Journal of Great Lakes Research xxx (xxxx) xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/ijglr

Results of the collaborative Lake Ontario bloater restoration stocking and assessment, 2012–2020

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ARTICLE INFO

Article history:
Received 31 May 2021
Accepted 3 November 2021
Available online xxxx
Communicated by: James Watkins

Keywords:
Bloater
Coregonus hoyi
Lake Ontario
Restoration
Reestablishment
Bottom trawl

ABSTRACT

Bloater, *Coregonus hoyi*, are deepwater planktivores native to the Laurentian Great Lakes and Lake Nipigon. Interpretations of commercial fishery time series suggest they were common in Lake Ontario through the early 1900s but by the 1950s were no longer captured by commercial fishers. Annual bottom trawl surveys that began in 1978 and sampled extensively across putative bloater habitat only yielded one individual (1983), suggesting that the species had been locally extirpated. In 2012, a multiagency restoration program stocked bloater into Lake Ontario from gametes collected in Lake Michigan. From 2012 to 2020, 1,028,191 bloater were stocked into Lake Ontario. Bottom trawl surveys first detected stocked fish in 2015, and through 2020 ten bloater have been caught (total length mean = 129 mm, s.d. = 44 mm, range: 96–240 mm). Hatchery applied marks and genetic analyses confirmed the species identification and identified stocking location for some individuals. Trawl capture locations and acoustic telemetry suggested that stocked fish dispersed throughout the main lake within months or sooner, and the depth distribution of recaptured bloater was similar to historic distributions in Lake Ontario and other Great Lakes. Predicted bloater trawl catches, based on modeled population abundance and trawl survey efficiency, were similar to observed catches, suggesting that post-stocking survival is less than 20% and contemporary bottom trawl surveys can quantify bloater abundance at low densities and track restoration.

Introduction

Bloater, *Coregonus hoyi*, were one of several native coregonines that primarily inhabited deepwater pelagic habitats of the four deepest Laurentian Great Lakes and Lake Nipigon (Eshenroder et al., 2016). As invertivores, bloater play a unique role in large, deep, oligotrophic lakes, vertically migrating through pelagic habitats (Hrabik et al., 2006) and serving as prey for native piscivore such as lake trout, *Salvelinus namaycush* (Fratt et al., 1997;

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[1] Given their role as Associate Editor, Timothy B. Johnson had no involvement in the peer-review of this article and has no access to information regarding its peer-review. Full responsibility for the editorial process for this article was delegated to James Watkins.

https://doi.org/10.1016/j.jglr.2021.11.014
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Pritchard et al., 1931). Bloater are frequently captured in the three most-upstream Great Lakes (Bunnell et al., 2006; Gorman et al., 2012; Harford et al., 2012); however, the Lake Ontario population was considered extirpated by the mid 1900s along with other deepwater coregonines, kiyi, *Coregonus kiyi* and shortnose cisco *Coregonus reighardi* (Christie, 1972; Owens et al., 2003). The decline and disappearance of Lake Ontario bloater has been attributed to anthropogenic impacts including degraded water quality, predation by sea lamprey, interactions with nonnative planktivores, and overfishing (Christie 1973; Smith 1972).

Our understanding of historical Lake Ontario bloater population dynamics is limited since the species was infrequently targeted in commercial fisheries and current commercial landings data do not differentiate most coregonine landings to species. Smith (1892) noted the Lake Ontario commercial fishery began targeting bloater in the late 1800s after other tributary and nearshore salmonid fisheries had been depleted. A commercial fishing landings database lists catches of deepwater 'chubs' (including bloater) and shallow water ('cisco', *Coregonus artedi*) as a single summed catch until 1951, and afterwards distinguished catches of these two groups of coregonines (Baldwin et al., 2018). By applying species composition data from fishery independent data from the mid-1900s to the commercial landing of 'chubs', we can assume bloater declined markedly from 1952, with the last reported landing of 1000 lb occurring in 1969 (Baldwin et al., 2018).

Fishery independent surveys also suggest the Lake Ontario bloater population declined during the mid-1900s, while the lack of observations in contemporary surveys suggests they were locally extirpated. In 1942, Stone (1947) caught over 2,300 deep water coregonines in 27 gill nets, with bloater comprising 92% of the catch. A similar 1964 survey captured only 13 deep water coregonines, nine of which were bloater (Wells, 1969). Wells (1969) estimated a decline in nightly gill net catch rate of deepwater coregonines from 52 per net night in 1942, to one per net night in 1964, and 0 in 1966. In 1972, a seasonally-distributed, lake-wide bottom trawl and gill net survey captured a single bloater near Port Credit, Ontario (O'Gorman et al., 1989). Contemporary annual fishery independent surveys began in 1962 in Canada and in 1978 in U.S. waters and despite thousands of gill net and bottom trawl samples, fished in putative bloater habitats, only one bloater was captured in a 1983 bottom trawl (Owens et al., 2003).

Lake Ontario fish community objectives seek to increase prey fish diversity by re-establishing deepwater coregonines, including bloater (Stewart et al., 2017). Bloater would provide native predators (e.g., lake trout and Atlantic salmon, *Salmo salar*) a prey fish alternative to alewife, *Alosa pseudoharengus*, which are the dominant Lake Ontario prey fish (Weidel et al., 2020). Alewife often have high thiaminase activity, a thiamine-degrading enzyme linked to reproduction deficiencies in salmonines (Honeyfield et al., 2005; Ketola et al., 2000). Increasing the diversity of the Lake Ontario prey fish community by restoring bloater can offer greater resilience to species invasions and a changing climate, and by restoring native prey fish could benefit native predator restoration by ameliorating the effects of thiaminase containing prey.

