Ann. Zool. Fennici 58: 161–175 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 30 August 2021

Contemporary and historic dynamics of lake whitefish (*Coregonus clupeaformis*) eggs, larvae, and juveniles suggest recruitment bottleneck during first growing season

Zachary J. Amidon[1,*], Robin L. DeBruyne[1], Edward F. Roseman[2] & Christine M. Mayer[1]

[1)] *University of Toledo Lake Erie Center, Department of Environmental Sciences, 6200 Bay Shore Rd., Oregon, OH 43616, USA (*corresponding author's e-mail: zachary.amidon@utoledo.edu)*
[2)] *U.S. Geological Survey, Great Lakes Science Center, 1451 Green Rd., Ann Arbor, MI 48105, USA*

Received 31 Aug. 2020, final version received 22 Jan. 2021, accepted 9 Feb. 2021

Amidon, Z. J., DeBruyne, R. L., Roseman, E. F. & Mayer, C. M. 2021: Contemporary and historic dynamics of lake whitefish (*Coregonus clupeaformis*) eggs, larvae, and juveniles suggest recruitment bottleneck during first growing season. — *Ann. Zool. Fennici* 58: 161–175.

To determine if a survival bottleneck occurs in Lake Erie's lake whitefish (*Coregonus clupeaformis*) population and explore possible mechanisms responsible, we examined contemporary and historical dynamics of lake whitefish eggs, larvae and juveniles. Widespread spawning and low overwinter egg retention were observed in 2016–2018, however subsequent larval CPUE remained consistent with historical observations when regular recruitment occurred. Highest larval CPUE was consistently observed in nearshore areas 3–11 km from mid-lake spawning locations. Fall age-1 juvenile presence was predicted by fall age-0 catches, indicating the bottleneck occurs during the first growing season. Our results suggest the following: (1) factors limiting recruitment affect survival during or after the pelagic larval stage to fall age-0, and (2) physical and biological processes underlying connectivity between spawning and nearshore nursery habitats may be limiting recruitment. Future research focusing on larval nursery habitat characterization and lake whitefish growth and survival may reveal mechanisms affecting recruitment.

Introduction

Before the 1950s, large numbers of adult lake whitefish (*Coregonus clupeaformis*) supported a valuable commercial fishery in Lake Erie (http://www.glfc.org/great-lakes-databases.php). During this time, multiple age classes were regularly harvested, suggesting consistent recruitment to the fishery. Due to spawning habitat losses, invasive species interactions, and increased harvest in the 1950s, the lake whitefish fishery collapsed, leaving only a remnant population (Hartman 1973). A change occurred during the 1990s where commercial harvest catches of age-3 and older lake whitefish increased following reduced phosphorus loading and sea lam-

Editor-in-charge: Juha Karjalainen

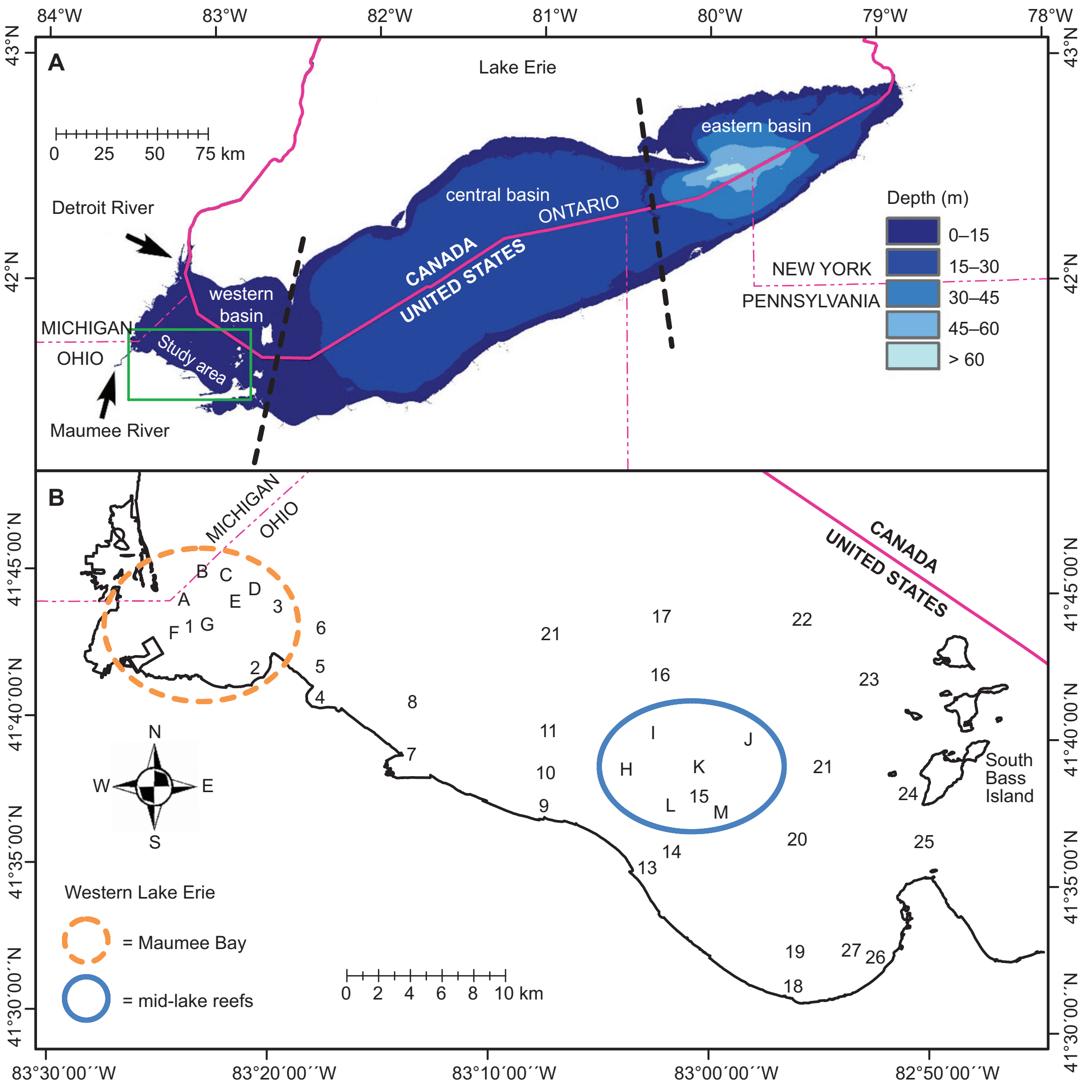

Fig. 1. (**A**) Bathymetric map of Lake Erie and boundary lines identifying the three basins. (**B**) Egg and larvae sampling locations in the southern part of Lake Erie's western basin. Letters represent individual egg sampling locations (A = MB1, B = MB2, C = MB3, D = MB4, E = MB5, F = MB6, G = MB8, H = Locust, I = Cone, J = Niagara, K = Crib, L = Toussaint, M = Round) and numbers represent individual larvae sampling locations.

prey (*Petromyzon marinus*) control (Cook *et al.* 2005, Ebener *et al.* 2008, Coldwater Task Group 2020). Catches again steadily declined in the early 2000s, likely due to poor recruitment during early life and juvenile stages as suggested by the lack of age-3 fish in the harvest (Coldwater Task Group 2020). Therefore, identifying life stages and environmental conditions under which recruitment bottlenecks occur for this population can provide insight into which variables influence recruitment.

Lake whitefish spawn in fall over shallow (< 5 m), hard substrate in the western basin of Lake Erie (Goodyear *et al.* 1982, Amidon *et al.* 2021) where their eggs incubate until hatching in the spring. While spawning occurs throughout the western basin, the highest egg abundances are found in Maumee Bay and on the mid-lake reefs (Amidon *et al.* 2021) (Fig. 1). In Maumee Bay, spawning occurs adjacent to the navigation channel on hard, shallow shoals created by dredged material (Amidon *et al.* 2021).

