

SPECIAL SECTION

Avoiding a Macabre Future for *Macrhybopsis*—Improving Management and Conservation of Chubs

Assessing potential spawning locations of Silver Chub in Lake Erie

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Abstract

Objective: Silver Chub *Macrhybopsis storeriana*, a predominately riverine species throughout its native range, exists within Lake Erie as the only known lake population. Its population declined in the 1950s and never fully recovered. Canada has listed Silver Chub in the Great Lakes–St. Lawrence River as endangered and has initiated a recovery plan that recognized the identification of spawning areas as a critical component to inform Silver Chub's recovery potential.**Methods:** We investigated potential spawning locations of Silver Chub using capture records, otolith microchemistry, and daily age analysis. Lapillus otolith Sr:Ca ratios from 27 age-0 Silver Chub were used to identify potential spawning areas. Daily ages estimated from lapilli were used to calculate hatch dates, which then were compared with capture data of adults and river flows to further inform potential spawning areas.**Result:** The Detroit River (and its nearshore area) was all but ruled out as a potential spawning location. The Maumee, Portage, and Sandusky rivers or their nearshore areas were all possible spawning locations. Projected hatch dates spanned the end of May through the end of June and occurred across a wide range of flows, although some peaks in hatch dates corresponded to flow peaks, indicating recruitment is potentially enhanced by high flows.**Conclusion:** Silver Chub spawning period and hypothesized spawning rivers or lacustraries overlap those of invasive Grass Carp *Ctenopharyngodon idella*, creating a need to jointly consider Grass Carp control efforts with conservation of Silver Chub when assessing management alternatives. Further research on spawning guild and the use of rivers themselves or nearshore areas influenced by rivers as spawning areas are required to maximize potential for conservation and recovery of Silver Chub.

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KEYWORDS

conservation, native species, restoration and enhancement, threatened and endangered species, water chemistry

INTRODUCTION

Silver Chub *Macrhybopsis storeriana* is a native leuciscid of the large rivers of central North America. Its primary range is the Mississippi River and its large tributaries (Gilbert 1978). Riverine populations outside of the Mississippi River basin include the Brazos, Mobile, Pascagoula, and Pearl rivers, which flow into the Gulf of Mexico; the Red River of the northern USA, which forms the border between the states of Minnesota and North Dakota; and the Assiniboine River of Manitoba (Gilbert 1978). Silver Chub populations have declined during the past several decades throughout most of their distributional range (e.g., Van Hassel et al. 1988; Hesse 1994; Berry and Young 2004; Haslouer et al. 2005; Perkin and Gido 2011; Steffenson et al. 2014). Increases in agricultural land use (Gammon and Gammon 1993), pollution (Krumholz and Minckley 1964), habitat fragmentation (Perkin and Gido 2011; Pierce et al. 2014; Perkin et al. 2015), and altered flow regimens (Koel and Sparks 2002; Durham and Wilde 2006; Layzer and Scott 2006; Gido et al. 2010) have been identified as likely causal mechanisms in declines of Silver Chub and other riverine species. Although globally secure, Silver Chub populations are listed as vulnerable in the states of Arkansas, Kansas, Texas, West Virginia, and Wisconsin, imperiled in the states of Georgia, South Dakota, and Nebraska and the Canadian Province of Ontario, critically imperiled in Michigan, and presumed extirpated in New York (NatureServe 2013).

Although primarily riverine, a Silver Chub population persists in Lake Erie. The dispersal pathway of Silver Chub into Lake Erie has not been rigorously investigated, but one possible pathway was when the outlet of glacial Lake Maumee flowed through what is now the Wabash River to the Mississippi River following the last glacial period (Dryer 1919; Lewis et al. 1994; Mandrak and Crossman 1992; also see Elbassiouny et al. 2023, this special section). Silver Chub was abundant in Lake Erie from the late 1800s (McCormick 1892) through the mid-1950s. Kinney (1954) reported capturing Silver Chub with bottom trawls in several locations around the islands of western Lake Erie and near the mouth of the Portage River, including a few large samples in and near the mouth of Sandusky Bay in 1953 (Figure 1). He also reported anecdotal evidence of a springtime fishery for Silver Chub along the shoreline east and northeast of the mouth of the Portage River. The population in Lake Erie declined in the mid-1950s (Britt 1955) and remained low until the late 1990s (USGS 2019a). There was a short-lived population

Impact statement

Conserving the Silver Chub is vital; it's an indicator of water quality, a food source for aquatic organisms, and preserves biodiversity. Identifying both locations and mode of spawning enhances the conservation of biodiversity in fish communities, ensuring ecosystem stability.

increase in the early 2000s (USGS 2019a), but there has never been a sustained recovery to the levels of the late 1800s through 1950s.

The conservation status of Silver Chub in Lake Erie varies by jurisdiction. New York (NatureServe 2013; NYS-DEC 2017) lists Silver Chub as endangered and probably extirpated. Michigan lists Silver Chub as critically imperiled (NatureServe 2013; Michigan Natural Features Inventory 2020). In Canada, Silver Chub in the Great Lakes and St. Lawrence River were identified by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2012) as a separate designatable unit from those in the Nelson and Assiniboine rivers in Manitoba and Saskatchewan. The Great Lakes–Upper St. Lawrence designatable unit was changed in 2012 from of special concern to endangered. Canada has a recovery potential assessment (McCulloch et al. 2013) and a management plan (Boyko and Staton 2010). Ohio (ODNR 2017) and Pennsylvania (Pennsylvania Natural Heritage Program 2019) give Silver Chub no special status and do not recognize separate riverine and lake populations.