Bloater were first stocked into Lake Ontario in November 2012 with fish raised from gametes collected in Lake Michigan. Gamete collection and culture details are fully described in Holey et al. (in press) and Smith et al. (in press). Here we describe restoration stocking and evaluation of bloater in Lake Ontario from 2012 to 2020. We report the number and characteristics of stocked fish and recaptures from fishery-independent bottom trawl surveys. We evaluate the presence of hatchery applied marks in bloater calcified structures and confirmed species identification with a GTseq panel (Campbell et al., 2015), currently in development to detect high differentiation loci for putative bloater. We summarize morphometric, meristic, and diet data from bloater captured from trawl surveys, and lake-wide acoustic telemetry data from fishes detected from 2015 to 2021. Finally, we developed a simple population model to estimate a population abundance range and likelihood of catching a bloater in the April bottom survey and compared those estimates to our observed bloater catches.

Methods

We summarized bloater stocking based on agency databases and annual reports including the New York State Department of Environmental Conservation (NYSDEC) Lake Ontario Fisheries Unit annual reports (https://www.dec.ny.gov/outdoor/27068.html) and the Ontario Ministry of Northern Development, Mines, Natural Resources, and Forestry (NDMNRF) Lake Ontario Management Unit (http://www.glfc.org/loc_mgmt_unit/, Fig. 1). All bloater stocked in Lake Ontario originated from either wild-collected gametes from Lake Michigan or from brood stock developed from that same source. From 2014 to 2020, bloater stocked in U.S. waters of Lake Ontario were marked with either calcein or alizarin red as described in Chalupnicki et al. (2016), and all releases in U.S. waters occurred offshore, adjacent to deep water, near Oswego, NY (Fig. 2). Bloater stocked in Canadian waters were not marked and were primarily released by tugs at various locations away from shore, however, some stocking also occurred along the shoreline and in conjunction with acoustic telemetry research (Table 1, Fig. 2).

Seasonally distinct bottom trawl surveys have been conducted annually in U.S. waters primarily in April, June, July, and October and target different Lake Ontario prey fishes and juvenile lake trout (Table 2). Surveys differ in their spatial and temporal extent; however, all were conducted during the day, with tows oriented along depth contours, over depths from 5 to 225 m. Two different trawl configurations were used including: a 12 m headrope nylon Yankee trawl, and an 18 m headrope polypropylene trawl with an elevated foot rope and cookie sweep. More detailed descriptions of trawl survey designs are available in Lantry et al. (2007).

Community index bottom trawl surveys have sampled Canadian waters since 1962. These surveys have primarily sampled in the Bay of Quinte, the Kingston Basin (Virdin et al., 2000), and south of Prince Edward County, Ontario, however, their effort was generally lower than surveys in U.S. waters (Table 2). Trawls in the Bay of Quinte used a 3/4 Western Trawl while Kingston

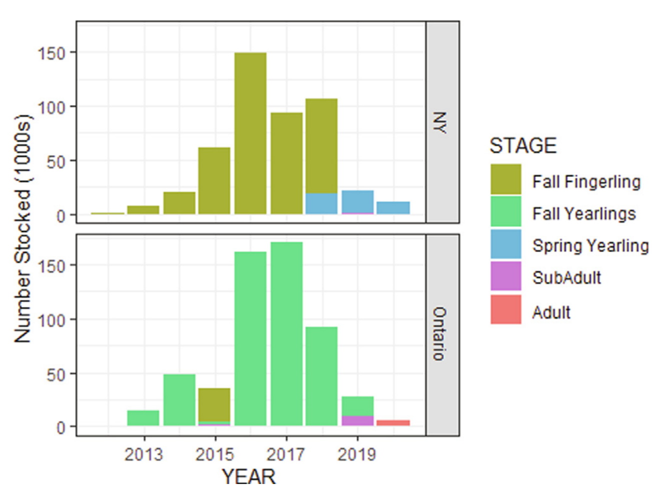

Fig. 1. The number and life stage of Bloater stocked into NY and Canadian waters of Lake Ontario, 2012–2020. The reduced number of bloater stocked in 2019 and 2020, resulted from transitioning from wild caught gametes to brood stock gametes and initial low levels of fertilization and survival in these new processes.

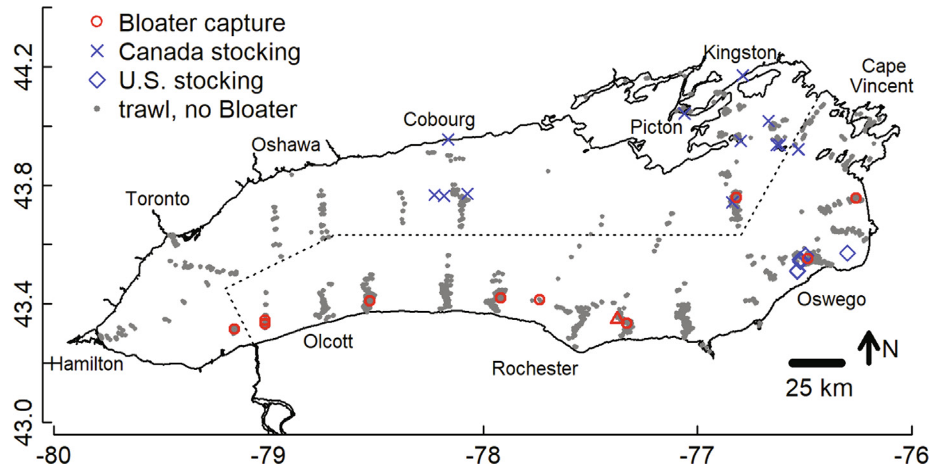

Fig. 2. Lake Ontario bloater stocking locations (blue symbols), bottom trawls that captured bloater (red open circles), and trawls where bloater were not captured (gray circles, n = 3380), 2013–2019. The red open triangle illustrates where the last native bloater was captured in 1983 prior to restoration stocking (Owens et al., 2003). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Bloater stocked into Lake Ontario waters of United States (U.S.) and Canada (CA) from 2012 to 2020. All fish were stocked by vessel unless otherwise indicated (pier, ramp). Age and weight values represent means.