The mid-lake reefs are a natural offshore complex of varied rocky substrate with numerous crevices and cavities (Herdendorf & Braidech 1972, Amidon *et al*. 2021). Adult lake whitefish utilize the same spawning areas and their hatching larvae enter the open water system at a similar time as walleye (*Stizostedion vitreum*) larvae. Therefore, lake whitefish and walleye larvae are likely subject to transport by the same wind-driven spring lake currents (Roseman *et al.* 2005, Zhao *et al.* 2009). As waters warm in June to the upper limits of lake whitefish tolerance, juveniles travel east to the central basin likely along the 17 °C isotherm seeking cooler waters, as they transition to benthic feeding (Reckahn 1970, Edsall 1999).

The lake whitefish is a cold-water species and Lake Erie is at the southern edge of its geographic range, therefore, more productive year classes may occur during unusually cold winters (Lawler 1965, Freeberg *et al.* 1990). Cold winters promote low water temperatures (0.5–6.0 °C) which are optimal for incubation of lake whitefish eggs, thereby resulting in higher hatch rates and fewer larval abnormalities as compared with higher incubation temperatures (Price 1940, Mueller *et al.* 2015). In addition to direct physiological effects, low water temperatures promote the formation of ice cover that prevents strong winds from producing turbulence capable of dislodging incubating eggs. The persisting ice cover retains eggs near the original spawning area which may be more suitable for incubation and survival (Taylor *et al.* 1987, Freeberg *et al.* 1990, Brown *et al.* 1993). Since 1900, Lake Erie has experienced a trend of lower ice cover duration, with a notable decline since the early 1960s, especially since the late 1970s (Assel 2004). If increased or fluctuating water temperature during incubation contributes to decreased recruitment, we would expect decreased overwinter egg survival in recent years.

Variability in year class strength of many fish species is primarily caused by variation in growth and survival during the early life stages (Hjort 1914, Houde 2008). Large fluctuations in fish recruitment can be precipitated by relatively small variations in mortality rates, growth rates, or stage durations in the egg, larvae, and juvenile stages (Houde & Hoyt 1987, Pangle *et al.* 2004, Houde 2008). Despite the importance of early life stages to recruitment, fishery-independent surveys of early life history stages are relatively rare due to collection difficulty and cost. In an effort to index early life stage success, the Ohio Department of Natural Resources (ODNR) has conducted fall (13 September–30 November) bottom trawl assessment surveys in Lake Erie's central basin since 1990 (hereinafter referred to as fall trawl). Consistent detection of a cohort in the trawl survey at age-0 and age-1 would provide evidence that some fish survived through the most vulnerable life stages. The lack of detection of a cohort in the trawl survey would provide evidence that factors responsible for poor recruitment occurred prior to the juvenile stage.

An improved understanding of lake whitefish early life history dynamics and factors affecting recruitment contribute information that may help answer prioritized ecological questions from Great Lakes fishery managers concerning impediments to population growth (Bronte *et al.* 2017). The goal of this study was to measure lake whitefish early life history stage dynamics and concurrent environmental parameters to narrow the period when a recruitment bottleneck occurs and identify potential mechanisms hindering recruitment. Our specific objectives were to (1) estimate overwinter egg abundance at known spawning locations, (2) quantify contemporary abundance of lake whitefish larvae to compare with historical data, identifying spatial and temporal changes between the two periods, (3) determine the relationship between age-0 and age-1 juvenile stages from fall trawl abundances, and (4) explore the relationship between environmental parameters and ontogeny.

Material and methods

Study area

Lake Erie is the southernmost and warmest Laurentian Great Lake, (Herdendorf 1992, Bolsenga & Herdendorf 1993). The lake consists of three basins (western, central, and eastern) (Fig. 1). The western basin, where larval sampling occurred, is the shallowest and warmest basin with most depths between 7 and 10 m (Herdendorf 1992). In contrast with the other two basins, the western basin has several bedrock islands and shoals along its eastern edge, forming a partial divide between the western and central basins (Herdendorf & Braidech 1972, Herdendorf 1992). The central basin where ODNR trawl surveys are conducted is deeper and cooler, with average and maximum depths of 18.5 and 26 m, respectively (Herdendorf 1992). The lake's long fetch and western basin's shallow depth increase potential for strong wave and current formation which keep the western basin well mixed (Busch *et al.* 1975).

Egg collection and processing

To estimate egg relative abundance and overwinter survival, egg sampling locations were selected in Maumee Bay and the mid-lake reef complex because the highest egg abundances are known to occur there (Amidon *et al*. 2021). Detailed site attributes are described in Amidon *et al*. (2021). Eggs were sampled over two spawning and incubation seasons. During each fall, all sites were sampled approximately once per week until winter ice conditions prohibited lake access. In the spring after retreating ice allowed for boat access, all sites were sampled again to document the catch-per-unit-effort (CPUE) of viable overwintered eggs in areas of confirmed spawning. The first season was from 1 November 2016 to 23 February 2017 and included four locations in Maumee Bay (MB3, MB4, MB5, and MB6) and six locations within the mid-lake reef complex (Round, Toussaint, Crib, Niagara, Cone, and Locust). Cone, Crib, and Round were not sampled on 2 November 2016 and MB3 was not sampled on 22 November 2016. Due to poor weather and ice conditions on the lake, no sites were visited between 30 November 2016 and 17 February 2017. Spring 2017 egg collections occurred on 17 February 2017 at Round, Toussaint, Crib, Niagara, Cone, Locust, MB4, and MB5, and on February 23, 2017 at MB3 and MB6. Although spring egg collections in Maumee Bay were split between two sample days, they are treated as one collection and reported on the mean sample day (20 February 2017). The second spawning and incubation season was from 1 November 2017 to 24 March 2018 and included six Maumee Bay (MB1, MB2, MB3, MB4, MB5, and MB8) and six mid-lake reef complex locations (Round, Toussaint, Crib, Niagara, Cone, and Locust) (Fig. 1). MB2 and MB8 were not sampled on 1 November 2017 and 6 November 2017. Due to poor weather and ice conditions on the lake, no sites were visited between 4 December 2017 and 23 March 2018. Spring 2018 egg collections occurred on 23 March 2018 at Round, Toussaint, Crib, Niagara, Cone, and Locust. Spring collections occurred at MB1, MB2, MB3, MB4, MB5, and MB8 on 24 March 2018.

For each egg sampling event, we used a boat to pull a 39 kg iron sled attached to a diaphragm pump on the boat deck by a flexible 5 cm diameter hose in a circle on top of known spawning locations for 2–5 minutes (Stauffer 1981, Amidon *et al*. 2021). Bottom substrate and debris were pumped to the boat deck where it was filtered through a series of sieves, retaining egg-sized particles (1.5–6 mm). This process was replicated three times at each site and mean depth (m), bottom temperature (°C), and substrate composition were recorded. Samples were stored on ice until laboratory processing where lake whitefish eggs were picked from samples, identified (Auer 1982), and counted. All sites in each region (Maumee Bay, mid-lake reefs) were sampled on the same day when possible. CPUE of eggs at a site was calculated as the number of eggs per minute sampled (pooled replicates), with standard error. Sites were then split between Maumee Bay and the mid-lake reefs where CPUE was calculated for each region as the mean (± SE) number of eggs per minute of all sites sampled on the same day. Region CPUE was plotted over each sample period for Maumee Bay and mid-lake reefs. This method of egg collection varies in efficiency between substrate types and depth. Consequently, we did not make between-site egg CPUE comparisons. However, we did compare CPUE within each region from fall to spring when the same sites were sampled.