Canada's assessment of recovery potential (McCulloch et al. 2013) identified several gaps in knowledge to be filled to inform recovery potential. Lack of knowledge of spawning areas was identified as a critical knowledge gap. Previous publications (e.g., Kinney 1954; Goodyear et al. 1982) indicate that Silver Chub spawned in the open lake or on beaches over clean gravel. However, these conclusions were based on timing of adult fish captures in the open lake (Kinney 1954) and assertions that Silver Chub spawned on beaches because “there are no suitable rivers remaining” (Goodyear et al. 1982). Neither study provided data or analyses supporting where spawning occurred. Here, we use otolith microchemistry, daily age analysis, and capture records to identify potential spawning locations. Otolith microchemistry, especially in the core region, has been used to identify spawning locations for numerous species, especially when water chemistry

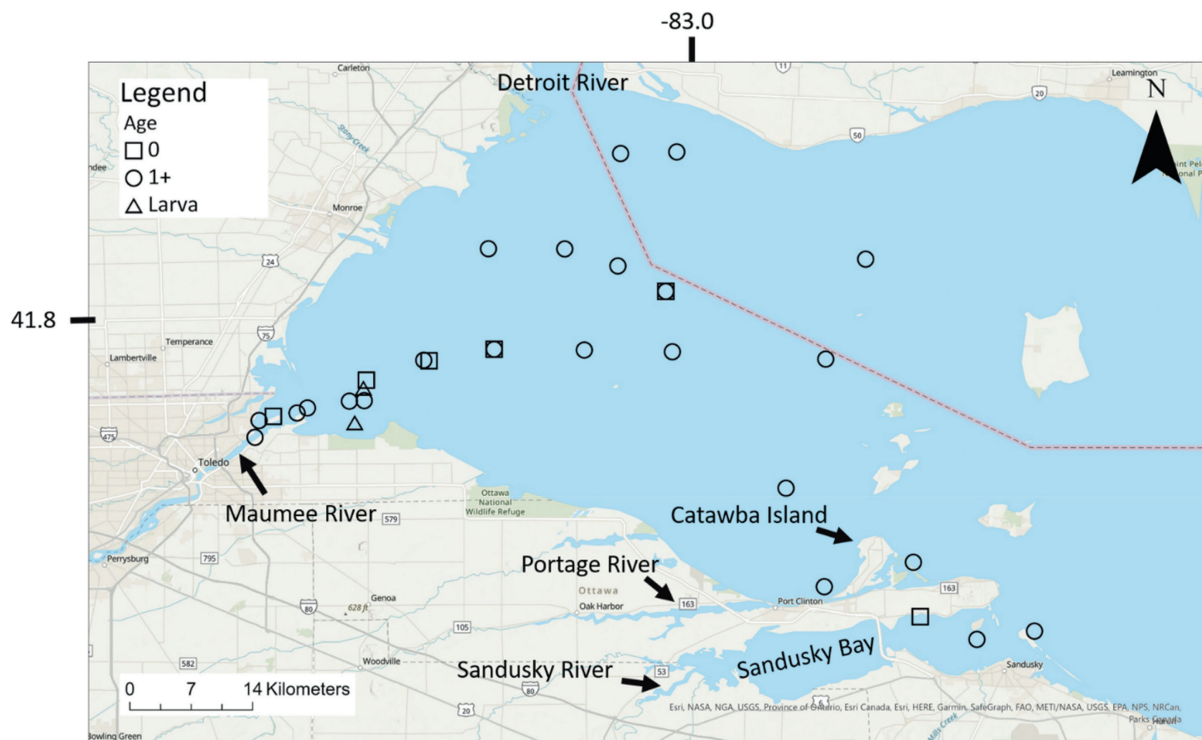


FIGURE 1 Capture locations of Silver Chub in western Lake Erie in 2017 and 2018. The red line indicates the international border between Canada and the USA.

differs among spawning locations because of the linear relationship between water and otolith chemistry (e.g., Pangle et al. 2010). In western Lake Erie, this is enhanced by the strong gradients of Sr:Ca that are very high in the Sandusky and Portage rivers, moderate in the Maumee River, and very low in the Detroit River. Daily age analyses of larval and early juvenile fish can also be used to determine the timing of spawning and relate this to associated environmental factors (Long and Grabowski 2017).

METHODS

Silver Chub were obtained for otolith microchemistry and daily age analyses in 2017 and 2018 from three sources: U.S. Fish and Wildlife Service (USFWS) comprehensive Aquatic Invasive Species Early Detection and Monitoring Program conducted in Maumee Bay and Sandusky Bay, Ohio Department of Natural Resources (DNR) and Ontario Ministry of Natural Resources and Forestry partnership Western Basin interagency August trawl survey, and U.S. Geological Survey (USGS) June and September forage fish index surveys (USGS 2019a). The USFWS efforts were conducted during spring to fall in Sandusky Bay and Maumee Bay, including the mouth of the Maumee River. The USFWS samples were from daytime bottom trawl tows at depths >2m, overnight sets from paired fyke nets at depths of 1–2m, and nighttime paired

ichthyoplankton nets fished at depths >1 m. Ohio DNR samples were from bottom trawl samples collected May through September in Ohio waters of western Lake Erie. Samples from the USGS were from bottom trawl samples collected in June and September in Ohio and Ontario waters of western Lake Erie. Both Ohio DNR and USGS samples were from open waters of western Lake Erie at depths of 3–11 m. All sampling and handling of fish during research was done in accordance with guidelines provided by the American Fisheries Society's Use of Fishes in Research Committee (2014).

Silver Chub specimens were either stored in 95% non-denatured ethanol or frozen in the field prior to otolith extraction. In the laboratory, lapilli were extracted and dried to remove any remaining tissue and placed dry into labeled vials. For young-of-year (age-0) specimens, one lapillus was used for microchemistry analysis and the other to estimate daily age. For the microchemistry analysis, lapilli were embedded in a two-part epoxy (West System 105 Epoxy Resin and 206 Slow Hardener). The otolith was then transversely sectioned using a low-speed diamond-tipped saw (South Bay Technology, Model 650). Both sides of the otoliths were wet polished with 3M silicon carbide sandpaper (400 and 600 grit) until the core was reached (typically to a thickness of ~200µm) then buffed using Precision Surface International lapping film (12µm, 3µm). The polished otoliths were mounted on standard petroscopic microscope slides (~16 otoliths per

slide) using cyanoacrylate adhesive (Loctite Super Glue). The otolith slides were triple-rinsed with Milli-Q (Millipore) ultrapure water and sonicated for 5 min in Milli-Q water. The slides were covered and allowed to dry overnight under a fume hood. The slides were stored in clean Petri dishes until the analysis was performed. All otolith preparation was conducted at Bowling Green State University.

