Larval lake whitefish (*Coregonus clupeaformis*) recruitment dynamics in Lake Huron

A Thesis Submitted to the Committee on Graduate Studies
in Partial Fulfillment of the Requirements for the Degree of Master of Science
in the Faculty of Arts and Science

TRENT UNIVERSITY
Peterborough, Ontario, Canada

Environmental and Life Sciences M.Sc. Graduate Program
May 2022

ABSTRACT

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Lake whitefish (*Coregonus clupeaformis*) recruitment has declined substantially in several regions of the Laurentian Great Lakes since the establishment of non-native dreissenid mussels in the early 1990's. In Lake Huron, the reasons for the observed recruitment declines are currently unknown and there is limited knowledge about larval life stage. In our study, we determined whether larval hatching and growth rates have changed before and after dreissenid mussel invasion, and the role of several key environmental variables in influencing annual variation in larval densities. Larval fish were collected in the Fishing Islands spawning shoal during two time periods: a historical period (1976-1986) and a contemporary period (2017-2019). Larval densities and growth were lower in recent years, suggesting that recruitment is being limited at the larval life stage and that reduced food availability may be further limiting the growth during the larval stage. Annual variation of larval densities were influenced by spawning stock biomass, water levels, and dreissenid mussel presence, with higher water levels and the presence of dreissenid mussels being associated with higher larval densities. The direction of the effect of spawning stock biomass was either negative or positive depending on the model. We also found that larval density was a significant predictor of age 4 recruitment, indicating that year-class strength may be partly established at the larval life stage.

Keywords: lake whitefish, Coregonus clupeaformis, recruitment, Lake Huron, larval, Great Lakes.

ACKNOWLEDGEMENTS

I have received a great deal of support throughout the duration of my Master's degree, for which I am extremely grateful.

I would first like to thank my supervisor, Dr. Erin Dunlop, for the opportunity to complete a research project in an area of fisheries science that I am passionate about. Her guidance and encouragement throughout this entire process has helped me to complete my thesis.

Thank you to my committee members, Dr. Nick Jones and Dr. Jim Schaefer, for their feedback and support.

This research project would not have been possible without the efforts of Erin's research team and the Upper Great Lakes Management Unit. Specifically: Mike Pinder, Derek Lipskie, Issac Herbert, Justin Trumpickas, Courtney Taylor, Camilla Ryther, Vicki Lee, Chris Davis, and Lawrence Skinner.

I would also like to thank the entire Raby Lab for their kindness and friendship throughout these past two years. Having good friends that I could turn to for advice was something I am grateful for.

Finally, I would like to thank my family for their love and continued support throughout this journey.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

CHAPTER 1: GENERAL INTRODUCTION

The invasion of non-native species, overharvesting, and loss of habitat have all contributed to dramatic shifts in fish abundance over the past century (Bunnell et al. 2014). For example, the establishment of sea lamprey (*Petromyzon marinus*) throughout the upper Great Lakes in the late 1930's corresponded with the loss of lake trout (*Salvelinus namaycush*), a top predator and commercially significant species (Christie 1974). Almost all other large fish species were affected by sea lamprey predation, leading to a collapse of fisheries in the upper Great Lakes (Christie 1974; Smith and Tibbles 1980). Perhaps the most drastic ecosystem changes occurred following the introduction of dreissenid mussels (*Dreissena* spp.). The filter-feeding activities of dreissenid mussels shifted nutrient cycling, altered benthic macroinvertebrate community composition, and enhanced water clarity in the Great Lakes (Higgins and Vander Zanden 2010; Bunnell et al. 2014). These changes ultimately led to declines in the recruitment of several key species, namely lake whitefish (*Coregonus clupeaformis*).