Larval collection and processing

Estimates of pelagic larval lake whitefish density and distribution were measured following spring egg collections in 2017 and 2018. The larval sampling locations and protocol for this study largely followed previous larval sampling in western Lake Erie conducted during spring 1994–1998 (Roseman *et al.* 2005), which allowed for comparison between the two periods. In total, 27 sites adjacent to the overwinter egg sampling sites were chosen in 2017–2018 (Fig. 1), and larvae were sampled at each site weekly from March to June. Samples were collected by boat towing a 60 cm diameter paired bongo net fitted with 500 µm mesh netting at approximately 1 m s^{-1} for five minutes. Nets were towed horizontally within the top 2 m of water during daylight hours, and all weekly samples were collected on the same day when possible. A flow meter was attached to the center of each net opening to estimate the volume of water sampled. Samples were rinsed from the net into a jar, preserved with 95% ethanol, and stored until laboratory processing.

In the laboratory, lake whitefish were identified and counted following keys and description provided in Auer (1982). The abundance of larval lake whitefish was estimated as the number of larvae per 1000 m^3 of water. We then calculated weekly mean larval abundance and standard error using mean densities from all sites sampled each week. Weekly abundance was reported on the mean date for the range of dates sampled each week.

Trawl juvenile assessment

To examine the relationship of survival through the juvenile stage, ODNR fall trawl assessment dataset was used (Ohio Department of Natural Resources 2020). Samples were collected from the lake bottom using a Yankee two-seam bottom trawl with a 10.4 m head rope, 25 mm bar mesh in the cod end, 13 mm stretched mesh liner, and 25.4 cm roller gear. Ten- and five-minute tows were conducted at sites with water depths greater and smaller than 10 m, respectively. Fish were identified to species, enumerated, and CPUE was calculated as the number of fish per hectare. For our analysis, CPUE data were organized by cohort, omitting cohorts where fish were not sampled at both age-0 and age-1, reducing our data set to the 1990–2018 cohorts. Exploratory analysis revealed that fall age-0, and age-1 CPUE data were not uniformly distributed, therefore we reduced quantitative CPUE data to nominal presence/absence count data and converted counts to contingency tables for hypothesis testing. Fisher's exact two-sided test for testing the null of independence (Fisher 1992) was used to calculate the probability that the observed proportion or those more extreme are caused by random chance. If the H_0 is accepted, the variables are independent, and there is no association between the cohort observations. If the H_0 is rejected in favor of the H_1, the variables are dependent, and there is an association between age-0 and age-1 observations, indicating the value of one variable helps to predict the value of the other variable.

Habitat

Mean water depth, water temperature at 1 m depth, and water transparency (Secchi disk to measurements nearest 0.1 m) were recorded in the field at each site. To create spatial representations of geographic patterns in larval fish, water depth, water temperature, and water transparency across our study area, we used ArcMap to plot the seasonal mean for each attribute at each sampling site as discrete point samples. We classified the data into five categories using the natural break function and applied graduated symbols so sites with higher values are represented by larger symbols. Additionally, changes in surface water temperature in 2017 and 2018 within the sample area were calculated by averaging the temperatures (± SD) from all sites sampled each week and reported on the mean date for the range of dates sampled. Daily water warming rate was calculated by subtracting the previous mean weekly temperature from the current mean weekly temperature and dividing the result by the number of days elapsed ([current temp – previous temp]/number of days). Wind velocity and direction data were recorded at South Bass Island in western Lake Erie located at the eastern edge of the study area (Fig. 1) for 1994–1998 and 2017–2018 (https://www.ndbc.noaa.gov/). Wind direction and frequency data for the period

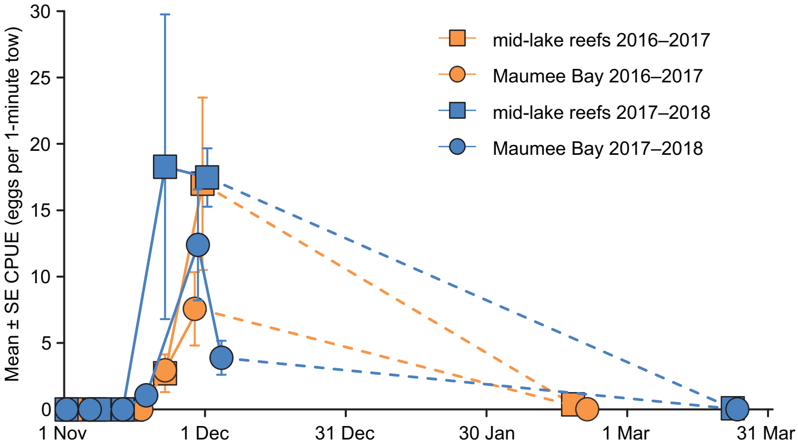

Fig. 2. Mean ± SE lake whitefish egg CPUE (eggs per 1-minute tow) from Maumee Bay and the mid-lake reefs. The dashed lines represent the periods when we were unable to sample due to weather and ice.

when peaks of pelagic lake whitefish larvae were observed (15 April–15 May) were summarized graphically using wind roses. To examine recent annual changes in ice cover (1973–2019), Lake Erie maximum ice cover data from the National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory (https://www.glerl.noaa.gov/data/ice/#historical) were plotted against time. Maximum Lake Erie ice cover during egg incubation for a cohort was plotted with fall age-0 lake whitefish CPUE for years with overlapping data (1990–2019).

Results

Egg collection and abundance

We detected eggs at all locations in fall 2016. Eggs were first detected in Maumee Bay (mean water temp. = 6.0 °C) and on the mid-lake reefs (mean water temp. = 7.0 °C) on 22 November 2016 with the highest CPUE (eggs per minute) observed on 29 November 2016 in Maumee Bay (mean CPUE ± SE = 7.58 ± 3.48) and 30 November 2016 on the mid-lake reefs (mean CPUE ± SE = 16.99 ± 6.50) (Fig. 2). In spring 2017 we detected no viable eggs in Maumee Bay, and few viable eggs on the mid-lake reefs (mean CPUE ± SE = 0.37 ± 0.15), resulting in a 97.8% decrease from our observed fall 2016 peak CPUE.

Also in fall 2017 we detected eggs at all locations. Eggs were first detected in Maumee Bay (mean water temp. = 5.6 °C) on 18 November 2017 and the mid-lake reefs (mean water temp. = 5.2 °C) on 22 November 2017 with the highest CPUE observed on 29 November 2017 in Maumee Bay (mean CPUE ± SE = 12.39 ± 4.18) and 22 November 2017 on the mid-lake reefs (mean CPUE ± SE = 18.28 ± 11.48) (Fig. 2). During spring 2018 we detected no viable eggs in Maumee Bay and few viable eggs on the mid-lake reefs (mean CPUE ± SE = 0.07 ± 0.05), resulting in a 99.6% decrease from our observed fall 2017 peak CPUE.

Larval lake whitefish abundance and distribution

Weekly larval samples were collected between 19 March and 2 June in 2017, and between 28 March and 24 May in 2018. The highest CPUE (mean ± SE = 69.96 ± 33.68) in 2017 was measured during the week of 23–29 April (Fig. 3). In 2018, pelagic larval dynamics were similar in magnitude (2018 mean CPUE ± SE = 38.86 ± 12.32) to the variation observed between 1994 and 1998 (mean CPUE ± SE = 37.85 ± 10.29) and 2017, however peak CPUE occurred between 29 April and 5 May which is later than previously observed (Fig. 3). Lake whitefish larvae were not detected at every site each week, however, they were detected at all sites at some point during the sample period except for site 24 in 2017 (Fig. 1). In 2017 and 2018, highest densities of lake whitefish larvae were collected at sites near the shallow southern

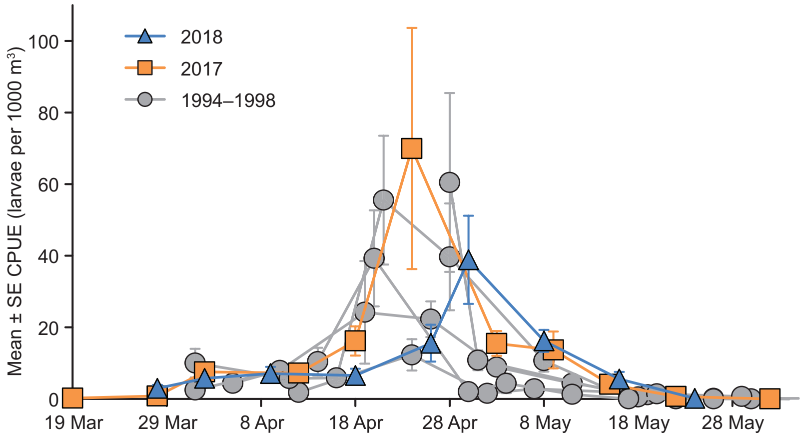

Fig. 3. Weekly larvae abundance (mean number of larvae per 1000 m^3 ± SE) of lake whitefish in western Lake Erie, 1994–1998 and 2017–2018.

shoreline where water temperatures were higher and water transparency was lower than those at the offshore sites (Fig. 4).