The otoliths were analyzed at the Great Lakes Institute for Environmental Research (University of Windsor, Ontario) using laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) with an Agilent 7900 fast-switching quadrupole mass spectrometer coupled with a PhotonMachines 193-nm laser. The laser was operated at a 100-Hz pulse rate, producing 0.059 mJ/pulse at the sample surface and a resulting laser ablation crater width of ~25 µm. The LA-ICPMS was operated in low-resolution peak-jumping mode (isotope dwell time: 10 ms, carrier gas: Ar), so that each element was measured every 250 ms. All laser traverses were run from the otolith edge through the core region to the opposite edge at a scan speed of 5 µm/s, monitoring for ^{43}Ca , ^{44}Ca , ^{86}Sr , and ^{88}Sr . The ^{120}Sn was monitored to establish when ablation of the otolith had begun and ended as the epoxy contains a trace amount of tin. The concentrations of all elements were above background and always greater than the limits of detection. The theoretical concentration of calcium in stoichiometric calcium carbonate ($400,432 \mu\text{g Ca/g CaCO}_3$) was used as an internal standard to correct for ablation yield differences between external calibration standard and the otoliths. A collection of background counts was taken for 60 s prior to analysis of each sample. Analysis of a certified standard reference glass (NIST 610) was conducted both before and after each set of 16 otoliths was analyzed to calibrate concentrations and correct for ablation yield and instrument drift. Data processing was performed in R using elementR 1.3.7 (Sirot et al. 2017; R Core Team 2021), an R package for reducing elemental data from LA-ICPMS. Images of postablation otoliths and graphs of Sr:Ca ratios versus unit time were used to identify location of the otolith core for assessing Sr:Ca ratio.

Although studies attempting to determine spawning areas of fishes frequently use ratios of other divalent cations to Ca (e.g., Whitley et al. 2019), Sr:Ca ratios are particularly useful for assessing potential spawning locations in western Lake Erie because of highly distinguishable levels of Sr among the Detroit, Maumee, Portage, and Sandusky rivers. Aquifers supply water enriched in Sr to the Maumee, Portage, and Sandusky rivers, resulting in Sr levels inversely related to flow. During low flows, Sr:Ca levels are high, and they decrease as surface runoff decreases the proportion of groundwater in streamflow (i.e., during high-flow events). Comparatively constant flow results in little fluctuation in Sr:Ca levels in the Detroit

River. The Portage and Sandusky rivers have high Sr:Ca ratios, the Maumee has moderate Sr:Ca ratios, and the Detroit River has low Sr:Ca ratios (Alexander et al. 1998; Hayden 2009; Ohio EPA 2010; Pangle et al. 2010; Kočovský and Farver 2019). Because the Detroit River supplies over 90% of the water to western Lake Erie, its influence dominates most of western Lake Erie and Sr:Ca levels in western Lake Erie are only slightly higher than those in the Detroit River. Discharge from the Maumee, Portage, and Sandusky rivers influence Sr:Ca values within a few kilometers of the southern shore, resulting in elevated Sr:Ca levels compared with offshore waters of western Lake Erie (Hayden 2009; Pangle et al. 2010).

Daily ages of age-0 Silver Chub were estimated from counts of rings in lapilli. We used USGS September trawling data from 2005 to 2018 to create a histogram to assist in the identification of age-0 Silver Chub (USGS 2019a; Figure 2). Lapilli were mounted to glass slides with thermoplastic cement and sanded to the core with 2000-grit sandpaper to expose daily rings (Starks et al. 2016; Long and Grabowski 2017). To improve clarity, sanded otoliths were polished with 0.3-µm alumina powder and a polishing cloth prior to viewing. To estimate daily age, counts of rings in otoliths were made under 100–200 magnification three times by one biologist with more than two decades of experience analyzing daily rings in otoliths (DiCenzo and Bettoli 1995; Starks et al. 2016; Long and Porta 2019). For each round of counts, lapilli were viewed in random order and without knowledge of fish length. For each otolith, we calculated the mean ring count and all pairwise differences. We used the average (rounded up) of the two ring counts that were closest to each other and within 10% of the mean count as the estimated age (Neilson 1992). If all pairwise differences were greater than 10% of the mean ring count, we estimated ring count a fourth time and calculated the new pairwise differences. If there were no pairs within 10% of the mean ring count after a fourth count, we eliminated the otolith from further analyses.

Because all other known Silver Chub populations are riverine spawners and high flows have been linked to spawning success of some *Macrhybopsis* spp. (e.g., Starks et al. 2016), we compared hatch dates to flow conditions in potential candidate rivers for spawning based on microchemistry signatures in identified potential natal waters (see Results) to qualitatively assess flow conditions on fertilization dates to assist in potential hypothesis development for when and under which hydraulic conditions spawning occurs. To estimate hatch dates, we subtracted the estimated age in days plus 1 day from the collection date (Starks et al. 2016) following Bottrell et al. (1964) and Secor et al. (1992), who reported that two pairs of otoliths (probably lapilli and sagittae) were present 24 h after hatching in congeneric Peppercorn Chub *M. tetranema*. Not

