly 1 million stocked) have been captured in Lake Ontario bottom trawls (two in 2015, one in 2017, five in 2018) at maximum distances of 203 km from the stocking location (Weidel, Holden, & Connerton, 2019), at mean depths of 82 m.

The findings from this study can be used to adapt stocking practices to increase the survival of stocked bloater, and thus optimise the costs of rearing hatchery fish. Considering the high rates of predation bloater experience post-stocking, survival might be increased if bloater were exposed to predators prior to release (Beck & Rooker, 2012; Tang et al., 2017). Since bloater are reared in a hatchery setting, they may not develop the appropriate predator avoidance cues that wild fish have. A *soft release* in which fish are held in underwater pens for several days or weeks to adjust to their new environment would provide bloater with an opportunity to become accustomed to predators without direct exposure, thereby reducing initial predation rates. If stocked bloater are experiencing difficulty acclimatising to other aspects of the lake such as the light levels, depth, and pressure, a soft release can also provide more of a transition period for bloater to adjust. Given the very shallow depth use of bloater at night, night-time stocking might increase survival by introducing bloater into an environment that they would normally be in based on their DVM cycle. Not only would night-time stocking allow more time for bloater to acclimatise in shallow water before subsequently moving to depth, but it would also provide refuge from visual predators.

This study used acoustic telemetry to reveal movement and behaviour of bloater that has never been observed before at this resolution, producing results valuable to management of a reintroduced species, and demonstrating the value of acoustic telemetry in stocking and restoration efforts. Future studies should focus on expanding acoustic receiver coverage in Lake Ontario, which would help determine the fate of bloater and allow for more detection data beyond the current spatial extent of the array. Expanded spatial coverage would also allow fish to be stocked at different locations in smaller numbers while still being monitored to determine if one large stocking event and several smaller stocking events in various locations yield different results. Future studies should also aim to understand the effects of barometric pressure on stocked bloater when they swim to deep water (>40 m, four atmospheres) and explore the use of underwater remote-operated vehicles with attached tags to mimic movements of fish and assess detectability in various habitats. The findings from this study not only contribute to our understanding of the fundamental ecology of bloater and deepwater ciscoes as whole, but also address existing knowledge gaps about the fate of fish post-stocking, particularly for deepwater species for which data are sparse or non-existent.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon request.

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REFERENCES

Ahrenstorff, T. D., Hrabik, T. R., Stockwell, J. D., Yule, D. L., & Sass, G. G. (2011). Seasonally dynamic diel vertical migrations of *Mysis diluviana*, coregonine fishes, and siscowet lake trout in the pelagia of western Lake Superior. *Transactions of the American Fisheries Society*, *140*(6), 1504–1520. https://doi.org/10.1080/00028487.2011.637004

Bates, D., Maechler, M., Boker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beck, J. L., & Rooker, J. R. (2012). Effect of predator exposure on the performance and survival of red drum (*Sciaenops ocellatus*). *Environmental Biology of Fishes*, *93*(2), 267–276. https://doi.org/10.1007/s10641-011-9912-1

Bivand, R., & Lewin-Koh, N. (2019). *Maptools: tools for handling spatial objects. R package version 0.9-5*. https://CRAN.R-project.org/package=maptools.

Brandt, S. B. (1986). Food of trout and salmon in Lake Ontario. *Journal of Great Lakes Research*, *12*(3), 200–205. https://doi.org/10.1016/S0380-1330(86)71719-X

Brandt, S. B., Mason, D. M., Patrick, E. V., Argyle, R. L., Wells, L., Under, P. A., & Stewart, D. J. (1991). Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(5), 894–908. https://doi.org/10.1139/f91-106

Bunnell, D. B., Barbiero, R. P., Ludsin, S. A., Madenjian, C. P., Warren, G. J., Dolan, D. M., … Weidel, B. C. (2014). Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *BioScience*, *64*(1), 26–39. https://doi.org/10.1093/biosci/bit001

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Clemens, B. J., & Crawford, S. S. (2009). The ecology of body size and depth use by bloater (*Coregonus hoyii* Gill) in the Laurentian Great Lakes: Patterns and hypotheses. *Reviews in Fisheries Science*, *17*(2), 174–186. https://doi.org/10.1080/10641260802618375