Trawl juvenile assessment

The numbers of total annual fall trawl hauls and fish collected were 18–78 and 0–52, respectively (Table 1). CPUE of fall juvenile lake whitefish (age-0 and age-1) was usually low, but still provided a measure of abundance prior to commercial harvest (Fig. 5). Assuming the variables are independent (true H_0), the probability of obtaining an effect at least as extreme as our sample data is < 0.01% (Fisher's exact test, 2-tailed, $p = 0.0001$). We reject the H_0 due to its unlikelihood in favor of the H_1, indicating the variables are dependent and that there is an association between the age-0 and age-1 cohort observations. The presence of lake whitefish at fall age-0 predicted the presence of lake whitefish at fall age-1 93% of the time and the absence of lake whitefish at fall age-0 predicts the absence of lake whitefish at fall age-1 80% of the time.

Table 1. Total fall trawl effort and number of fish collected for age-0 and age-1 by cohort in 1990–2019. The 2019 cohort age-1 data were not available at the time of publication.

Cohort	Age-0: number of trawls (number of fish)	Age-1: number of trawls (number of fish)	Cohort	Age-0: number of trawls (number of fish)	Age-1: number of trawls (number of fish)
1990	35 (0)	34 (0)	2005	58 (16)	57 (1)
1991	34 (0)	45 (0)	2006	57 (0)	57 (0)
1992	45 (6)	38 (9)	2007	57 (1)	57 (0)
1993	38 (18)	38 (13)	2008	57 (0)	55 (0)
1994	38 (27)	58 (43)	2009	55 (0)	18 (0)
1995	58 (12)	65 (30)	2010	18 (0)	56 (0)
1996	65 (52)	76 (30)	2011	56 (0)	57 (0)
1997	76 (0)	58 (0)	2012	57 (0)	57 (0)
1998	58 (2)	75 (10)	2013	57 (0)	20 (0)
1999	75 (4)	73 (3)	2014	20 (0)	23 (2)
2000	73 (0)	47 (0)	2015	23 (4)	78 (20)
2001	47 (3)	75 (41)	2016	78 (0)	57 (1)
2002	75 (0)	71 (3)	2017	57 (0)	24 (0)
2003	71 (51)	54 (18)	2018	24 (2)	36 (2)
2004	54 (4)	58 (5)	2019	36 (0)	

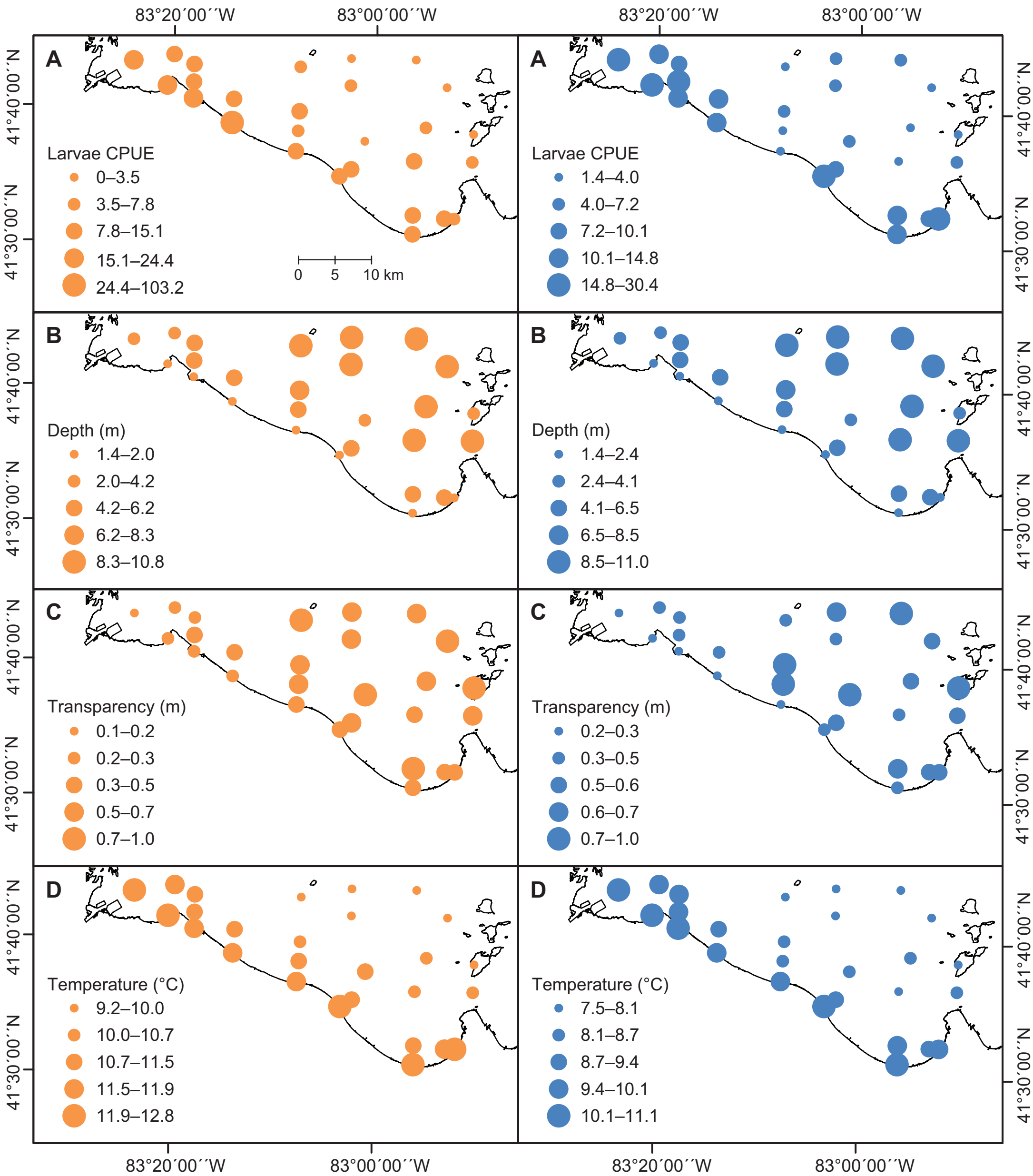

Fig. 4. Spatial distribution of mean annual measurements of (**A**) lake whitefish larvae CPUE (mean number of larvae per 1000 m^3), (**B**) depth (m), (**C**) water transparency (m), and (**D**) water temperature (°C) at sampling sites in the southern part of western Lake Erie for spring 2017 (left) and spring 2018 (right).

Habitat

Weekly surface water temperatures ranged from 1.5 °C to 19.0 °C during the 2017 sampling period. When compared with available data from 1994–1998, 2017 waters warmed at a relatively faster rate from March to mid-April, a slower rate from mid-April until mid-May, and moderate rate until June at a mean daily warming rate of 0.23 °C during the sampling period (19 March–1 June) (Fig. 6).