	Month	Year	Location	Depth (m)	Stage	Mark	Number	Age (Months)	Weight (g)
U.S.	11	2012	Oswego	105	FF		1200	6.4	6.2
	11	2013	Oswego	105	FF		7310	7.4	10.6
	11	2014	Oswego	109	FF	calcein	20,000	7.5	8.5
	11	2015	Oswego	105	FF	calcein	61,617	6.8	7.6
	11	2016	Oswego	104	FF	alizarin	149,353	6.8	3.2
	11	2017	Oswego	105	FF	calcein	93,553	6.4	5.1
	5	2018	Oswego	60	SY	AD- double calcein	11,721	11.7	9.8
	5	2018	Oswego	59	SY	double calcein	6911	11.7	9.8
	11	2018	Oswego	58	FF	single calcein	87,674	6.4	2.8
	5	2019	Oswego	40	SY	AD- calcein	3815	12.2	5.9
	5	2019	Oswego	40	SY	double calcein	17,295	12.4	9.9
	11	2019	Oswego	40	Sub	AD- calcein	960	30.5	69.5
	5	2020	Mexico Bay	40	SY	single calcein	11,153	13.0	11.1
CA	11	2013	Rocky Point	99	FY		15,187	20.0	26.6
	11	2014	Cobourg	41	FY		13,256	19.0	36.0
	11	2014	Cobourg Deep	98	FY		35,239	19.0	24.0
	11	2015	Main Duck Isl.	18	FY		2100	31.0	92.0
	11	2015	Glenora Pier	5	FF		1027	20.0	49.1
	11	2015	Main Duck Isl.	18	FY		625	19.0	58.1
	11	2015	Main Duck Isl.	51	FF		31,845	8.0	3.6
	11	2016	Main Duck Isl.	51	FY		539	31.0	90.9
	11	2016	Main Duck Isl.	51	Sub		117,580	20.9	23.7
	11	2016	Station 81	36	FY		43,561	18.0	17.7
	4	2017	Main Duck Isl.	51	Adult		110	54.5	208.5
	4	2017	Main Duck Isl.	51	SY		880	13.0	5.7
	11	2017	Main Duck Isl.	51	FY		23	55.0	250.0
	11	2017	Main Duck Isl.	51	FY		26	32.0	150.0
	11	2017	Main Duck Isl.	51	Sub		12,441	20.0	36.1
	11	2017	Cobourg Deep	92	Adult		156,930	19.2	24.8
	5	2018	Main Duck Isl.	51	Sub		1074	26.0	36.0
	9	2018	Finkle's Ramp	8	FY		2850	19.0	24.6
	11	2018	Cobourg	71	FY		31,004	20.0	34.0
	11	2018	Main Duck Isl.	38	FY		9023	20.0	25.6
	11	2018	Cobourg Deep	98	FY		47,702	18.7	20.6
	11	2019	Cobourg	66	FY		9703	31.0	66.1
	11	2019	Cobourg Deep	66	Sub		17,733	18.0	19.0
	11	2020	Cobourg Deep	98	Adult		5171	43.0	126.1

FF = fall fingerling, FY = fall yearling, Sub = subadult, SY = spring yearling, AD = adipose fin clip. Calcein and alizarin are chemical marks applied in the hatchery that leave marks on bony structures of fishes and have been applied as a single or double mark.

Basin and lake sites were sampled using a 12 m headrope Yankee trawl (Christie et al., 1987). All tows were conducted in summer months (June–September). Additional details on trawls and survey design are available in Christie et al. (1987) and Hoyle et al. (2012).

Bottom trawl catches were sorted to species, counted, weighed, and measured. For large catches (>5 kg), the catch was subsampled with rare fishes, including bloater, picked from the discarded portions. Putative bloater were identified in the field and distin-

Table 2
Lake Ontario bottom trawl survey effort prior to bloater restoration stocking (1962–2012, upper five rows) and since stocking began (2013 – 2019, lower six rows). Bloater stocking in 2012 occurred after all surveys had been completed such that the first surveys that could have captured stocked bloater were in 2013. Precautions related to COVID-19 prevented some 2020 surveys from being conducted.

Area	Month	Year Range	Years (n)	Mean tows ($n \cdot yr^{-1}$, s.d.)	Mean Trawl Time ($hrs \cdot yr^{-1}$)	Mean Prop. Lake ($prop. \cdot yr^{-1}$)	Bloater (n)
U.S.	Apr	1978–2012	35	103 (20)	15.5	8.5×10^{-5}	1
U.S.	Jun	1978–2012	35	92 (10)	13.6	6.9×10^{-5}	0
U.S.	Jul	1978–2012	35	93 (17)	15.1	7.6×10^{-5}	0
U.S.	Oct	1978–2012	34	54 (19)	8.1	4.5×10^{-5}	0
CA	Jun-Sep	1962–2012	56	47 (25)	5.5	3.3×10^{-5}	0
U.S.	Apr	2013–2019	7	131 (29)	15.7	9.2×10^{-5}	5
U.S.	Jul	2013–2019	7	94 (36)	15.2	8.2×10^{-5}	2
U.S.	Oct	2013–2020	8	86 (18)	6.5	5.0×10^{-5}	2
CA	Apr	2016–2019	4	65 (15)	6.8	3.6×10^{-5}	0
CA	Oct	2015–2020	6	43 (8)	3.6	2.3×10^{-5}	0
CA	Jun-Sep	2013–2019	7	44 (25)	3.5	2.2×10^{-5}	1

guished from cisco, based on fin length ratios. Identifications were verified with genetic analyses and by observing hatchery-applied marks on rib bones. Bloater were photographed and frozen whole for morphometric analysis. Tissue, stomach, and calcified structures were collected and analyzed in the lab. Bloater rib bones were mounted in epoxy, sectioned, and observed under a compound microscope equipped with epi-fluorescence capability to determine if calcein marks were present as described in Chalupnicki et al. (2016). Bloater stomach contents were examined with a stereo microscope and contents were identified to the lowest practical taxon and counted.