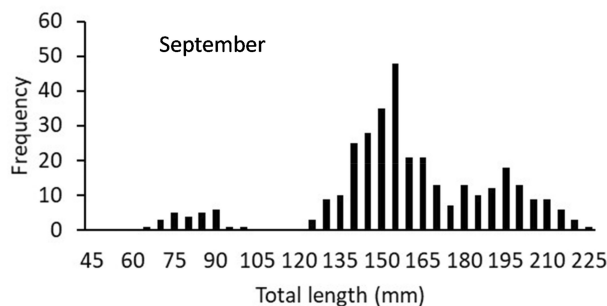


FIGURE 2 Length-frequency histogram for Silver Chub captured in USGS bottom trawl nets in western Lake Erie in September 2005–2020 ($n = 340$) to aid identification of putative age-0 individuals.

all young of year collected were used in both age and microchemistry analyses because we were not able to extract both lapilli from all young of year. When only one otolith was available, we randomly assigned the fish to have either microchemistry or daily age analysis. We overlaid histograms of hatch dates with plots of discharge from USGS gauges 04193500 on the Maumee River, 04195500 on the Portage River, and 04198000 on the Sandusky River (waterwatch.usgs.gov) for age-0 Silver Chub collected in 2018 to qualitatively examine potential relationships between discharge and spawning. We did not make this comparison for 2017 young of year because of small sample size ($n = 5$).

Statistical analysis

We used a threshold analysis for interpreting potential spawning locations based on outcomes of the otolith microchemistry analysis on 27 age-0 Silver Chub. For the hatch date of each young of year, we retrieved mean daily flow data from the USGS streamflow gauges mentioned previously for the Maumee, Sandusky, and Portage rivers and estimated water Sr:Ca on hatch date using the following equations:

$$\text{Maumee: } \log(\text{water Sr:Ca}) = -0.2388 \cdot \log(Q_{\text{cms}}) + 1.1422$$

(Alexander et al. 1998),

$$\text{Portage: } \log(\text{water Sr:Ca}) = -0.1533 \cdot \log(Q_{\text{cms}}) + 1.1212$$

(Kočovský and Farver 2019),

$$\text{Sandusky: } \log(\text{water Sr:Ca}) = -0.3346 \cdot \log(Q_{\text{cms}}) + 1.4239$$

(Alexander et al. 1998),

where Q_{cms} is river discharge measured in cubic meters per second (cms). Because the flow of the Detroit River is much less variable, we did not use a regression equation and instead used the maximum value for the Detroit River from Kočovský and Farver (2019). We then divided otolith core microchemistry by a partition coefficient of

0.43 (Table A.1 in the Appendix) to estimate water Sr:Ca on the hatch date. For example, for an otolith with a core Sr:Ca of 4.0, we estimated water Sr:Ca as $4.0/0.43 = 9.3$. The final step in assessing potential for spawning in a tributary or the nearshore area influenced by it was to compare the otolith core Sr:Ca adjusted for flow to the expected river Sr:Ca on the hatch date. If the adjusted otolith Sr:Ca was higher than that of the water for a river, it was excluded as a possibility. This also applies to nearshore areas influenced by a river, which would necessarily be lower than that of the river itself (Hayden 2009).

RESULTS

Age-0 Silver Chub were captured throughout western Lake Erie in 2017 and 2018 (Figure 1). Thirty-six Silver Chub were collected in trawl samples by the USFWS in late May and early June 2017 in the lower reaches of the Maumee River and within approximately 3 km of its mouth. Young-of-year Silver Chub were captured at six locations near the mouth of the Maumee River, in offshore waters of western Lake Erie, and near Sandusky Bay. Two larval Silver Chub genetically confirmed by the USFWS Whitney Genetics Laboratory were collected in ichthyoplankton nets, one on May 23, 2017, in Maumee Bay, approximately 5 km east of the mouth of the Maumee River and ~1 km north of shore, the other on July 7, 2017, approximately 7 km northeast of the mouth of the Maumee River in the open waters of western Lake Erie.

Core Sr:Ca values for all but one Silver Chub were too high for the otolith to have been influenced by Detroit River water (Table 1). Core Sr:Ca ratios were also too high for the open lake, which has lower values than the tributaries and their nearshore areas. Ten fish had values too high to have been influenced by Maumee River water. The Sandusky River was eliminated as a possibility for only three fish, and the Portage River was not eliminated for any. Based on less difference between predicted Maumee River water Sr:Ca and core Sr:Ca values compared with differences between otoliths and either Portage or Sandusky river water, we infer most spawning was likely associated with the Maumee River.

We estimated daily ages for 48 age-0 Silver Chub, 5 from 2017 and 43 from 2018. Otoliths were not recovered from the two larvae captured in 2017. Daily ages ranged from 44 to 84 days, with estimated hatch dates between June 18 and July 3 in 2017 and between May 27 and June 25 in 2018 (Long and Kocovsky 2022). The average difference between mean estimated age and each of the two ring counts that contributed to the mean was 1.08 d (SD = 0.9) for the 2018 young of year. We estimated the larvae captured on May 23

TABLE 1 River discharge (m^3/s), otolith core Sr:Ca ratio (mmol/mol), projected water Sr:Ca based on a partition coefficient of 0.43, and estimated water Sr:Ca on projected hatch dates (maximum for Detroit River) of age-0 Silver Chub from western Lake Erie in 2017 and 2018. Abbreviations are as follows: D = Detroit River, M = Maumee River, P = Portage River, and S = Sandusky River.