In the 2018 sampling period, weekly surface water temperatures ranged from 3.8 °C to 17.5 °C. When compared with available data

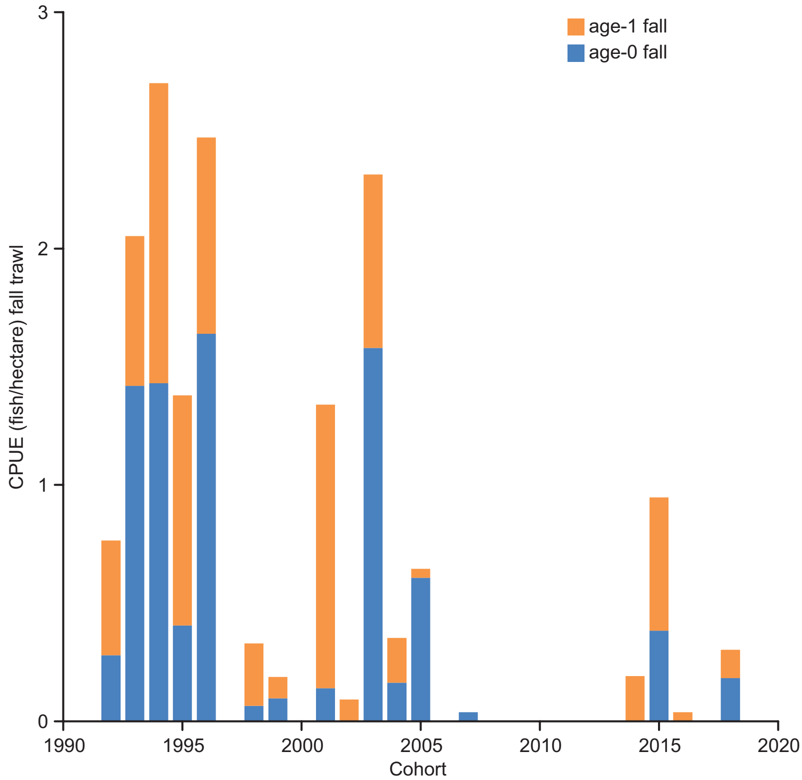

Fig. 5. Estimation of mean age-0, and age-1 lake whitefish post-stratification (fall) catch per hectare by cohort. Age-0 and age-1 data were collected at the end of the first and second growing seasons, respectively. For example, the 1996 bar shows the 1996 cohort sampled at age-0 in fall 1996 (blue) and the 1996 cohort sampled at age-1 in fall 1997 (orange). Data were collected in Lake Erie's Ohio central basin between October 13 and November 1990–2019 (Ohio Department of Natural Resources 2020). Mean age-1 data from the 2019 cohort were not available at the time of publication.

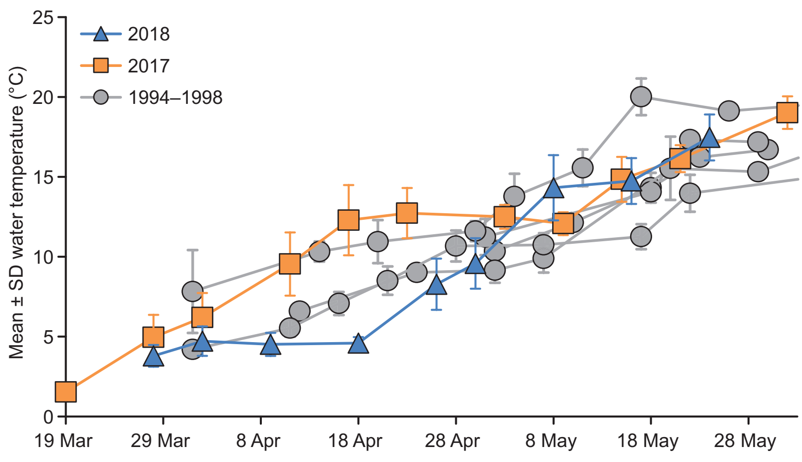

Fig. 6. Weekly surface water temperatures (mean ± SD) measured at spring larvae sites in the western basin of Lake Erie.

from 1994–1998, 2018 waters warmed at a relatively slow rate until mid-April, a faster rate from mid-April until mid-May, and moderate rate until June at a daily warming rate of 0.25 °C during the sampling period (28 March–24 May) (Fig. 6).

In 2017 and 2018, nearshore water temperatures were consistently higher than the offshore ones (Fig. 4). Water depth was shallowest nearest the mainland shoreline, increasing moving offshore. Secchi depth varied widely among sampling sites and dates, but water transparency was generally lower at nearshore and shallow Maumee Bay sites than at offshore sites in both years (Fig. 4). Wind direction and speed at South Bass Island varied each year, but the highest

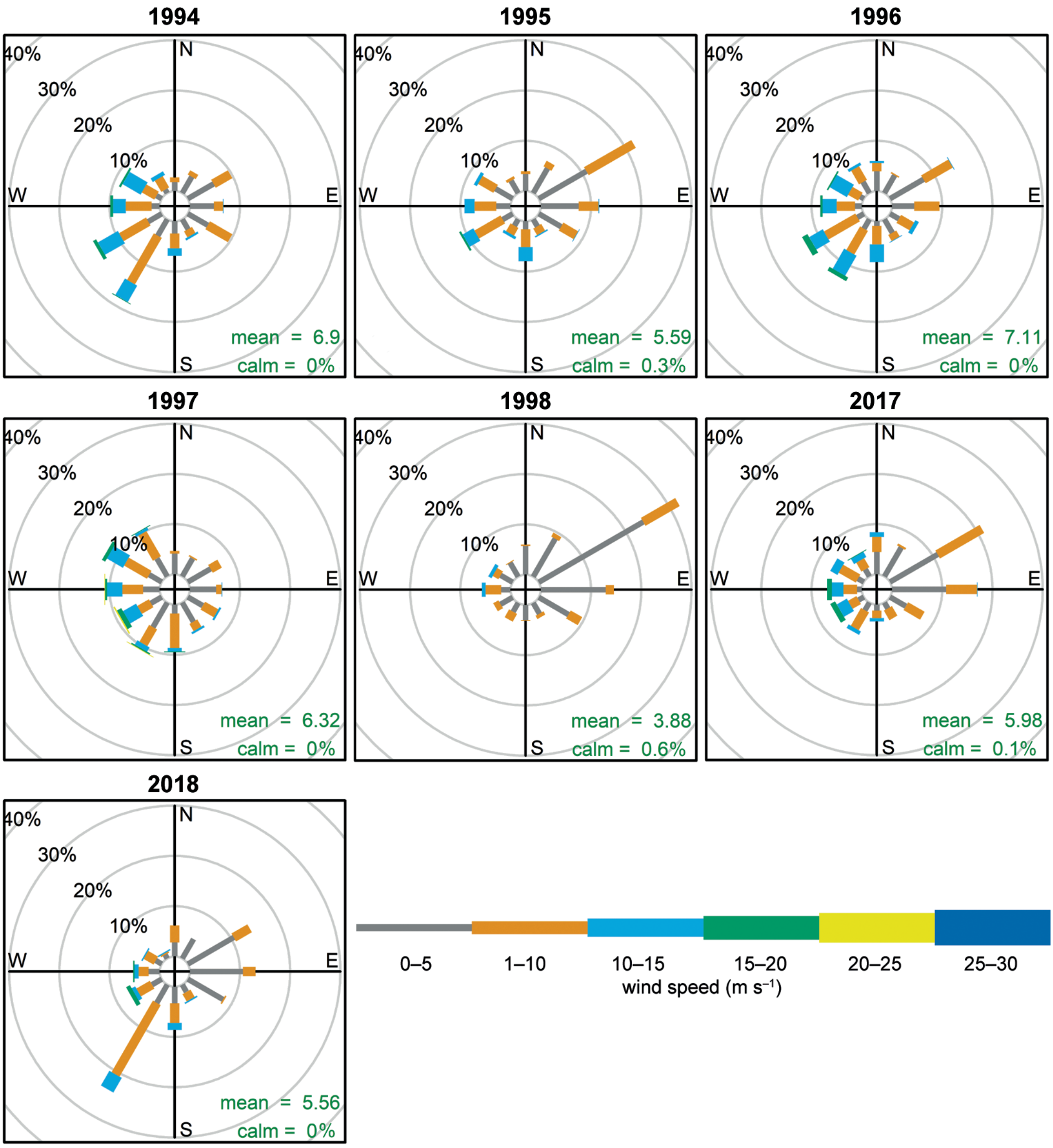

Fig. 7. Wind rose diagrams with wind speed (m s^{-1}) and frequency of count by wind direction (%) information recorded at South Bass Island, Lake Erie, during the pelagic larval lake whitefish period (April 15–May 15), 1994–1998 and 2017–2018.