Lake whitefish are a commercially significant species that have undergone several major fluctuations in abundance across the Great Lakes over the past century, with the exception of Lake Superior (Mohr and Nalepa 2005; Ebener et al. 2008). Historically, lake whitefish comprised a significant proportion of the total commercial catch in the Great Lakes until the beginning of the 1940's when population abundances began to decline (Mohr and Nalepa 2005). Lake whitefish abundance reached an all-time low during the 1950's and remained depressed throughout the 1960's (Mohr and Nalepa 2005). These historical fluctuations have been primarily attributed to overharvesting, predation by sea lamprey, and the degradation of habitat and water quality due to human activities (Christie 1974; Mohr and Nalepa 2005; Ebener et al. 2008). During the 1980's, a resurgence of lake whitefish populations occurred due to a combination of effective management strategies, including sea lamprey control, restrictions on commercial harvesting, and habitat restoration (Ebener 1997; Ebener et al. 2008). In the late 1980's, zebra mussels (*Dreissena polymorpha*) first invaded the Great Lakes, followed by quagga mussels (*Dreissena bugensis*) in 1993 (Griffiths et al. 1991; Mills et al. 1993; Bunnell et al. 2014). The establishment of zebra and quagga mussels (hereafter dreissenid mussels) coincided with the decline of the energy-rich benthic amphipod *Diporeia* spp. (hereafter *Diporeia*), an important food source for adult lake whitefish (Ebener 1997; Mohr and Nalepa 2005; Ebener et al. 2008). Declines in growth, condition, feeding ecology, and age 4 recruitment of lake whitefish throughout the Great Lakes resulted following the loss of *Diporeia* (Mohr and Nalepa 2005; Fera et al. 2015; Fera et al. 2017; Gobin et al. 2015; Cottrill et al. 2020).

Lake whitefish are a cold-water species found in freshwater lakes and rivers across Canada and parts of northeastern United States (Scott and Crossman 1973). Within the Great Lakes system, lake whitefish adults tend to occupy regions with water temperatures around 10°C at depths during the summer stratified period ranging from 20 to 85 m (Scott and Crossman 1973; Selgeby and Hoff 1996). Lake whitefish reach maturity between 3.5-4.5 years of age, with males typically reaching maturity at a younger age than females (Scott and Crossman 1973). The diet of adult lake whitefish varies, but aquatic insects (e.g., Chironomidae larvae), molluscs, and amphipods are the primary foods (Koelz 1929; Scott and Crossman 1973; Ihssen et al. 1981). Lake whitefish have also been observed to occasionally consume small fish and fish eggs (Scott and

Crossman 1973; Pothoven 2005; Herbst et al. 2013). The food habits of age-0 lake whitefish are less well known, but recent research indicates that diet varies based on location and prey availability during the larval life stage (Claramunt et al. 2010; Pothoven and Olds 2020).

In the Great Lakes, the lake whitefish spawning season occurs from late October to early December in shallow embayments 1-8 m deep (Scott and Crossman 1973). Adult lake whitefish are broadcast spawners that deposit their eggs randomly across rocky substrates (Scott and Crossman 1973; Lane et al. 1996). Developing embryos incubate under the ice throughout the winter months at water temperatures ranging from 0.5°C to 6°C (Price 1940; Brooke 1975). The average incubation period is inversely related to temperature, and ranges from 59 days at 6°C to 141 days at 0.5°C (Price 1940; Brooke 1975). Hatching begins in April or May as water temperatures approach 6°C (Price 1940; Scott and Crossman 1973). Newly hatched embryos swim to the surface and remain epipelagic for approximately 14-21 days before being transported by wind and wave currents to adjacent nursery habitats (Hart 1930; Reckahn 1970; Frederick 1982). During the larval life stage, lake whitefish transition from endogenous feeding to exogenous feeding (Balon 1975). Larval lake whitefish are transported to nearby shallow beachy areas (<3 m deep) by winds or currents in late June and early July (Hart 1930; Reckahn 1970). Larval fish occupy this area for about two months before descending into deeper waters as water temperatures continue to increase throughout the summer months (Reckahn 1970).