Capture date	Age (d)	Hatch date	Discharge (m^3/s)				Otolith Sr:Ca	Water Sr:Ca	Hatch date Sr:Ca in water				Ruled out as spawning river
			M	P	S				D max	M	P	S	
Aug 17, 2017	48	Jun 30, 2017	55.8	2.7	6.7		4.0	9.3	2.3	5.3	11.4	14.0	D, M
Aug 16, 2017	59	Jun 18, 2017	92.9	4.8	24.4		3.5	8.1	2.3	4.7	10.4	9.1	D, M
	58	Jun 19, 2017	56.4	4.0	14.2		2.9	6.7	2.3	5.3	10.7	10.9	D, M
Aug 22, 2018	74	Jun 9, 2018	56.9	0.1	6.1		1.4	3.3	2.3	5.3	18.6	14.5	D
Aug 23, 2018	80	Jun 4, 2018	125.4	0.2	18.9		1.7	4.0	2.3	4.4	16.6	9.9	D
	72	Jun 12, 2018	430.4	1.6	291.7		1.3	3.1	2.3	3.3	12.3	4.0	D
	79	Jun 5, 2018	92.3	0.1	12.1		1.3	3.0	2.3	4.7	17.9	11.5	D
	72	Jun 12, 2018	430.4	1.6	291.7		2.0	4.7	2.3	3.3	12.3	4.0	D, M, S
	73	Jun 11, 2018	120.6	1.8	157.4		1.6	3.7	2.3	4.4	12.1	4.9	D
	74	Jun 10, 2018	63.7	0.8	15.6		1.7	4.0	2.3	5.1	13.7	10.6	D
	77	Jun 7, 2018	47.0	0.1	7.8		1.3	3.0	2.3	5.5	19.3	13.3	D
	75	Jun 9, 2018	56.9	0.1	6.1		1.4	3.3	2.3	5.3	18.6	14.5	D
	84	May 31, 2018	94.9	0.1	12.4		1.8	4.1	2.3	4.7	19.1	11.4	D
	79	Jun 5, 2018	92.3	0.1	12.1		1.5	3.5	2.3	4.7	17.9	11.5	D
	72	Jun 12, 2018	430.4	1.6	291.7		2.0	4.7	2.3	3.3	12.3	4.0	D, M, S
	72	Jun 12, 2018	430.4	1.6	291.7		1.5	3.5	2.3	3.3	12.3	4.0	D, M
	81	Jun 3, 2018	87.8	0.5	36.2		1.4	3.3	2.3	4.8	14.8	8.0	D
	64	Jun 20, 2018	62.9	0.1	12.5		1.0	2.3	2.3	5.2	18.6	11.4	None
	76	Jun 8, 2018	59.2	0.1	6.9		1.4	3.3	2.3	5.2	19.7	13.9	D
	71	Jun 13, 2018	651.3	2.0	294.5		1.8	4.2	2.3	3.0	11.8	4.0	D, M, S
	79	Jun 5, 2018	92.3	0.1	12.1		1.6	3.7	2.3	4.7	17.9	11.5	D
	73	Jun 11, 2018	120.6	1.8	157.4		1.4	3.3	2.3	4.4	12.1	4.9	D
	59	Jun 25, 2018	1042.1	0.4	20.4		1.8	4.2	2.3	2.6	15.5	9.7	D, M
	70	Jun 14, 2018	591.8	1.0	222.3		1.3	3.0	2.3	3.0	13.2	4.4	D
	72	Jun 12, 2018	430.4	1.6	291.7		1.5	3.5	2.3	3.3	12.3	4.0	D, M
	59	Jun 25, 2018	1042.1	0.4	20.4		1.8	4.2	2.3	2.6	15.5	9.7	D, M
	71	Jun 13, 2018	651.3	2.0	294.5		1.3	3.0	2.3	3.0	11.8	4.0	D

(5.4 mm TL) and July 7 (6.1 mm TL), 2017, were no more than 1 day old at capture owing to lack of otoliths; hence, their hatch dates were May 22 or 23 and July 6 or 7.

Based on results of the microchemistry analysis, we overlaid a histogram of hatch dates for fish for which the Maumee, Portage, and Sandusky rivers were potential spawning associations (i.e., were not eliminated) on graphs of discharge for each river. Hatching occurred across a range of flows (Figure 3). Estimated hatch dates corresponded with the ascending limb or peak of one high-flow event on each river, but estimated hatch dates also corresponded with lower flows.

DISCUSSION

Our analyses identified the Maumee River and the Portage and Sandusky rivers or their associated nearshore areas as the most likely potential spawning areas for Silver Chub in western Lake Erie. Many of the otoliths

we analyzed had core ratios of Sr:Ca, indicating the developing larvae or female parent during vitellogenesis (see below) were in the Maumee River, its mouth, or nearshore areas influenced by Maumee River water. Collection of ripe females at the mouth of the Maumee River a few days prior to a larva being captured in Maumee Bay further corroborates the Maumee River, Maumee Bay, or nearshore areas influenced by Maumee River water as a possible spawning area. Evidence from other sampling efforts includes capture by the USFWS of a 49-mm, age-0 Silver Chub in the Maumee River approximately 6 km from Maumee Bay in September 2019 and Ohio Environmental Protection Agency records of a 44-g Silver Chub captured during the spawning season 11 km upstream of the confluence with Maumee Bay (June 25, 2012; C. Boucher, Ohio Environmental Protection Agency, written communication; The Ohio State University Museum of Biological Diversity specimen OSUMU 442227). Using length-weight data from the USGS trawl data used to generate length histograms (USGS 2019a), this fish was