Tissue for genetic assignment was available from 9 out of the 11 putative bloater (1 from 1983, 10 recent). DNA was extracted and amplified at 514 target loci from an in-development GT-seq (Campbell et al., 2015) panel refined from restriction site-associated DNA sequencing (RAD-seq) data from populations across the Great Lakes following the protocols described in Bootsma et al. (2021). Sequence data were filtered and processed in GTScore v1.3 (McKinney et al., 2020). GT-seq genotypes for 148 reference individuals from Lakes Michigan & Huron (bloater) and Lake Ontario (cisco) were mined from RAD-seq data that was generated following methods described in Ackiss et al. (2020). A final dataset of shared loci genotyped in both reference individuals and putative bloater samples assigned putative bloater to source populations with the R package assignPOP (Chen et al., 2018). Detailed genetic assignment methods can be found in Electronic Supplementary Material Appendix S1 and locus information in Table S1.

A total of 360 acoustic tagged bloater (age-1 to age-3) have been released in Lake Ontario since 2015. Post-stocking survival and behavior results have been described from the St. Lawrence channel of eastern Lake Ontario (Klinard et al., 2021, 2020, 2019). We reported the spatial extent and depths where bloater were detected in the rest of Lake Ontario. Other receivers were deployed in western Lake Ontario (n = 5 in 2015; 12 in 2016; 48 in 2017; 56 in 2018; 77 in 2019), the Bay of Quinte, Toronto Harbour, Hamilton Harbour, and the Niagara River (Fig. 3). Tagged bloater were released in the St. Lawrence channel array from November 2015 through September 2020. Receivers included a logging hydrophone suspended ~2 m above the lake bottom and were downloaded annually during the summer. Depth distribution of acoustic tag detections was reported according to the receiver depth in 20 m depth categories across seasonal time periods defined as spring (May-Jun), summer stratified (Jul-Oct), fall turnover (Nov-Dec), and winter isothermal (Jan-Apr). Tag detections were filtered to remove detections believed to be dead or predated bloater based on repeated detections over multiple days at a single receiver (Klinard et al., 2020). Because the depth distribution of receivers was uneven within 20 m categories, we reported the mean number of bloater detections per receivers within a depth strata.

Morphometry and meristic traits of Lake Ontario bloater were quantified and compared to bloater from other lakes and to Lake Ontario cisco. Bloater gill rakers were counted and morphometric measurements were collected from thawed fish using a digital caliper as described O'Malley et al. (2020). We converted morphometric measurements to ratios to account for size differences among samples and compare to the same measurements from Lake Superior (2004–2010) and Michigan (2008–2011) bloater in Eshenroder et al. (2016), and from small (<250 mm TL) cisco captured in Lake Ontario surveys (2015–2020). For each trait, we considered Lake Ontario bloater to be different from other populations if the difference between means was more than twice that of the smallest of the two standard deviations using these values (Eshenroder et al., 2016). We compared morphology of bloater to Lake Ontario cisco with t-tests.

We evaluated the effectiveness of current bottom trawl surveys for tracking the bloater restoration using a simple population model with assumed survival rates and bottom trawl survey effort. We calculated bloater abundance in U.S. waters in April, assuming post-stocking survival of 5% or 20% from U.S. fall stocking to the following April and 58% annual survival each year thereafter (Brown et al., 1985). The proportion of U.S. waters swept by bottom trawls was calculated as the annual summed area swept by all bottom trawls (wing widths) and a value of 9101 km^2 for the U.S. area of Lake Ontario. We assumed a catchability of one for bloater within the area swept by the bottom trawl. The expected bloater catch was the product of the annual low and high population estimates and the proportion of the lake swept in a year.

Results

Between 2012 and 2020, 1,028,191 bloater were stocked in Lake Ontario (Table 1, Fig. 1). Stocking locations in U.S. waters were initially in ~100 m depth near Oswego, NY; but since 2019, bloater have been released in approximately 50 m depth, from stocking trucks loaded on to barges to reduce handling stress (Fig. 2). Stocking in Canada was more dispersed and included acoustic tagged fish. The majority of bloater (65%) were stocked as either fall yearlings in Ontario or fall fingerlings in New York (Fig. 1, Table 1).

From 1962 to 2012, only a single bloater was caught in annual Lake Ontario bottom trawl surveys that sampled putative bloater habitats (Table 2). From 2013 to 2020, 10 bloater have been captured by bottom trawls in Lake Ontario with the first catch in 2015 (Table 3). Nine of the bloater were caught along the lake's south shoreline (Fig. 2). Seven of the 10 recaptured bloater contained calcein marks indicating they were from the U.S. stockings (Table 3).

Eight of the nine bloater could be assigned to the Lake Michigan/Huron bloater population with >94% membership probability