Lake whitefish recruitment has substantially declined over the past two decades in the main basins of lakes Huron, Michigan, Erie, and Ontario accompanied by declines in population abundance and yield (Mohr and Nalepa 2005; Cottrill et al. 2020; Ebener et al. 2021). In Lake Huron, declines in age 4 lake whitefish recruitment have been most pronounced in the northern and central main basin and southern Georgian Bay (Cottrill et al. 2020; Ebener et al. 2021). Lake whitefish recruitment first began to decline following the invasion of dreissenid mussels in the late 1980's and reductions in *Diporeia* abundance that followed (Griffiths et al. 1991; Nalepa et al. 1995; Mohr and Nalepa 2005). Consequently, some lake whitefish populations were forced to shift into deeper habitats in search of alternative foraging grounds (Mohr and Ebener 2005a; Bence and Mohr 2008), while other populations moved into more shallow waters (Fera et al. 2017). This switch in diet proceeded dramatic declines in adult lake whitefish growth and condition throughout the lake (Rennie et al. 2015; Fera et al. 2017). The age composition of populations has also been impacted by the recruitment decline, with the average age of lake whitefish increasing to 10 years or more in most parts of Lake Huron (Cottrill et al. 2020). Presently, it is unclear at what life stage the recruitment bottleneck is occurring and what factors have contributed to the recruitment decline. We do not know the extent to which environmental variables influence recruitment. Several hypotheses for these recruitment declines exist including the presence of invasive dreissenid mussels, the collapse of *Diporeia*, and limited food availability, yet there has been limited research on the larval life stage of lake whitefish specifically in Lake Huron (Henderson et al. 1983; Gobin et al. 2015).

In this thesis, I examined the lake whitefish recruitment dynamics in Lake Huron, focusing on the larval life stage in an effort to better understand the population declines. In the first chapter, I determined whether lake whitefish recruitment was being limited at the larval life stage and whether changes in larval hatching and growth rates had changed before and after dreissenid mussel invasion. I hypothesized that lake whitefish recruitment was being limited at the larval life stage and that recruitment was declining because of reduced food availability caused by the presence of dreissenid mussels. I predicted that if recruitment was being limited at the larval stage and dreissenid mussels were causing changes in the food web leading to reduced food availability, then contemporary estimates of larval density and growth rates would be lower than historical estimates. In the second chapter of this thesis, I examined the effect of climate on larval lake whitefish density and whether there was a relationship between larval densities and future year-class strength. I hypothesized that climate variation was an important determinant of larval lake whitefish density. I predicted that if recruitment was being limited at the larval life stage and climate variation was an important determinant of year-class strength that there would be a relationship between annual larval lake whitefish abundance and future year-class strength. In the general discussion, I summarized the main findings of each chapter and discussed the implications of my findings.

CHAPTER 2: LONG-TERM CHANGES IN DENSITY AND GROWTH OF LARVAL LAKE WHITEFISH (*COREGONUS CLUEAFORMIS*) IN LAKE HURON

ABSTRACT

Lake whitefish (*Coregonus clupeaformis*) are an ecologically and commercially significant species across the Laurentian Great Lakes. Over the past 20 years, lake whitefish populations in Lake Huron have shown drastic declines, potentially linked to the invasion of dreissenid mussels and resulting ecosystem changes. In this study, larval fish were sampled from the Fishing Islands region in Lake Huron to determine if declines in recruitment are linked to poor growth and survival during the larval period. Larval fish were collected during two time periods: a historical time period prior to dreissenid mussel establishment (1976-1986) when population abundances were higher, and a contemporary time period (2017-2019) when population abundances were low. Substantial year-to-year variability was observed in both time periods in larval production and growth, pointing to the possible role of environmental factors (e.g., ice cover) affecting larval dynamics. Importantly, we observed lower larval lake whitefish densities in recent years, suggesting that recruitment is being limited at the larval life stage. We furthermore observed a lower larval growth rate in recent years after accounting for variation in growing degree days. These slower larval growth rates are consistent with the hypothesis that reduced food availability during critical early life stages contribute to reduced recruitment of lake whitefish, potentially due to dreissenid mussel establishment.

INTRODUCTION

Over the past century, the establishment of numerous invasive species has resulted in significant ecosystem changes throughout the Laurentian Great Lakes (Mills et al. 1993; Sturtevant et al. 2019). Two such species are zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*), hereafter referred to collectively as dreissenid mussels. The establishment of dreissenid mussels led to declines in several native fish species and shifts in zooplankton community composition throughout the Great Lakes (Christie 1974; Bunnell et al. 2014). The effects of such species invasions over the past century were exacerbated further by overfishing, eutrophication, and habitat changes (Christie 1974; Meisner et al. 1987).