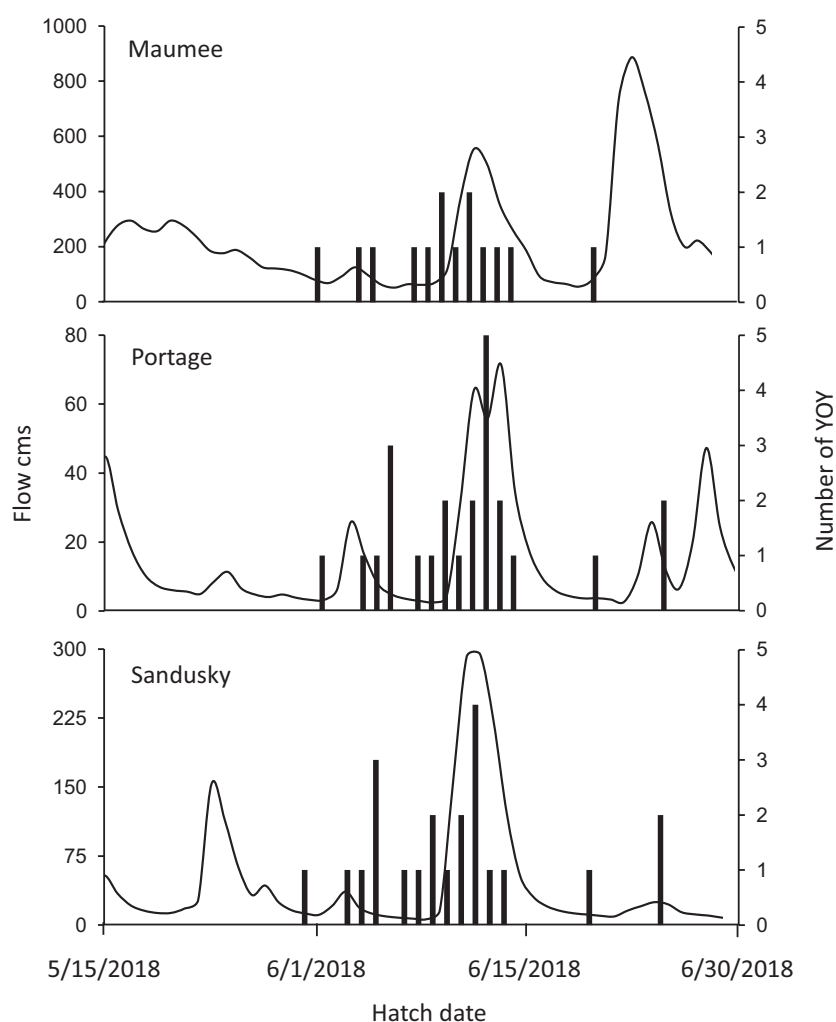


FIGURE 3 Histogram of calculated hatch dates of Silver Chub overlaid on hydrographs for the Maumee, Portage, and Sandusky rivers in 2018 for 27 young-of-year (age-0) Silver Chub collected in 2018 that were assigned to these respective rivers as a likely spawning location.

159–177 mm total length, which is likely a 2-year-old fish (i.e., spawning age).

Dual influences on chemical composition of otolith cores might complicate interpretation of our results. Otolith chemistry at the time of otolith formation is influenced by water mass chemistry during larval development and potentially by the effect of water mass chemistry on yolks during vitellogenesis (Kalish 1990). This effect would likely be highest for species with large yolks and those that rely on those yolks for long periods of time, such as those in family Salmonidae (e.g., Kalish 1990). Species in the genus *Macrhybopsis* that have been studied absorb most of their yolks during their comparatively short development, and the yolks are nearly completely absorbed at hatching (e.g., Bottrell et al. 1964). The effect of yolk chemistry on otolith chemistry for *Macrhybopsis* spp. is undoubtedly lower than that for Salmonidae but might not be negligible, allowing for Sr:Ca ratios to become more variable as larval fish drift and develop. For example, nearshore movement of Silver Chub into waters adjacent to Catawba Island in mid-March, up to 3 months prior to spawning (Kinney 1954), includes the period prior to and during vitellogenesis. That area is near the outflow of the Portage River, which has very high Sr:Ca ratios compared with other tributaries. Our observation of Silver Chub congregating near the mouth of the Maumee River in May could be indirect evidence of spawning-related nearshore movement. Furthermore, residence in waters along the southern shore during vitellogenesis would result in yolks having higher Sr:Ca concentrations for fish in areas influenced by the Maumee, Portage, and Sandusky rivers, which cover the entire southern shoreline of western Lake Erie, compared with those that resided in open waters of western Lake Erie or near the mouth of the Detroit River. Therefore, it is possible that a fish resided in a water mass prior to spawning that was different from the water mass in which it spawned, meaning Sr:Ca from the resident water mass was incorporated into hard parts of developing fish, possibly complicating direct interpretation of the results. However, because yolks were not present in the two likely day-old larval Silver Chub we captured in this study, contribution of Sr:Ca during the period of vitellogenesis (and thus in yolk) is probably not sufficient to hinder interpretation of Sr:Ca representing natal areas.

For many fish, otolith core Sr:Ca ratios were so high that larvae or the female parent during vitellogenesis could only have been in the Sandusky or Portage rivers or nearshore areas with substantial amounts of water from the Sandusky or Portage rivers during periods of low flow. Kinney's (1954) report of recreational anglers catching Silver Chub and Ohio DNR trawl records of Silver Chub being captured in nearshore areas along Catawba Island, which is in the Portage River plume east of the mouth

of the Portage River (Figure 1), corroborate our findings that the Portage River, its mouth, or nearshore areas influenced by Portage River water could be spawning areas. Few Silver Chub age 1 and older have been captured in Sandusky Bay. Furthermore, no Silver Chub eggs or larvae have been reported from the Sandusky River or Sandusky Bay despite having been sampled intensively in 2015–2020 for early life history stages of Grass Carp as part of a long-term assessment of spawning potential (Kočovský et al. 2018). These results cast doubt on the Sandusky River as a spawning area for Silver Chub, but they do not rule out Sandusky Bay or nearshore waters affected by its flow, especially if Silver Chub is not a pelagophil (see below).