Cowx, I. G. (1994). Stocking strategies. *Fisheries Management and Ecology*, *1*(1), 15–30. https://doi.org/10.1111/j.1365-2400.1970.tb00003.x

Crowder, L. B., & Crawford, H. L. (1984). Ecological shifts in resource use by bloaters in Lake Michigan. *Transactions of the American Fisheries Society*, *113*(6), 694–700. https://doi.org/10.1577/1548-8659(1984)113<694:ESIRUB>2.0.CO;2

Eckmann, R. (1991). A hydroacoustic study of the pelagic spawning behaviour of whitefish (*Coregonus lavaretus*) in Lake Constance. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(6), 995–1002. https://doi.org/10.1139/f91-116

Eshenroder, R. L., Argyle, R. L., & TeWinkel, L. M. (1998). Evidence for buoyancy regulation as a speciation mechanism in Great Lakes ciscoes. *Archiv Für Hydrobiologie Special Issues, Advances in Limnology*, *50*, 207–217.

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

Favé, M.-J., & Turgeon, J. (2008). Patterns of genetic diversity in Great Lakes bloaters (*Coregonus hoyi*) with a view to future reintroduction in Lake Ontario. *Conservation Genetics*, *9*(2), 281–293. https://doi.org/10.1007/s10592-007-9339-6

Fleming, C. H., & Calabrese, J. M. (2017). A new kernel density estimator for accurate home-range and species-range area estimation. *Methods in Ecology and Evolution*, *8*(5), 571–579. https://doi.org/10.1111/2041-210X.12673

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator. *Ecology*, *96*(5), 1182–1188. https://doi.org/10.1890/14-2010.1

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

Gorman, O. T., Yule, D. L., & Stockwell, J. D. (2012b). Habitat use by fishes of Lake Superior. II. Consequences of diel habitat use for habitat linkages and habitat coupling in nearshore and offshore waters. *Aquatic Ecosystem Health and Management*, *15*(3), 355–368. https://doi.org/10.1080/14634988.2012.711664

Honeyfield, D. C., Hinterkopf, J. P., Fitzsimons, J. D., Tillitt, D. E., Zajicek, J. L., & Brown, S. B. (2005). Development of thiamine deficiencies and early mortality syndrome in lake trout by feeding experimental and feral fish diets containing thiaminase. *Journal of Aquatic Animal Health*, *17*(1), 4–12. https://doi.org/10.1577/H03-078.1

Hrabik, T. R., Jensen, O. P., Martell, S. J. D., Walters, C. J., & Kitchell, J. F. (2006). Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(10), 2286–2295. https://doi.org/10.1139/F06-124

Jobes, F. W. (1949). The age, growth, and bathymetric distribution of the bloater, *Leucichthys hoyi* (Gill) in Lake Michigan. *Papers of the Michigan Academy of Science, Arts, and Letters*, *33*, 135–172.

Karam, A. P., Kesner, B. R., & Marsh, P. C. (2008). Acoustic telemetry to assess post-stocking dispersal and mortality of razorback sucker *Xyrauchen texanus*. *Journal of Fish Biology*, *73*(3), 719–727. https://doi.org/10.1111/j.1095-8649.2008.01947.x

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6420), aaa2478-1. https://doi.org/10.1126/science.aaa2478

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

Klinard, N. V., Halfyard, E. A., Matley, J. K., Fisk, A. T., & Johnson, T. B. (2019). The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. *Animal Biotelemetry*, *7*(17), 1–17. https://doi.org/10.1186/s40317-019-0179-1

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

Koelz, W. (1929). Coregonid fishes of the Great Lakes. *Bulletin of the United States Bureau of Fisheries*, *43*(2), 297–643.

Long, J. (2014). *wildlifeDI: calculate indices of dynamic interaction for wildlife telemetry data. R package version 0.2*. https://CRAN.R–project.org/package=wildlifeDI.