The introduction of dreissenid mussels in Lake Huron is associated with profound changes throughout the lake's ecosystem. Zebra mussels first became established in Lake Huron in 1989 and continued to colonize both deep offshore and nearshore ecosystems throughout the early 1990's (Griffiths et al. 1991; Nalepa et al. 1995). Quagga mussels then invaded the lake in 1997, primarily occupying soft sediments in deep waters (Mills et al. 1999; Nalepa 2010; Karatayev et al. 2015). The proliferation of dreissenid mussels in Lake Huron resulted in an increase of water clarity, reductions in primary productivity, and shifts in the benthic invertebrate community (Rennie et al. 2009; Fera et al. 2017). The establishment of dreissenid mussels also coincided with dramatic declines in the energy-rich benthic amphipod *Diporeia* spp. (hereafter *Diporeia*; Dermott et al. 2005; Nalepa et al. 2005; Nalepa et al. 2007), a preferred prey item for some fish species, including lake whitefish (*Coregonus clupeaformis*; Scott and Crossman 1973; Pothoven et al. 2001; Hondorp et al. 2005). Ecosystem changes during the past two decades have also been associated with declines in key fish populations, for example the collapse of alewife (*Alosa pseudoharengus*), a non-native prey fish that once dominated the offshore fish community in Lake Huron (Riley et al. 2008; Riley et al. 2019).

Lake whitefish, a widely distributed and commercially harvested species in the Great Lakes, have been significantly impacted by the establishment of dreissenid mussels and the associated changes in the food web. Following the loss of *Diporeia*, an important food source for later stage juveniles and adults, lake whitefish switched to consuming prey with lower energetic value, primarily dreissenid mussels (Pothoven et al. 2001; McNickle et al. 2006). In addition, the distribution of lake whitefish populations changed, with some populations shifting to inhabit deeper waters in search of the remaining pockets of *Diporeia* (Mohr and Ebener 2005a; Rennie et al. 2015), and others moving more inshore with an increased reliance on nearshore benthic production (Rennie et al. 2009; Rennie et al. 2015; Fera et al. 2017). The switch in diet and changes in depth distribution of lake whitefish resulted in declines in growth and body condition, which preceded reductions in the relative abundance of juveniles, adults, and the number of new recruits (age 3+; Pothoven et al. 2001; Pothoven and Madenjian 2008; Cottrill et al. 2020).

In Lake Huron, lake whitefish are the most widely distributed and sought-after commercially harvested species, occupying all four major interacting water bodies or basins (Ebener et al. 2008a). Between 2010 and 2017, lake whitefish accounted for the majority of the total commercial harvest from Lake Huron, with catches averaging 2.09 million kg annually (Cottrill et al. 2020). Lake whitefish yield peaked in 2000 with 4.43 million kg harvested but since that peak, yield has been declining continuously (Cottrill et al. 2020). Substantial declines in current lake whitefish yield have been observed throughout Lake Huron, particularly in the northern and central regions of the main basin of the lake (Cottrill et al. 2020). Reductions in lake whitefish yield have been primarily attributed to declines in population abundance and the loss of *Diporeia* (Pothoven et al. 2001; Nalepa et al. 2005; Pothoven 2005). In addition to reduced yield, declines in lake whitefish spawning stock biomass (Fig. 2.1A) and juvenile recruitment (age 4+; Fig. 2.1B) have occurred throughout Lake Huron. However, the reasons for the observed declines in juvenile lake whitefish recruitment are currently unknown.

One explanation as to why declines in juvenile recruitment are occurring is that food availability has been reduced during the critical early larval fish stage, leading to slower growth and reduced survival to the juvenile stage (Ebener et al. 2021). Larval fish growth is largely dependent upon zooplankton abundance as explained by the match/mismatch hypothesis, which proposes that the timing of larval hatching and the production of food is crucial for survival, growth, and ultimately recruitment (Cushing 1974; Cushing 1990). The establishment of dreissenid mussels have changed zooplankton abundances, altering the number and type of prey species available, due to the mussels' filter feeding activity (Higgins and Vander Zanden 2010). Dreissenid mussel presence is also associated with declines in phytoplankton biomass and the re-direction of energy from pelagic to benthic pathways (Higgins and Vander Zanden 2010). For lake whitefish, these ecosystem changes have likely caused reductions in food availability upon hatching and could result in poor larval growth rates.