wind frequencies were from SW and NE with the greatest wind speeds from the W–SW vectors (Fig. 7). Since 1973, Lake Erie exceeded 70% maximum peak ice cover for 40 winters and fell short of 70% maximum peak ice cover during seven winters (Fig. 8). Five of the seven low ice-cover years occurred between the most recent half of the time series (1996–2019), indicating a change towards warmer winters during recent years. A threshold relationship between ice cover and fall age-0 CPUE in agency trawl surveys was evident: lake whitefish recruitment was highest in years when the lake ice cover during egg incubation in the previous winter was greater than 85% (Fig. 8). However, not all cohorts that experienced greater than 85% ice cover recruited to fall age-0 in detectable numbers.

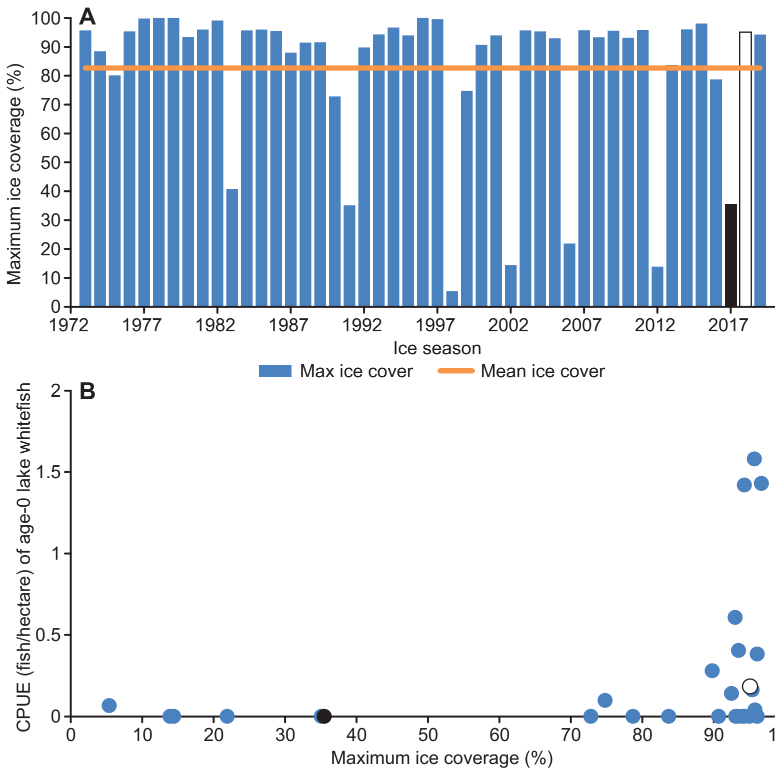

Fig. 8. (**A**) Maximum Lake Erie ice cover and mean series ice cover for 1973–2019 (https://www.glerl.noaa.gov/data/ice/#historical). (**B**) Maximum ice cover plotted against age-0 lake whitefish catch per hectare for overlapping years (1990–2019). Years 2017 (black) and 2018 (white) highlighted.

Discussion

The lack of age-3 lake whitefish entering the Lake Erie fishery since 2009 suggests a recruitment bottleneck occurs during life stages prior to harvesting from the fishery. The goal of this study was to assess early life history stage dynamics and environmental parameters to identify when a recruitment bottleneck occurs and potential mechanisms responsible. The following observations suggest that the recruitment bottleneck occurs after spring hatch and before fall of age-0:

1. A bottleneck is unlikely before or during the egg stage:
   a. Egg collections using a diaphragm pump provided evidence for widespread lake whitefish spawning in the western basin indicating abundant spawning habitat (Amidon *et al*. 2021).
   b. Although overwinter egg CPUE declined by 97.8% and 99.6%, larvae were widely dispersed the following spring and were of the same magnitude as in 1994–1998 when adult lake whitefish were consistently recruiting to the fishery in higher numbers.
2. A bottleneck likely occurs before fall of age-0:
   a. The presence of a lake whitefish cohort at fall age-0 in fall bottom trawls predicts the presence at fall age-1 indicating that severe mortality is unlikely after fall age-0.

Additionally, there are multiple biotic and abiotic conditions potentially contributing to survival within our recruitment bottleneck window (pelagic larval stage to fall age-0), and preliminary environmental data suggest that year-class success during this period may be associated with spatial and temporal overlap of pelagic larvae and favorable conditions in nursery areas such as high prey abundance, warm water temperatures, and few predators. Therefore, future research following yellow perch (*Perca flavescens*) and walleye framework (Roseman *et* *al.* 2005, Zhao *et al.* 2009, Fraker *et al.* 2015, Brodnik *et al.* 2016) coupling physical and biological processes to evaluate growth and survival through the larval stage may reveal specific factors influencing recruitment.

Evidence suggests a bottleneck is unlikely before or during the egg stage in Lake Erie, even though lake whitefish eggs in Lake Erie may experience less optimal environmental conditions than in colder lakes. In Grand Traverse Bay, Lake Michigan, 5.6% overwinter egg survival was observed in a high ice-cover year *vs*. 1.7% egg survival in a low ice-cover year. The difference in overwinter egg survival was attributed to ice cover protection from wave action which retains eggs on suitable incubation substrate, increasing survival to the larval stage (Freeberg *et al.* 1990). In our study, we observed less overwinter egg survival than Freeberg *et al.* (1990) after the low ice-cover year, even though peak ice cover differed substantially between the two years studied (36% in 2016–2017 *vs*. 95% in 2017–2018). Despite evidence of low overwinter egg survival, larval CPUE was similar in 2017 and 2018 to those observed in the same location in 1994–1998 when age-3 lake whitefish were recruiting to the fishery, indicating that strong year classes occur despite low overwinter egg survival. The lack of evidence for an ice-cover effect may be a result of Lake Erie's southern location within the Great Lakes. Lake Erie does not freeze for the duration of lake whitefish egg incubation, especially in the western basin where most of the spawning occurs. Western basin ice typically begins to form in December after the fall spawn, and begins to break up in mid-February with last ice usually near the end of March, well before hatch (Assel 2005, Wang *et al.* 2012), leaving eggs exposed to wind-driven lake currents. Even during a cold year, Lake Erie ice cover may not last long enough to detect its consistently positive effect on overwinter egg survival. Therefore, low overwinter egg survival should be expected in lakes where the egg incubation period extends beyond the period of ice cover.

Our larval data cannot confirm if the bottleneck occurs during or after the pelagic larval stage. Larval abundance peaked in Lake Erie on 24 April 2017 and 30 April 2018 and gradually decreased thereafter, but the cause of this decrease could be attributed to either mortality or gear avoidance due to morphological development. Lake whitefish larvae hatch at 11–13 mm (Price 1940) and can live off their yolk-sac resources without exogenous food sources for two weeks before the yolk-sac is depleted (Taylor & Freeberg 1984). Once yolk-sac resources are depleted, there is a total reliance on exogenous food sources and mortality rates dramatically increase (Taylor & Freeberg 1984). During this transition to exogenous food (~16 mm), they also begin to develop fins that facilitate mobility to actively evade ichthyoplankton nets, move outside of the study area, and leave the surface waters seeking benthic prey items which would be seen in catches as a decline (Hoagman 1974, McKenna & Johnson 2009, Ryan & Crawford 2014). The combination of larval development and the limitations of our sampling gear prohibit assessment of survival during or beyond this stage based on abundance only. Therefore, we suggest that the recruitment bottleneck is likely occurring during or after the pelagic larval stage, but the exact timing of the bottleneck could not be determined by our study design.