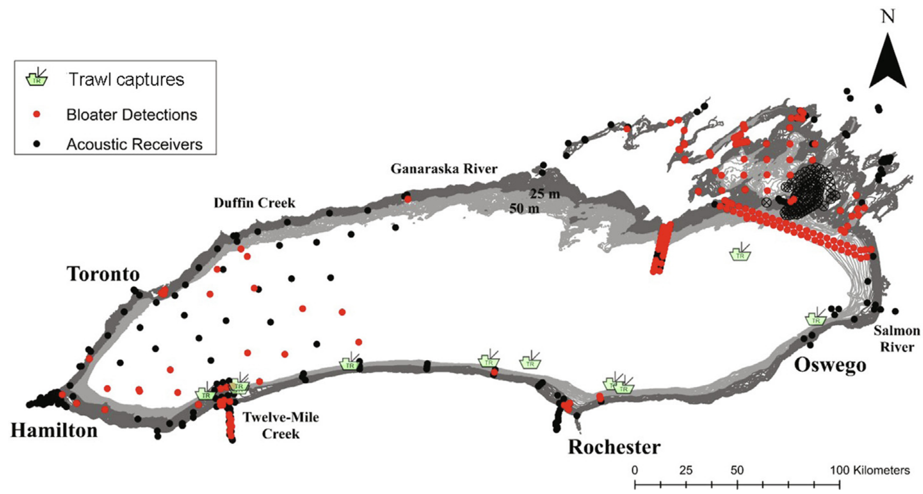

Fig. 3. Lake Ontario acoustic telemetry receiver locations that did (red filled circles) and did not (black filled circles) detect acoustic tagged bloater, 2015–2020. Detections in St. Lawrence Channel array, where bloater were released (dense cluster of open circles, eastern Lake Ontario) were excluded to illustrate the pattern of detections in the remaining portions of the lake. The dark gray region illustrates bathymetric regions to a depth of 25 m while the lighter gray regions illustrate bathymetry to 50 m depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Lake Ontario bloater catches from bottom trawl surveys, 1983–2019. Depth represents the depth of capture in bottom trawls. Empty spaces represent no data available. A 'c' in the mark column denotes a calcein mark was present. The Tissue ID column is included to match individual fish data from this table to Table 4.

Date	Depth (m)	Temp. (C°)	Length (mm)	Wt. (g)	Sex	Mark	Region	Latitude	Longitude	Tissue ID
28-Apr-1983	110.0	3.6	272	182.0			Smoky Pt.	43.34667	−77.37333	
8-May-2015	95.0	3.5	125	10.2		c	Oswego	43.55329	−76.48644	HOY6139
5-Jul-2017	90.0		130	14.0		c	Rocky Pt.	43.75896	−76.81866	
22-Apr-2018	60.0	2.7	108	6.0		c	Youngstown	43.33334	−79.01683	HOY6142
22-Apr-2018	75.0	2.7	102	4.0		c	Youngstown	43.34472	−79.01634	HOY6143
25-Apr-2018	95.0	2.6	96	5.0		c	Hamlin	43.41968	−77.92026	HOY6144
14-Oct-2018	75.0	4.1	117	8.9		c	30-Mile Pt.	43.41018	−78.52961	HOY6138
23-Oct-2018	78.0	9.8	240	122.0	F		Smoky Pt.	43.33526	−77.32985	HOY6140
23-Apr-2019	65.0	2.6	87	2.8			Fairhaven	43.41498	−77.73905	HOY6141
19-Jul-2019	26.0	4.1	160	20.9	M		Southwicks	43.75657	−76.26048	HOY6136
24-Jul-2019	72.6	4.1	123	13.6	M	c	Niagara	43.31502	−79.16077	HOY6137

Table 4
Statistics for genotyped bloater. Primer-probe reads are the total number of sequences that contained both the forward primer and the SNP probe. The % of genotyped loci is the proportion of loci in the final dataset of 849 SNPs that were genotyped in the bloater specimens. Membership probability to either cisco of Lake Ontario origin or bloater of Lake Michigan/Huron origin was generated from a panel of 590 SNPs shared between reference and bloater samples calculated in assignPOP (Chen et al., 2018).

Tissue ID	Collection date	# Primer-probe reads	% missing data (# loci)	Membership probability		Genetic ID
				C. artedi	*C. hoyi*	
HOY6136	7/19/2019	24,675	0.000 (0)	0.034	0.966	*C. hoyi*
HOY6137	7/24/2019	40,379	0.004 (3)	0.038	0.962	*C. hoyi*
HOY6138	10/14/2018	16,293	0.005 (4)	0.052	0.948	*C. hoyi*
HOY6139	5/8/2015	9,775	0.001 (1)	0.050	0.950	*C. hoyi*
HOY6140	10/23/2018	29,030	0.000 (0)	0.061	0.939	*C. hoyi*
HOY6141	4/23/2019	40,594	0.000 (0)	0.053	0.947	*C. hoyi*
HOY6142	4/22/2018	20,337	0.001 (1)	0.028	0.972	*C. hoyi*
HOY6143	4/22/2018	1,047	0.647 (549)	–	–	–
HOY6144	4/25/2018	3,957	0.019 (16)	0.017	0.983	*C. hoyi*

(Table 4). A total of 566,325 sequences were generated for the nine specimens genotyped with the GTseq panel. Of these, 186,087 sequences contained both the forward primer and a target SNP region with genotype information (probe; see Table 4). One sample (HOY6143, Table 4) was dropped from the analysis due to high amounts of missing data likely due to tissue sample quality. After filtering, 590 SNPs were shared between the reference individuals and the 8 genotyped bloater specimens and used for genetic assignment (ESM Table S1 for amplicon sequence and SNP information).

Over 500,000 detections of acoustic tagged bloater were observed on Lake Ontario receivers between November 2015 and June 2021, excluding detections within the St. Lawrence channel receiver array (Fig. 3). After data filtering procedures for dead or predated tagged bloater there were ~18,000 detections, from 53 of 360 tagged bloater, that were detected on 172 different acoustic receivers in Lake Ontario (Fig. 3, Table 5). Time of detection post-release ranged from 2.2 to 656.8 days with an average of 147.4 days. Depth distribution of detections differed with depth and season (Table 5).

Table 5
Total acoustic telemetry receivers and the number of those that detected tagged bloater in Lake Ontario over depth strata. Seasonal values represent the mean number of acoustic tag bloater detections per receiver per depth strata in Lake Ontario between Nov 2015 and Jun 2020. Acoustically tagged bloater were stocked in November (n = 297) or May (n = 67). Bloater detected on receivers in the St Lawrence Channel array were excluded from the analysis (Fig. 3). Seasonal categories were divided according to spring mixing (May–Jun), summer stratified (Jul–Oct), fall turnover (Nov–Dec), and winter isothermal (Jan–Apr).