In addition to food availability during the larval period, other factors may influence lake whitefish recruitment including adult spawning stock biomass, overwinter conditions, and spring water temperatures. Spawning stock biomass represents an estimate of the total weight of spawning adult fish in a stock, which can influence recruitment. Moderate levels of adult spawning stock biomass are associated with greater levels of recruitment, while lower and higher spawning stock biomass levels tend to result in poorer recruitment, presumably due to increased competition for resources (Henderson et al. 1983; Taylor et al. 1987; Brown et al. 1993). Overwinter conditions, namely water temperature and ice cover, are important in the survival of lake whitefish eggs and larvae (Taylor et al. 1987; Freeberg et al. 1990). As a cold-water species, the optimum incubation temperature for lake whitefish eggs is between 2-8 °C, with colder water temperatures typically resulting in increased egg survival and hatching rates (Price 1940; Christie 1963; Brooke 1975; Taylor et al. 1987). The duration of ice cover during the winter months is also crucial in lake whitefish survival, potentially by preventing the developing eggs and larvae from being shifted off important nursery habitats by strong winds and currents (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993). Early winters with prolonged ice cover are associated with increased survival of lake whitefish eggs and larvae (Freeberg et al. 1990). Additionally, warm spring temperatures result in increased larval lake whitefish survival and growth (Reckahn 1986; Freeberg et al. 1990); however, Ryan and Crawford (2014) found no relationship between water temperature at the timing of hatching and larval lake whitefish distribution or abundance.

Most research on the population dynamics of lake whitefish has focused primarily on the juvenile and adult life stages and little is known about the earlier life stages. Our present knowledge about lake whitefish recruitment comes from several key studies, most of which involve data collected prior to the invasion of dreissenid mussels (Taylor et al.

1987; Freeberg et al. 1990; Brown et al. 1993; Claramunt et al. 2010; Lynch et al. 2015; Zischke et al. 2017). By examining the effect of numerous variables on lake whitefish recruitment at sites in Lake Michigan, Taylor et al. (1987) found that spawning biomass, winter ice cover, and spring water temperatures were important determinants of juvenile and adult recruitment (age 2+). Similar findings regarding the effects of ice cover and spring water temperatures were reported by Brown et al. (1993) and Lynch et al. (2015), although the degree to which ice cover influenced juvenile recruitment (age 3+) varied among the study sites sampled. Claramunt et al. (2010) examined the potential role of diet in age-0 lake whitefish in lakes Michigan and Superior. Ontogenic shifts in larval diets were found to influence the growth and survival of lake whitefish, indicating the potential role of diet in recruitment (Claramunt et al. 2010). Freeberg et al. (1990) aimed to identify the determinants of lake whitefish year-class strength in Grand Traverse Bay, Lake Michigan. Overwinter conditions and food availability were found to be important; however, lake whitefish data were only collected for only two years. While these studies have provided insight into some of the drivers of larval recruitment, only a handful of studies have focused on lake whitefish recruitment in Lake Huron specifically (Henderson et al. 1983; Gobin et al. 2015). Over the past two decades, lake whitefish recruitment in Lake Huron has continuously declined but the reasons why are unknown (Gobin et al. 2015; Cottrill et al. 2020). Presently, it is unclear whether the observed declines in juvenile recruitment are caused by reduced hatching rate or reduced survival at the larval stage, and the role that dreissenid mussels have played in the declines of lake whitefish.