Good habitat conditions, generally characterized by high prey abundance, warm water, and few predators, are typically patchy in the environment. Larvae must encounter these patches in sufficient frequency in order to grow, survive, and recruit to the population (Cushing 1990, Roseman *et al.* 2005). We found lake whitefish larvae concentrated in shallow nearshore areas where water temperatures were higher and water clarity relatively lower than at offshore sites in both years of our study (Fig. 4), similar to patterns in 1994–1998 suggesting continuity between periods. Warmer, shallow waters are known to produce abundant prey resources and are favorable as nursery habitat for pelagic lake whitefish larvae as they transition to benthic-feeding juveniles (Taylor & Freeberg 1984, Brown & Taylor 1992, Frost & Culver 2001). However, with over 80% of Lake Erie's shoreline armored and limited connectivity of favorable habitat, high quality nursery area may be reduced (Herdendorf 1987). While broad scale temperature changes remain consistent, spatial evaluation of multiple habitat quality metrics, including prey abundance, water temperatures, and predation risk, would more clearly identify the quality and distribution of nursery habitat to inform survival estimates through the pelagic larval stage.

In the same way that habitat quality varies spatially at a given point in time, habitat quality varies temporally at a given location. Strong adult year classes are produced when fall water temperatures drop early and remain low during egg incubation, without fluctuating throughout the winter, before increasing slowly in late spring during larval emergence (Christie 1963, Lawler 1965); suggesting spring water temperature and prey abundance may affect recruitment. Lake whitefish are the first species to hatch in the western basin when zooplankton biomass is relatively low (Frost & Culver 2001, Roseman *et al.* 2005). After a warm winter (e.g., 2016–2017), water temperatures may rise early in spring, resulting in an earlier hatch that may not coincide with an increase in zooplankton biomass even in shallow nearshore areas (Frost & Culver 2001), thus causing possible starvation mortality for the larval fish. Therefore, to characterize nursery habitat quality and distribution for lake whitefish larvae, a sampling design which incorporates both spatial and temporal aspects would be most effective.

Since ichthyoplankton have little ability to maintain their location directly after hatch and are subject to movement by lake currents (Grioche *et al.* 2000, McKenna & Johnson 2009), their presence in these shallow nearshore locations does not confirm the quality of this habitat. Lake current direction at the time of hatch has been found to influence walleye transport to poor-quality offshore areas or high-quality inshore areas in western Lake Erie, which affects survival (Roseman *et al.* 2005, Zhao *et al.* 2009). Given the similarity between walleye and lake whitefish early life history events we suspect that wind-driven lake currents may influence lake whitefish survival as well. In all years that lake whitefish larvae were collected, wind direction frequencies were dominated by SW and NE vectors with the greatest wind speeds originating from the W–SW vectors (Fig. 7). Pelagic larvae exposed to a dominant SW–W wind would likely move offshore and larvae exposed to a dominant NE wind would likely move inshore implying potential for contrasting nursery quality conditions. While wind is one major driver of surface lake currents, inflows from the Detroit and Maumee Rivers also contribute to circulation patterns in Lake Erie's western basin (Beletsky *et al.* 2013). Therefore, at this time we can only hypothesize that wind-driven currents are responsible for the spatial distribution of pelagic lake whitefish larvae in western Lake Erie. Definitive modeling studies that solve for waterbody motions, transport, and mixing of simulated particles are needed to determine post-hatch distribution.

Our data did not show evidence for increased larval abundance due to physical ice cover, however cold winters that promote ice cover also promote low stable water temperatures and a late spring warm that may influence larval survival (Christie 1963, Lawler 1965). The two years of intensive sampling during the larval period in this study revealed similar larval densities despite very different ice cover conditions, but the relationship between ice cover and fall age-0 CPUE remained consistent for 2017 and 2018. Year-class strength is usually determined in the first year of life (Pangle *et al.* 2004, Houde 2008) and ODNR fall bottom trawl assessment collects lake whitefish at 0.5 and 1.5 years post-hatch. Examination of the trawl data revealed that years when a cohort was present at fall age-0, it was usually present the following year at fall age-1 and in years when a cohort was absent from trawl data at fall age-0, it was usually absent the following year at fall age-1. Therefore, the presence or absence of a cohort at fall age-1 is usually predicted by fall age-0, suggesting the bottleneck limiting recruitment occurs prior to fall age-0. Coupled with results from egg and larvae collections we conclude that the bottleneck limiting recruitment likely occurs during or after the pelagic larval stage and prior to fall age-0.

In recent years, the Lake Erie lake whitefish population has experienced a decline in age-3 recruitment (Coldwater Task Group 2020) and juvenile lake whitefish index surveys have indicated that year class strength is set before fall age-0. Despite evidence of high overwinter egg CPUE decline, larval abundances were similar to those observed in the same location from 1994–

1998 when age-3 lake whitefish were recruiting to the fishery regularly. The consistent presence of larvae in spring collections in 1994–1998 and 2017–2018 indicates that eggs hatched and larvae survived to the pelagic stage with the potential to recruit to the fishery, affirming the recruitment decline is likely not from reduced spawning and hatching success, but is occurring during or after the pelagic larval stage and before fall age-0. Preliminary exploration of environmental variables suggests spatial and temporal overlap of pelagic larvae and favorable nursery areas may influence recruitment. Although this study does not address the exact cause of the recruitment bottleneck, we do identify the life stages when the bottleneck may be occurring for future work evaluating growth and survival through the larval and early juvenile stages.

Acknowledgments

This work was supported by the Great Lakes Restoration Initiative. The authors acknowledge the contributions of numerous field and laboratory staff that assisted with various phases of this project to include B. Kuhaneck, M. Tomczak, B. Schmidt, R. Young, and the boat captain, A. Lytten. Invaluable graphic assistance was provided by A. Sodeman and J. Fischer. Handling of fishes followed the guidelines provided in the "Guidelines for the use of fishes in research" published by the American Fisheries Society, Bethesda, MD. Use of trade names is for descriptive purposes and does not imply endorsement by the U.S. Geological Survey.

References

Amidon, Z., DeBruyne, R., Roseman, E. F. & Mayer, C. H. 2021: Spatial extent of contemporary lake whitefish spawning in western Lake Erie. — *Advances in Limnology* 66. [In press].

Assel, R. A. 2004: *Lake Erie ice cover climatology: basin averaged ice cover, winters 1898–2002*. — US Department of Commerce, National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.

Assel, R. A. 2005: *Great Lakes weekly ice cover statistics*. — US Department of Commerce, National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan.

Auer, N. A. 1982: *Identification of larval fishes of the Great Lakes basin with emphasis on the Lake Michigan drainage*. — Great Lakes Fishery Commission, Ann Arbor, Michigan.

Beletsky, D., Hawley, N. & Rao, Y. R. 2013: Modeling summer circulation and thermal structure of Lake Erie. — *Journal of Geophysical Research: Oceans* 118: 6238–6252.

Bolsenga, S. J. & Herdendorf, C. E. 1993: *Lake Erie and Lake St. Clair handbook*. — Wayne State University Press, Detroit, Michigan.

Brodnik, R. M., Fraker, M. E., Anderson, E. J., Carreon-Martinez, L., DeVanna, K. M., Heath, D. D., Reichert, J. M., Roseman, E. F. & Ludsin, S. A. 2016: Larval dispersal underlies demographically important intersystem connectivity in a Great Lakes yellow perch (*Perca flavescens*) population. — *Canadian Journal of Fisheries and Aquatic Sciences* 73: 416–426.