Depth strata (m)	Total receivers	Receivers detecting bloater	May–Jun	Jul–Oct	Nov–Dec	Jan–Apr	Total
0–20	95	78	15	2	33	29	79
20–40	64	48	45	59	52	16	172
40–60	50	24	64	29	15	28	137
60–80	20	7	2	2	0	0	4
80–100	6	6	7	6	4	0	17
100–120	8	5	71	0	3	0	74
120–140	5	1	87	0	0	0	87
140–160	3	2	12	4	0	0	16
160–180	1	1	0	124	0	0	124

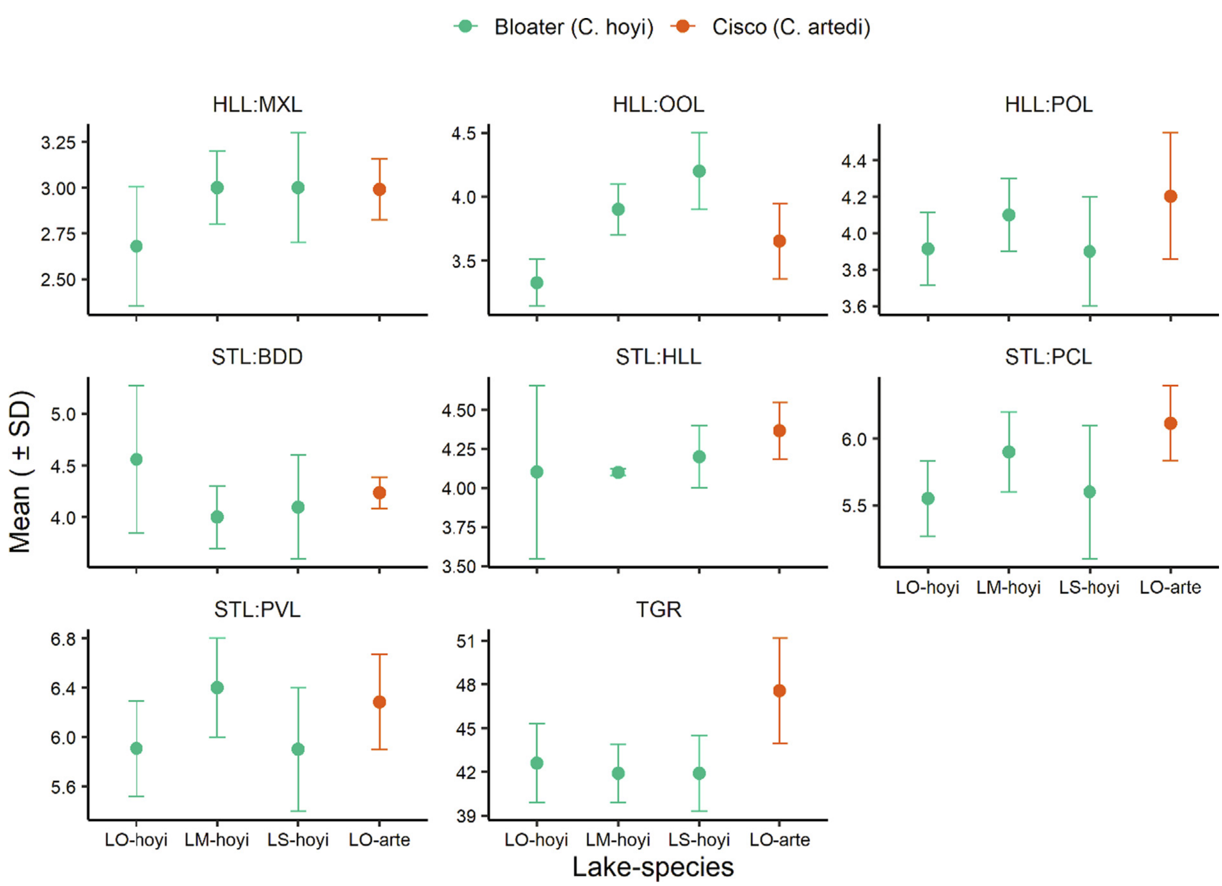

Fig. 4. Mean (±s.d.) morphometric ratios and one meristic of Lake Ontario bloater, *Coregonus hoyi* (LO-hoyi), Lake Michigan bloater (LM-hoyi), Lake Superior bloater (LS-hoyi), and Lake Ontario cisco (LO-arte), *Coregonus artedi*. Lakes Michigan and Superior bloater data is from (Eshenroder et al., 2016). Morphometric and meristic measurements are as follows: BDD = body depth; HLL = head length; MXL = maxillary length; OOL = orbital length; PCL = pectoral fin length; POL = preorbital length; PVL = pelvic fin length; STL = standard length; TGR = total gillraker count.

Morphological analysis indicated that recaptured Lake Ontario bloater had shorter snouts and heads, and shallower bodies than wild counterparts in Lakes Michigan and Superior (Fig. 4). The head to orbital length ratio was lower in Lake Ontario stocked bloater than in Lakes Michigan and Superior. Gillraker counts of Lake Ontario bloater (42.6 ± 2.7 SD) were similar to Lakes Michigan and Superior but significantly lower than Lake Ontario cisco (47.6 ± 3.6, p = 0.01). Compared to Lake Ontario cisco, Lake Ontario bloater differed by two out of seven morphometric ratios. The mean head to orbital length ratio in bloater (3.3 ± 0.2) was lower than for cisco (3.7 ± 0.3), and the standard length to pectoral fin length ratio was lower in bloater (5.6 ± 0.3) than for cisco (6.2 ± 0.3).

We examined seven bloater stomachs and five of those were empty. The individual captured on 14 October 2018 at a depth of 75 m contained 13 *Mysis diluviana*. The individual captured on 19 July 2019 in 26 m of water contained 37 cyclopoid copepods, six *Daphnia* sp., two *Daphnia galeata mendotae*, and 1 *Daphnia retrocurva*.