Mehner, T., Kasprzak, P., & Hölker, F. (2007). Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(6), 874–886. https://doi.org/10.1139/F07-067

Mills, E. L., Casselman, J. M., Dermott, R., Fitzsimons, J. D., Gal, G., Holeck, K. T., … Stewart, T. J. (2003). Lake Ontario: Food web dynamics in a changing ecosystem (1970–2000). *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 471–490. https://doi.org/10.1139/F03-033

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

Noonan, M. J., Tucker, M. A., Fleming, C. H., Akre, T. S., Alberts, S. C., Ali, A. H., … Calabrese, J. M. (2019). A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs*, *89*, e01344. https://doi.org/10.1002/ecm.1344

Ontario Ministry of Natural Resources & Forestry. (2015). *Stocking strategy for the Canadian waters of Lake Ontario*. Lake Ontario Management Unit, Ontario Ministry of Natural Resources & Forestry, Picton, ON, Canada.

Owens, R. W., O'Gorman, R., Eckert, T. H., & Lantry, B. F. (2003). The offshore fish community in southern Lake Ontario, 1972–1998. In M. Munawar (Ed.), *State of Lake Ontario – past, present and future* (pp. 407–441). Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Ontario, Canada.

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/.

R Development Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Schoen, E. R., & Beauchamp, D. A. (2010). *Predation impacts of lake trout and Chinook salmon in Lake Chelan, Washington: implications for prey species and fisheries management*. U.S. Geological Survey Report #WACFWRU-010-01, Washington Cooperative Fish and Wildlife Research Unit, University of Washington, Seattle.

Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimate of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movement. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(1), 23–32. https://doi.org/10.1139/F01-191

Tang, L., Jacquin, L., Lek, S., Liu, H., Li, Z., Liu, J., & Zhang, T. (2017). Differences in anti-predator behavior and survival rate between hatchery-reared and wild grass carp (*Ctenopharyngodon idellus*). *Annales De Limnologie – International Journal of Limnology*, *53*, 361–367. https://doi.org/10.1051/limn/2017020

Taylor, M. D., Laffan, S. W., Fairfax, A. V., & Payne, N. L. (2017). Finding their way in the world: Using acoustic telemetry to evaluate relative movement patterns of hatchery-reared fish in the period following release. *Fisheries Research*, *186*, 538–543. https://doi.org/10.1016/j.fishres.2016.07.003

TeWinkel, L. M., & Fleischer, G. W. (1999). Vertical migration and night-time distribution of adult bloaters in Lake Michigan. *Transactions of the American Fisheries Society*, *128*(3), 459–474. https://doi.org/10.1577/1548-8659(1999)128<0459:VMANDO>2.0.CO;2

Thorstad, E. B., Uglem, I., Finstad, B., Chittenden, C. M., Nilsen, R., Økland, F., & Bjørn, P. A. (2012). Stocking location and predation by marine fishes affect survival of hatchery-reared Atlantic salmon smolts. *Fisheries Management and Ecology*, *19*(5), 400–409. https://doi.org/10.1111/j.1365-2400.2012.00854.x

Weidel, B. C., Holden, J. P., & Connerton, M. J. (2019). *Bottom trawl assessment of Lake Ontario prey fishes* (pp. 12.1–12.18). NYSDEC 2018 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.

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

Wells, L. (1969). *Fishery survey of U.S. waters of Lake Ontario. Great Lakes Fishery Commission Technical Report No. 14* (pp. 51–57). Great Lakes Fishery Commission, Ann Arbor, MI.

Wells, L., & Beeton, A. M. (1963). Food of the bloater, *Coregonus hoyi*, in Lake Michigan. *Transactions of the American Fisheries Society*, *92*(3), 245–255. https://doi.org/10.1577/1548-8659(1963)92%5B245%3AFOTBCH%5D2.0.CO%3B2

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., … Zeller, D. (2009). Rebuilding global fisheries. *Science*, *325*(5940), 578–585. https://doi.org/10.1126/science.1173146

Zimmerman, M. S., & Krueger, C. C. (2009). An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. *North American Journal of Fisheries Management*, *29*(5), 1352–1372. https://doi.org/10.1577/M08-194.1

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