Bronte, C. R., Bunnell, D. B., David, S. R., Gordon, R., Gorsky, D., Millard, M. J., Read, J., Stein, R. A. & Vaccaro, L. 2017: *Report from the workshop on coregonine restoration science*. — US Geological Survey, Reston, Virginia.

Brown, R. & Taylor, W. 1992: Effects of egg composition and prey density on the larval growth and survival of lake whitefish (*Coregonus clupeaformis* Mitchill). — *Journal of Fish Biology* 40: 381–394.

Brown, R. W., Taylor, W. W. & Assel, R. A. 1993: Factors affecting the recruitment of lake whitefish in two areas of northern Lake Michigan. — *Journal of Great Lakes Research* 19: 418–428.

Busch, W.-D. N., Scholl, R. L. & Hartman, W. L. 1975: Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960–70. — *Journal of the Fisheries Board of Canada* 32: 1733–1743.

Christie, W. J. 1963: Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. — *Journal of the Fisheries Board of Canada* 20: 597–646.

Coldwater Task Group 2020: *2019 Report of the Lake Erie Coldwater Task Group, March 2020*. — Presented to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission, Ann Arbor, Michigan, USA.

Cook, H. A., Johnson, T. B., Locke, B. & Morrison, B. J. 2005: *Status of lake whitefish (Coregonus clupeaformis) in Lake Erie*. — The Great Lakes Fishery Commission, Ann Arbor, Michigan.

Cushing, D. 1990: Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. — In: Blaxter, J. H. S. & Southward, A. J. (eds.), *Advances in marine biology*: 249–293. Elsevier, Cambridge, MA.

Ebener, M. P., Kinnunen, R. E., Schneeberger, P. J., Mohr, L. C., Hoyle, J. A. & Peeters, P. 2008: Management of commercial fisheries for lake whitefish in the Laurentian Great Lakes of North America. — In: *International governance of fisheries ecosystems: Learning from the past, finding solutions for the future*: 99–143. American Fisheries Society, Bethseda, Maryland

Edsall, T. A. 1999: Preferred temperatures of juvenile lake whitefish. — *Journal of Great Lakes Research* 25: 583–588.

Fisher, R. A. 1992: *Statistical methods for research workers*.

— Springer, New York, NY.

Fraker, M. E., Anderson, E. J., May, C. J., Chen, K.-Y., Davis, J. J., DeVanna, K. M., DuFour, M. R., Marschall, E. A., Mayer, C. M. & Miner, J. G. 2015: Stock-specific advection of larval walleye (*Sander vitreus*) in western Lake Erie: implications for larval growth, mixing, and stock discrimination. — *Journal of Great Lakes Research* 41: 830–845.

Freeberg, M. H., Taylor, W. W. & Brown, R. W. 1990: Effect of egg and larval survival on year-class strength of lake whitefish in Grand Traverse Bay, Lake Michigan. — *Transactions of the American Fisheries Society* 119: 92–100.

Frost, P. C. & Culver, D. A. 2001: Spatial and temporal variability of phytoplankton and zooplankton in western Lake Erie. — *Journal of Freshwater Ecology* 16: 435–443.

Goodyear, C., Edsall, T., Dempsey, D. O., Moss, G. & Polanski, P. 1982: *Atlas of the spawning and nursery areas of Great Lakes fishes*. — U.S. Fish and Wildlife Service, Washington, DC.

Grioche, A., Harlay, X., Koubbi, P. & Lago, L. F. 2000: Vertical migrations of fish larvae: Eulerian and Lagrangian observations in the Eastern English Channel. — *Journal of Plankton Research* 22: 1813–1828.

Hartman, W. L. 1973: *Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie*. — Great Lakes Fishery Commission, Ann Arbor, Michigan

Herdendorf, C. E. 1987: *The ecology of the coastal marshes of western Lake Erie: a community profile*. — Ohio State University, Columbus, Ohio.

Herdendorf, C. E. 1992: Lake Erie coastal wetlands: an overview. — *Journal of Great Lakes Research* 18: 533–551.

Herdendorf, C. E. & Braidech, L. L. 1972: *A study of the physical characteristics of the major reef areas in western Lake Erie*. — Ohio Dept of Natural Resources, Div of Geological Survey, Project AFCS-1, Columbus, Ohio.

Hjort, J. 1914: *Fluctuations in the great fisheries of northern Europe viewed in the light of biological research*. — Andr. Fred. Høst & Fils, Copenhagen, Denmark.

Hoagman, W. 1974: Vital activity parameters as related to the early life history of larval and post-larval lake whitefish (*Coregonus clupeaformis*). — In: Blaxter, J. H. S. (eds.), *The early life history of fish*: 547–558. Springer, Berlin.

Houde, E. & Hoyt, R. 1987: Fish early life dynamics and recruitment variability. — *Transactions of the American Fisheries Society* 2: 17–29.

Houde, E. D. 2008: Emerging from Hjort's shadow. — *Journal of Northwest Atlantic Fishery Science* 41: 53–70.

Lawler, G. H. 1965: Fluctuations in the success of year-classes of whitefish populations with special reference to Lake Erie. — *Journal of the Fisheries Board of Canada* 22: 1197–1227.

McKenna, J. E. & Johnson, J. H. 2009: Spatial and temporal variation in distribution of larval lake whitefish in eastern Lake Ontario: signs of recovery? — *Journal of Great Lakes Research* 35: 94–100.

Mueller, C. A., Eme, J., Manzon, R. G., Somers, C. M., Boreham, D. R. & Wilson, J. Y. 2015: Embryonic critical windows: changes in incubation temperature alter survival, hatchling phenotype, and cost of development in lake whitefish (*Coregonus clupeaformis*). — *Journal of Comparative Physiology B* 185: 315–331.

Ohio Department of Natural Resources 2020: *Ohio's Lake Erie fisheries, 2019*. — Ohio Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Units, Fairport and Sandusky.

Pangle, K. L., Sutton, T. M., Kinnunen, R. E. & Hoff, M. H. 2004: Overwinter survival of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. — *Transactions of the American Fisheries Society* 133: 1235–1246.

Price, J. W. 1940: Time-temperature relations in the incubation of the whitefish, *Coregonus clupeaformis* (Mitchill). — *The Journal of general physiology* 23: 449–468.

Reckahn, J. A. 1970: *Ecology of young lake whitefish (Coregonus clupeaformis) in South Bay, Manitoulin Island, Lake Huron*. — University of Manitoba, Winnipeg, Manitoba.

Roseman, E. F., Taylor, W. W., Hayes, D. B., Tyson, J. T. & Haas, R. C. 2005: Spatial patterns emphasize the importance of coastal zones as nursery areas for larval walleye in western Lake Erie. — *Journal of Great Lakes Research* 31: 28–44.

Ryan, K. M. & Crawford, S. S. 2014: Distribution and abundance of larval lake whitefish (*Coregonus clupeaformis*) in Stokes Bay, Lake Huron. — *Journal of Great Lakes Research* 40: 755–762.

Stauffer, T. M. 1981: Collecting gear for lake trout eggs and fry. — *The Progressive Fish-Culturist* 43: 186–193.

Taylor, W. & Freeberg, M. 1984: Effect of food abundance on larval lake whitefish, *Coregonus clupeaformis* Mitchill, growth and survival. — *Journal of Fish Biology* 25: 733–741.

Taylor, W. W., Smale, M. A. & Freeberg, M. H. 1987: Biotic and abiotic determinants of lake whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan. — *Canadian Journal of Fisheries and Aquatic Sciences* 44: s313–s323.

Wang, J., Bai, X., Hu, H., Clites, A., Colton, M. & Lofgren, B. 2012: Temporal and spatial variability of Great Lakes ice cover, 1973–2010. — *Journal of Climate* 25: 1318–1329.

Zhao, Y., Jones, M. L., Shuter, B. J. & Roseman, E. F. 2009: A biophysical model of Lake Erie walleye (*Sander vitreus*) explains interannual variations in recruitment. — *Canadian Journal of Fisheries and Aquatic Sciences* 66: 114–125.