The current study examines whether larval hatching rates and growth rates have changed before and after dreissenid mussel invasion. To do this, we compared the trends in larval density and growth between: 1) a historical time period (pre-dreissenid; 1976-1986) and 2) a contemporary time period (post-dreissenid; 2017-2019). Our study was conducted in the Fishing Islands region, an important spawning shoal for lake whitefish located in the main basin of Lake Huron, where significant declines in juvenile recruitment have been reported (Ebener et al. 2021). We predicted reduced larval densities in the contemporary time period if declines in larval lake whitefish recruitment are occurring prior to the larval hatching stage, for example if fewer embryos are being produced or surviving overwinter. If low food availability during the larval stage contributes to reduced survival and impaired recruitment, we predict slower growth rates in the contemporary time period. We know of no other published dataset of larval lake whitefish densities in the Great Lakes that span these two time periods and that permit a closer examination of the early life history dynamics that might have contributed to the observed declines in juvenile recruitment.

METHODS

Study area

Our study focuses on the Fishing Islands spawning shoal, located in the main basin of Lake Huron. Lake Huron is composed of four major interacting water bodies or basins: the main basin, north channel, Georgian Bay, and Saginaw Bay (Lake Huron Partnership 2018). Our specific study area spans from Stokes Bay to Chiefs Point (Fig. 2.2). The Fishing Islands is thought to represent a historically important lake whitefish spawning shoal in the main basin of Lake Huron (Goodyear et al. 1982). This spawning shoal is also a region where there have been declines in lake whitefish recruitment and larval production (Ebener et al. 2021; Fig. 2.3).

Historical larval fish sampling (1976-1986)

For our study, we made use of larval fish trawling surveys conducted by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (OMNDMNRF) between 1976-1986 (hereafter referred to as the historical time period) in the Fishing Islands (Loftus 1977; Loftus 1978). A total of sixteen sites were sampled historically in the Fishing Islands region (Fig. 2.4; Table 2.1). Larval fish sampling was typically conducted from ice out (mid-April) until early June on a weekly basis to ensure sampling throughout the spring larval fish hatching period. The duration of the historical larval sampling period varied from year-to-year. Each trawl was associated with one of the sixteen sampling sites, although no detailed global positioning system (GPS) coordinates were recorded at the precise location for each individual trawl conducted.

Larval fish trawls were conducted using circular fish nets (80 cm diameter; 300 cm long) towed at approximately 1.0 m below the surface from the side of a vessel. Tows were conducted for 5-20 minutes at sites where the lake depth was greater than 2.0 m. Tows were replicated by making a second tow immediately following the first, and a maximum of two replicate tows were performed at each site. Tow velocities were measured with a General Oceanics flowmeter that was mounted in the net opening. For a subset of tows, vessel speeds were recorded and ranged between 0.30 m/s and 1.27 m/s (mean of 0.69 m/s). Environmental data were also simultaneously collected for each larval fish tow including surface water temperature, wind velocity, and general weather conditions (Loftus 1977; Loftus 1978). After each tow, larval fish were preserved in 5-

10% formalin. Larval samples were later identified in the laboratory with a microscope using keys available in Fish (1932) and May and Gasaway (1967). All identified lake whitefish were then enumerated and body lengths were measured to the nearest 0.5 mm.

Contemporary larval fish sampling (2017-2019)

Larval fish surveys were conducted annually from 2017-2019 (hereafter referred to as the contemporary time period) in the Fishing Islands by the OMNDMNRF, with the sampling region covering the same area as the historical Fishing Islands larval survey (Fig. 2.4; Table 2.1). The contemporary sampling was not meant to exactly replicate the historical sampling but was rather designed to study the correspondence between larval fish density and food availability. Nonetheless, given the similarity of key aspects of the sampling (e.g., surface larval fish tows conducted frequently over the entirety of the spring hatching period), the historical and contemporary sampling offered a good opportunity to compare larval lake whitefish densities before and after dreissenid mussel establishment. For the contemporary sampling, we sampled a combination of fixed and random sites throughout the spring larval hatching period. Fixed sites (11 in total) were sampled at least once a week and random sites were selected using the quantum geographic information system (QGIS) random points tool. Larval fish surveys began after ice out (mid-April) and continued until larval fish were no longer being captured in nets (end of May). In 2017, we conducted surveys every other week, with multiple days of sampling occurring during the weeks when trawling occurred. In 2018 and 2019, larval sampling occurred every week.