Based on our assumptions about stocked bloater survival, the estimated number of bloater in U.S. waters of Lake Ontario ranged from 60 to 45,124 from 2013 to 2019 (Table 6). The proportion of

Table 6
Lake Ontario bloater stocking, estimated population size, expected trawl catch, and observed trawl catch in U.S. waters of Lake Ontario, 2013–2019. Population estimates assumes bloater survival during the initial year of stocking as 5% (low) or 20% (high) and 58% annual survival for all years after that (Brown et al., 1985). Expected catch values are the low and high population estimates multiplied by the proportion of U.S. waters of Lake Ontario swept by the April bottom trawl survey each year.

Year	Stocked	Population estimate		Proportion	Expected catch		Observed
	prev. year	low	High	Swept	low	high	catch
2013	1200	60	240	6.7×10^{-5}	0.0	0.0	0
2014	7310	400	1601	9.1×10^{-5}	0.0	0.1	0
2015	20,000	1232	4929	1.1×10^{-4}	0.1	0.6	1
2016	61,617	3795	15,182	1.2×10^{-4}	0.5	1.9	0
2017	149,353	9669	38,676	9.1×10^{-5}	0.9	3.5	0
2018	93,553	10,286	41,143	7.4×10^{-5}	0.8	3.0	3
2019	106,306	11,281	45,124	8.4×10^{-5}	0.9	3.8	1

U.S. waters swept by bottom trawls during the April survey ranged from 6.9×10^{-5} to 1.2×10^{-4}. The expected bloater trawl catch in U.S. waters during the April survey ranged from 0 to 3.8 per year while the observed number caught was similar and ranged from 0 to 3 (Table 6).

Discussion

The appearance of bloater in Lake Ontario trawl survey catches, 32 years after the species was last observed, is a testament to the diverse and effective collaboration between commercial fishers, fish culturists, scientists, and administrators. Gamete collection and rearing of a species that had not been previously cultured has proven challenging, but likely would not have been possible without this collaborative approach (Holey et al., in press; Smith et al. (in press)). Efforts to refine gamete collection and culture are evident in the increased stocking numbers through the first five years of the restoration program (Holey et al., in press). The reduced number of bloater stocked in 2019 and 2020, resulted from transitioning from wild caught gametes to brood stock gametes and initial low levels of fertilization and survival in these new processes. As brood stock culture methods have improved, projections suggest over 500,000 bloater may be released into Lake Ontario in 2021, which would be 60% more than the previous maximum annual number stocked.

Genetic species differentiation panels and hatchery applied marks were critical for confirming species identification given the difficulty in distinguishing among coregonine species (George et al., 2018; Schlei et al., 2008). The subtle morphometric and meristic differences between Lake Ontario bloater and cisco illustrate the potential difficulty of differentiating these species in the field. Recent questions about possible remnant deep water coregonines in Lake Ontario (Favé and Turgeon, 2008) also highlights the value of evaluating the origin of recaptured fishes. The presence of calcein marks on stocked fish was also critical for identifying that seven of the ten recaptured bloater originated from U.S. stockings. While it would be beneficial to batch mark all stocked bloater, regulations and logistical constraints have prevented those practices. Genetic parentage or otolith microchemistry methods would be potentially useful for determining the source of recaptured bloater if these methods can be validated.

The spatial distribution of bloater captures and acoustic telemetry results suggest these fish disperse quickly from stocking sites. Weidel et al. (2019a) noted the three 4–6 g, calcein-marked bloater, captured in April 2018 were likely from the calcein-marked fish stocked in November 2017 near Oswego, NY. These relatively small fish moved at least 114 and 203 km from their stocking site in approximately 5 months. Similarly, acoustic telemetry observed a bloater moved 13.4 km from release site in eastern Lake Ontario in only 24 h. This tendency to disperse relatively quickly after stocking contrasts with observations of other stocked species like lake trout, that are frequently recaptured with trawls within 15 km of their stocking location (Elrod, 1997). The greater bloater catches in U.S. waters relative to Canadian waters could be indicative of habitat preference but is also likely due in part to sampling effort since effort was three to four times higher in U.S. waters relative to Canadian waters. Additionally, boulder substrates, at depths less than 85 m along the north shore (Thomas et al., 1972; Virdin et al., 2000), limits bottom trawling in Canada at the depths where bloater were most frequently captured in U.S. waters.

The depth distribution of trawl catches was similar to historic depth distributions described from Lake Ontario and other systems. In the 1930s and 1940s, Lake Ontario gill net surveys fished a wide range of depths but found bloater catches were greatest between 55 and 110 m (Pritchard et al., 1931; Stone, 1947). Similarly, in Lakes Superior and Huron bloater densities have been described to be greatest in 50–90 m (Gorman et al., 2012; Riley and Adams, 2010). Wells (1968) found similar depth distributions for Lake Michigan bloater, but also observed depth distribution shallowed in the summer. This behavior may be associated with feeding on metalimnetic zooplankton since the shallowest Lake Ontario bloater (26 m, July) had consumed zooplankton, while the bloater caught in October in 75 m contained *Mysis diluviana*. Preference for depths greater than 50 m may also partly explain low survival and rapid movements of acoustic-telemetry tagged bloater released in eastern Lake Ontario where depths greater than 50 m are rare (Klinard et al., 2020; Virdin et al., 2000). Interestingly, bloater depth distributions based on acoustic telemetry suggests a shallower distribution than trawls with most acoustic detections occurring between 20 and 60 m. In contrast to depth distributions based on bottom-fished trawls and gillnets, acoustic telemetry can quantify depth behavior of fish that may be off the lake bottom. Additional bloater telemetry observations made over the full range of Lake Ontario depths could help to identify seasonal or spatial trends in bloater habitat use, informing surveys and possibly identifying spawning areas.