Our analyses do not completely rule out the Detroit River or its mouth as a potential spawning area, but the evidence for it not being a spawning area is conflicting. Trawl samples near the mouth of the Detroit River in mid-June sometimes include large numbers of adult Silver Chub, while samples at the same sites in September produce few or no Silver Chub (USGS 2019a), suggesting a spawning migration consistent with what we observed at the mouth of the Maumee River and Kinney's (1954) observation of nearshore movement in the months that precede spawning. Furthermore, the USFWS captured eight Silver Chub in the Detroit River with bottom trawls in August 2019 near the south end of Fighting Island (A. Bowen, USFWS, personal observation). The potential influence of resident water mass on core otolith microchemistry during vitellogenesis leaves open the possibility the female parent could have resided in water of higher Sr:Ca during vitellogenesis (southern shore, Portage or Maumee rivers or plumes, Sandusky River or Sandusky Bay) and moved into Detroit River waters only to spawn as opposed to migrating there earlier in the spring as has been reported for Silver Chub along the southern shore. However, only one of the 27 fish we analyzed had low enough Sr:Ca in the otolith core to have possibly spent time in the Detroit River as a larvae. Moreover, no Silver Chub eggs or larvae have been reported in the literature in the Detroit River (Pritt et al. 2014; Tucker et al. 2018). The weight of evidence seems to nearly rule out the Detroit River or its mouth as a successful potential spawning area.

Our interpretations of potential spawning areas from otolith microchemistry relied on accurate partition coefficients. Here, we used an average partition coefficient of 0.43 calculated from freshwater species because we did not have a partition coefficient for Silver Chub. A higher partition coefficient for Silver Chub would mean that water Sr:Ca predicted from otolith chemistry would be lower than we estimated (Table 1). However, we would still predict that little successful reproduction occurs in the mouth of the Detroit River. A few of the Silver Chub we associated with the Maumee River or its nearshore

areas may have had high enough otolith core Sr:Ca that they could have originated from the Portage and Sandusky rivers if the true partition coefficient from water to otolith was lower than 0.43. A laboratory study would be required to establish a species-specific partition coefficient for Silver Chub.

As a riverine species in a lake environment, the question of where Silver Chub spawn in the Lake Erie basin is not only of interest to recovery and persistence of the Lake Erie population, but is potentially of evolutionary significance. Evidence to date leaves open the question of Silver Chub spawning guild, which also complicates our interpretation of spawning areas. Balon (1975) classified Silver Chub as a phytolithophil, but Simon (1999) argued Silver Chub cannot be a phytolithophil because the larvae lack cement glands and suggested the proper guild is lithopelagophil. Silver Chub spawning over clean gravel as reported, without supporting evidence, by Goodyear et al. (1982) would be consistent with Silver Chub being phytolithophils or lithopelagophils. However, several *Macrhybopsis* spp. that have been investigated have semibuoyant, nonadhesive eggs (e.g., Speckled Chub *M. aestivalis* [Bottrell et al. 1964; Platania and Altenbach 1998]; Sturgeon Chub *M. gelida* and Sicklefin Chub *M. meeki* [Albers and Wildhaber 2017]) and pelagic larvae (Speckled Chub, Sturgeon Chub, Sicklefin Chub, Silver Chub; Reeves and Galat 2010). Larson et al. (2016) and Camacho et al. (2019) reported that genetically confirmed Silver Chub eggs were collected in surface ichthyoplankton nets in the upper Mississippi River basin, indicating eggs might be semibuoyant, which would mean Silver Chub are pelagophils. Furthermore, Perkin et al. (2023, this special section) reported greater Silver Chub recruitment in longer pools of the Ohio River, which is consistent with the species being a pelagophil (i.e., longer drift potential leading to greater hatching success). In Lake Erie, the only two confirmed Silver Chub larvae were collected in western Lake Erie in ichthyoplankton nets deployed near the surface. These observations indicate that Silver Chub larvae are pelagic, which is typical for species in the pelagophil and lithopelagophil spawning guilds.

Another consideration for interpretation of spawning areas is the potential for Silver Chub in Lake Erie to have evolved a different spawning mode than riverine populations. The 14,000- to 11,000-year separation of Silver Chub in Lake Erie from the riverine progenitor (Mandrak and Crossman 1992) has resulted in their becoming genetically distinct from populations in the Assiniboine, Mississippi, Missouri, Ohio, and Wabash rivers (Elbassiouny et al. 2023 this issue). It is possible the novel evolutionary pressures of the lake environment that resulted in genetic differentiation also drove an evolution of spawning mode.

A laboratory study analogous to those conducted by Albers and Wildhaber (2017) would be required to settle the question of Silver Chub spawning guild.

Another gap in understanding is whether Silver Chub recruitment is higher when river flows are higher. Durham and Wilde (2006) found that some pelagophil species (i.e., Arkansas River Shiner *Notropis girardi*, Plains Minnow *Hybognathus placitus*, and Flathead Chub *Platygobio gracilis*) had the highest reproductive success during early spring when water discharge was consistently at its highest level. After accounting for a 1-day error in age estimates based on the standard deviation from our 2018 young of year, peaks in hatch dates still align with high-flow events. Although our results show that hatch dates were across a wide range of flows, indicating that spawning is not triggered by a high-flow event, peaks in hatching were sometimes aligned with high-flow events (Figure 3), suggesting a possible link between hatching success and high flows.

Viewed across years, densities of age-1-and-older Silver Chub in USGS trawl samples in autumn 2019 further support a possible influence of river flow on recruitment. In 2017 and 2018, there were several high-flow events on the Maumee River (waterwatch.usgs.gov, gauge 04193500). Spawning by Grass Carp, a pelagophil known to spawn during high-flow events (Shireman and Smith 1983; Embke et al. 2016), was documented during several of those events (Kočovský et al. 2018), including June 12–13, 2018, when Silver Chub hatch dates peaked (Figure 3). Furthermore, Grass Carp recruitment from the Maumee River on those dates was demonstrated by capture of larvae (USGS 2019b). Densities of age-1-and-older Silver Chub in USGS trawl samples (USGS 2019a) in autumn 2019 (i.e., 1-year-olds from 2018 and 2-year-olds from 2017) was 187 fish/ha, more than an order of magnitude higher than in 2017 (15.6 fish/ha) and 2018 (16.6 fish/ha). In 2013 and 2014, there were fewer and lower-magnitude flow events on the Maumee River, and density of age-1-and-older Silver Chub in USGS trawl samples in autumn 2015 (i.e., age 2 from 2013 and age 1 from 2014) was only 4 fish/ha (USGS 2019a). Successful recruitment related to high-flow events is characteristic of pelagophils and believed to be necessary to their persistence (e.g., Perkin and Gido 2011). These observational data indicate a potential link between high flows on the Maumee River and recruitment success of Silver Chub.