Larval fish trawls were conducted using a circular net (500 μm mesh; 50 cm diameter; 150 cm long) towed approximately 1.0 m below the surface of the water between 15-30 cm from the side of the vessel. Tows were conducted for 10 minutes at sites where the lake depth was greater than 1.5 m at tow speeds of 3.5-5.5 km/hr (mean of 3.85 km/hr). Immediately following each larval fish trawl, we sampled the same transect again with a plankton net (although the tow duration was shortened to be 3-5 minutes); the plankton data were not used in this study. We also recorded environmental data prior to starting each tow including air temperature, water temperature, wind velocity, and general weather conditions. In the laboratory, larval fish were enumerated and body lengths were measured to the nearest 0.01 mm using a microscope and digital camera.

Larval fish were genetically identified to species through DNA barcoding using a portion of the caudal fin (Appendix 1). In 2017 each larval coregonid was genetically identified, whereas in 2018 and 2019 a subset of coregonids sampled were genetically identified because of constraints in the number of samples that could be processed. For each tow in all three sampling years, we first separated larval coregonid fish from other fish samples collected using visual identification. A subset of coregonid fish were then identified to species through DNA barcoding. The proportion of confirmed larval lake whitefish were then used to estimate the number of lake whitefish in each tow conducted.

Statistical analysis: larval density

For the historical survey data, we assigned each larval trawl a GPS coordinate (latitude and longitude) based on the sampling site identified on a map (Loftus 1977; Loftus 1978). For the contemporary survey data, we used trawl GPS coordinates to assign each individual trawl to one of the sixteen historical sampling sites if that trawl was conducted within a 5 km diameter of that site. We explored the effect of varying the sampling diameter (ranging from 1-5 km) on our results and report those in Appendix 2.

The potential effect of this distance on larval density was assessed because historical trawl records did not indicate how far from each site sampling was conducted. Each trawl sample was then assigned a day of year and week of year.

Catch-per-unit effort ($CPUE$) was used as the measure of larval lake whitefish density. $CPUE$ was calculated using two units of effort. First, we calculated larval catches per unit area per tow minute (no. larval fish/m^2/min), denoted as $CPUE_A$. However, owing to a potential difference in vessel speeds between time periods, $CPUE$ was also calculated per volume (no. larval fish/m^3), denoted as $CPUE_V$. While $CPUE$ measured on a per-volume basis takes into account vessel speed differences, it does require an estimate of the distance travelled for each trawl. For the historical time period, the distance travelled was calculated for a subset of trawls from the flowmeter data (with no data collected in 1976). For the contemporary time period, we calculated distance travelled using the GPS coordinates that were recorded at the start and end of each trawl.

For both $CPUE$ measures, the area A of the net is simply πr^2, where the radius of the net r was 0.40 m historically and 0.25 m currently. To calculate $CPUE_A$, the catch per tow was divided by the area and divided by the tow duration (in minutes). To calculate $CPUE_V$ (in units of no. larval fish/m^3), we calculated the tow volume for each individual trawl by multiplying the tow distance (m) by the net area (m^2). For the historical time period, we calculated tow distance based on flowmeter data and these data were used to calculate tow volume. Distance travelled (m) using flowmeter data was calculated as follows:

$$(1) \qquad Distance = \frac{C_{Diff} \times R_{Const}}{999{,}999}$$

where C_{Diff} is the difference in counts (calculated by subtracting the initial count from the final count) and R_{Const} is the standard speed rotor constant, which is 26,873 (General Oceanics 2018). For the contemporary time period, the start (Lat0 and Lon0) and end (Lat1 and Lon1) GPS coordinates were used to calculate tow distance (m). All subsequent analyses and results reported hereafter in the main text are presented for $CPUE_V$, while the results for $CPUE_A$ are reported in Appendix 3.

Potential outliers in $CPUE$ values were identified by calculating z-scores for each time period as follows:

$$(2) \qquad Z = \frac{CPUE_V - \overline{CPUE}_V}{SD}$$

where $\overline{CPUE}_V$ is the mean and SD is the standard deviation of the untransformed individual trawl $CPUE_V$ values. $CPUE_V$ values were identified as outliers and removed from subsequent analysis if their absolute value of z-scores differed by more than three standard deviations from the mean (Schiffler 1988). A total of 20 outliers were identified and removed from our analysis because of larval catches that were substantially greater than other trawls conducted around the same time (> 500 larval fish per trawl). Larval density values were then log-transformed to approximate normality, as a visual assessment showed that the untransformed data were not normally distributed in either time period. The log-transformed density data without outliers were then used for all subsequent statistical analysis reported in the main text; however, we also conducted the same analyses with the outliers included (Appendix 4).