We expected hatchery bloater to have greater morphometric and meristic differences relative to wild fish, however observations suggest they were generally similar. The one difference we found between hatchery and wild fish, in the ratio of head length to orbital length, was likely an artifact of hatchery rearing since this phenomenon has been observed across multiple species (Belk et al., 2008; Vehanen and Huusko, 2011; Wintzer and Motta, 2005). It is unknown if the phenotypic changes we observed were sufficient to influence behavior or physiology of stocked fish relative to their wild counterparts. Unfortunately, we were unable to size-correct the Eshenroder et al. (2016) data used in comparison and therefore, did not size-correct data from Lake Ontario bloater. Future research should explicitly compare similar sized bloater or account for allometric differences (Albrecht et al., 1993) to confirm our results and improve our understanding of morphologic variability across populations.

The similarity between observed bloater catches and predicted catches based on assumed low survival provide additional evidence supporting the idea that stocked bloater experience low survival in Lake Ontario. Klinard et al. (2020) found only 32% of acoustic tagged bloater, 181–320 mm fork length, survived longer than 12 days in the St. Lawrence channel array and suggested predation was a likely source of early mortality (Klinard et al., 2019). Low survival of a stocked prey fish species may not be that surprising because over 48 million predator fish were stocked in Lake Ontario concurrently with approximately one million bloater (Connerton, 2020; Lake, 2018). Low survival rates have been observed for other Lake Ontario stocked fish by Brenden et al. (2011) in age-1 lake trout (8–24%; 1995–2008) and by Murry et al. (2010) in Chinook salmon (14.6%). Recent efforts to improve post-stocking bloater survival in the U.S. stocking include stocking fish directly from trucks loaded on barges to reduce handling stress as well as stocking in the spring when zooplankton and *Mysis diluviana* abundance is increasing, as opposed to the fall when their densities are decreasing (Holeck et al., 2020; Johannsson, 1995). Canadian bloater stocking has also recently shifted from shallow eastern Lake Ontario stocking locations to the north shore near Cobourg, Ontario, so that stocked individuals have more immediate access to deep waters and possibly less predation risk. Brown and Day (2002) reviewed stocking practices and suggested that predator and food acclimation as well as soft release procedures (e.g. acclimatizing in the lake prior to release) have potential to improve released fish survival. Such practices have doubled survival rate of stocked salmonines in Lake Ontario (Connerton, 2021); however, these practices have yet to be incorporated into bloater stocking.

Our conceptual model of bloater habitat use and evidence of recaptures at low densities suggests existing bottom trawl surveys can track the Lake Ontario bloater restoration status. Bloater are described to be near the lake bottom during the day with a portion of the population migrating off the bottom at night (Brandt et al., 1991; Gorman et al., 2012; Klinard et al., 2020; Tewinkel and Fleischer, 1999). Bottom trawl surveys as well as acoustic and midwater trawl surveys have both been used to assess bloater populations and appear to generate similar biomass estimates in Lake Huron (O'Brien et al., 2017; Riley et al., 2017), Lake Michigan (Bunnell et al., 2017; Warner et al., 2017), and Lake Superior (Yule et al., 2007). Given the apparent effectiveness of Lake Ontario bottom trawl surveys for collecting bloater at low densities, these surveys could evaluate stocking strategy effectiveness, similar to lake trout in Lake Ontario (Elrod et al., 1993, 1989; Lantry et al., 2011); however, this would require methods to mark or to differentiate different stocking treatments.

Ultimately, Lake Ontario bloater restoration depends on stocked individuals successfully reproducing. Bloater are believed to spawn in relatively deep lake habitats (Scott and Crossman, 1973), but it is not known whether specific substrate or environmental conditions are needed for successful egg incubation since neither egg deposition nor emergence has ever been observed. One of the few studies that evaluated bloater spawning success found that spawn timing and variable temperature regimes influenced early life stage survival in Lake Michigan (Rice et al., 1987). Unfortunately, Lake Ontario's downstream position and land use history result in the highest cumulative anthropogenic stress and habitat degradation among the Great Lakes, which could ultimately limit bloater reproduction (Allan et al., 2013). Conversely, the natural recovery of Lake Ontario deepwater sculpin (Weidel et al., 2019b), which are also thought to spawn during similar seasons and depths as bloater, may indicate deep Lake Ontario habitats can support native species reproduction. Ultimately, the restoration stocking and recaptures of bloater in Lake Ontario would not have been possible without a diverse, collaborative approach. Expanding that collaboration to identify conditions that contribute to successful bloater reproduction in upstream Great Lakes will be invaluable to the Lake Ontario bloater restoration process.

Declaration of Competing Interest

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

Acknowledgements

We thank the commercial fishers who collected Lake Michigan bloater gametes as well as the culture, vessel, administrative, and biological staff members of the USFWS, NDMNRF, NYSDEC, and USGS. We thank D. Yule, O, Gorman, D. Bunnell, and D. Warner for bloater advice, background information, and identification assistance. We thank A. Beezel, A. Heisey, P. Kohn, and journal reviewers for clarifying and editorial suggestions. We thank A. Ropp for GTseq library preparation and sequencing at the Ann Arbor Great Lakes Science Center. Trawl data are available at DOI:10.5066/F74M92QQ or at https://www.sciencebase.gov/catalog/item/ 57ed1b5de4b090825011d3db. Funding for this research was from the NDMNRF and the Canada-Ontario Agreement on Great Lakes Water Quality and Ecosystem Health, the Federal Aid in Sportfish Restoration grants to NYSDEC, Great Lakes Fishery Commission (GLFC), and the USGS Ecosystems mission area, Species Management Research Program. Acoustic telemetry projects were funded through the USFWS, Great Lakes Restoration Initiative, GLFC, and Canada Foundation for Innovation. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. For U.S. Fish and Wildlife Service authors, the findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. All USGS sampling and handling of fish during research are 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).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2021.11.014.

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