The Silver Chub population in Lake Erie represents a rare and unique element of biodiversity. It is the only known extant self-sustaining population in a large lake. Canadian collection data include a few specimens from Lake Huron and Lake St. Clair during 1982–1991

(McCulloch et al. 2013) and a single specimen from Lake St. Clair in 2022 (M. Thorn, Ontario Ministry of Natural Resources and Forestry, written communication). One Silver Chub reported in the gut of a Lake Trout *Salvelinus namaycush* captured in Lake Huron during 2009–2011 (Roseman et al. 2014) was determined to have been a database coding error upon our inquiry (E. Roseman, USGS, written communication). NatureServe lists Silver Chub as extirpated from Lake Michigan (NatureServe 2013), implying they were once present, but neither Becker (1983) nor Greene (1935) included Silver Chub as present in Wisconsin waters of Lake Michigan. Stewart and Watkinson (2004) reported Silver Chub from Lake Winnipeg, but none have been reported since 2005 (D. Watkinson, Fisheries and Oceans Canada, written communication). Silver Chub has been reported in large reservoirs, such as Lake Texoma on the Red River (Gido et al. 2002) and Lewis and Clark Reservoir on the Missouri River (Nelson and Walburg 1977; Kaemingk et al. 2007), but there are Silver Chub populations in both rivers; hence, the reservoir-dwelling Silver Chub might not be separate from the river populations.

Our research has helped identify potential spawning areas for Silver Chub, but our method did not allow us to definitively determine if spawning occurs in rivers. Conserving Silver Chub in Lake Erie is a priority in Canada, which lists Silver Chub in the Great Lakes as endangered (COSEWIC 2012) and has a recovery plan (Boyko and Staton 2010). Fish community objectives for Lake Erie include maintaining a native fish community, including rare, indigenous species (Francis et al. 2020).

A primary reason for the need to better understand Silver Chub spawning in rivers relates to efforts to manage invasive Grass Carp in Lake Erie. Grass Carp spawn in the Sandusky (Embke et al. 2016) and Maumee rivers (USGS 2019b) and potentially a third yet unidentified tributary (Whitledge et al. 2021), and their spawning season overlaps with that of Silver Chub. The current management plan for Grass Carp in the Sandusky River is to use a seasonal barrier (AECOM 2021) to prevent Grass Carp from reaching their spawning grounds (Kočovský et al. 2021). If Silver Chub spawn in the Sandusky River, any seasonal barrier that prevents Grass Carp spawning might also prevent Silver Chub spawning. We reiterate that presently there is only weak evidence of the possibility of Silver Chub spawning in the Sandusky River. If Silver Chub use the Maumee River to spawn, which our analyses indicate is probable, any similar efforts there to interfere with Grass Carp spawning could adversely affect Silver Chub spawning. Definitive studies to determine spawning guild and use of rivers for spawning are the next steps to ensuring the long-term persistence and recovery of Lake Erie Silver Chub.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

U.S. Geological Survey data are publicly available at the websites in the references section. Western Basin interagency August trawl survey data are available from the Forage Task Group of the Lake Erie Committee (<http://www.glfc.org/lake-erie-committee.php>) by request. Data collected by the U.S. Fish and Wildlife Service are available upon request from Anjanette Bowen (anjanette_bowen@fws.gov). Silver Chub otolith microchemistry data are available upon request from John Farver or Jeff Miner (jfarver@bgsu.edu or jminer@bgsu.edu, respectively).

ETHICS STATEMENT


We followed the American Fisheries Society's *Guidelines for the Use of Fishes in Research* (Use of Fishes in Research Committee 2014) for field data collection.

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Appendix: Additional data

TABLE A.1 Sources and species used for calculating a mean partition coefficient for otolith core Sr:Ca ratios for freshwater fish species.

Source	Species	Partition coefficient
Zimmerman (2005)	Chinook Salmon <i>Oncorhynchus tshawytscha</i>	0.37
	Coho Salmon <i>Oncorhynchus kisutch</i>	0.35
	Sockeye Salmon <i>Oncorhynchus nerka</i>	0.43
	Rainbow Trout <i>Oncorhynchus mykiss</i>	0.38
	Arctic Char <i>Salvelinus alpinus</i>	0.44
Tabouret et al. (2010)	European Eel <i>Anguilla anguilla</i>	0.49
Wells et al. (2011)	Cutthroat Trout <i>Oncorhynchus clarkii</i>	0.40
Chapman et al. (2013)	Grass Carp <i>Ctenopharyngodon idella</i>	0.68
Fukushima et al. (2014)	Siamese Mud Carp <i>Henicorhynchus siamensis</i>	0.41
	Notched Mud Carp <i>H. lobatus</i> ^a	0.50
Farver and Miner (2014)	Common Carp <i>Cyprinus carpio</i> ^b	0.36
	Common Carp ^c	0.47
Strohm et al. (2017)	June Sucker <i>Chasmistes liorus</i>	0.39
Bounket et al. (2021)	European Chub <i>Squalius cephalus</i>	0.40

^aFukushima et al. (2014) used the name “Siamese Mud Carp” for *Henicorhynchus siamensis* and *H. lobatus*. Here, we use the currently accepted common name for *Henicorhynchus lobatus* (www.fishbase.org).

^bFarver and Miner (2014) reported a regression equation predicting otolith Sr:Ca from water Sr:Ca with a slope of 0.359.

^cMean value for partition coefficients calculated from data presented in Farver and Miner (2014) Tables 1 and 2.