For all statistical analyses we used R version 3.5.2. Recognizing the spatial and temporal variability of our dataset, we conducted a nested analysis of variance (ANOVA) to examine the effect of year, sampling week, and site on contemporary log-transformed larval densities (aov function). The statistical model used was as follows:

(3) $aov(\log(CPUE_V) \sim Year + Year|Week + Year|Site + Year|Week|Site)$

An analysis of variance (ANOVA) was performed to test for a difference in larval $CPUE$ between the historical and contemporary time periods, $aov(\log(CPUE_V) \sim time\ period)$. A permutation test, or randomization test, was also conducted as there were only 3 years of contemporary larval data to compare with historical data (Quinn and Keough 2002). In the permutation test, the observed difference in mean larval densities between the historical and contemporary time period was first calculated. $CPUE_V$ values were then randomly reassigned to a time period and the difference in means of the two groups was calculated. The data were reshuffled 10,000 times, with the difference in means calculated each time. To compute the p value, the proportion of permuted test statistics greater than or equal to the observed test statistic was determined:

(4) $p = (no. D_1 \geq no. D_0) \div total\ no. of\ D_1$

where p is the calculated p value, D_0 is the observed difference in density means, and D_1 is the calculated difference in density means.

Larval lake whitefish were identified to species using two different techniques in each time period. Historically, larval whitefish were visually assessed with the aid of reference keys whereas in the contemporary time period, DNA barcoding was used to identify larval lake whitefish to species. To account for the potential misidentification of larval lake whitefish historically, we examined the reliability with which larval fish were correctly identified to species. In a comparison of visual and genetic identification using larval fish samples from Stokes Bay, Overdyk et al. (2016) determined that larval lake whitefish were correctly identified to species with 90.7% accuracy. Based on these findings, 10% of larval fish from each trawl were removed from each sampling year in the historical time period to examine the potential effects on calculated historical larval densities. Larval densities with 10% of larval fish removed ($CPUE_{V-10\%}$) were calculated using the steps outlined above. $CPUE_{V-10\%}$ values were then compared to assess for differences in larval densities between the two time periods using an ANOVA. The statistical model used was, $aov(\log(CPUE_{V-10\%}) \sim time\ period)$. The density comparisons were also conducted with the outliers included (Appendix 5).

In addition to examining larval fish trends over a broader spatial scale, we also wanted to examine site-specific temporal trends for key sites within the Fishing Islands region that were sampled frequently during both time periods. The frequency of sampling at these key sites allowed for finer scale analysis of larval density trends. Annual $CPUE_V$ values were examined at Howdenvale, Pike Bay, Red Bay, and Stokes Bay (Fig. 2.4). The site of Stokes Bay encompassed larval densities from Garden Island, Irish Harbour, and Tamarack (Fig. 2.4). We conducted ANOVAs to test for potential differences in larval densities between the historical and contemporary time periods at each of the four sites individually with outliers removed, $aov(\log(CPUE_V) \sim site)$. The ANOVAs were also conducted with the density outliers included (Appendix 6).

Statistical analysis: larval growth

To determine if there was a difference in larval growth rates between historical and contemporary time periods, we analyzed annual trends in the length at capture of larval lake whitefish. Given the linear relationship between warmer water temperatures and faster larval growth (Price 1940; Reckahn 1986), we calculated the growing degree days (GDD) for our larval fish samples. GDD represent an indicator of annual water temperatures and are often used to help explain variation in fish growth (Neuheimer and Taggart 2007). In the context of our study, GDD were calculated to provide us with an estimate of the variation in water temperature on the size of larval fish. To estimate GDD, we first predicted the daily water temperature for each day based on the linear regressions between observed water temperature (taken at each trawl) and day of year (DOY):

(5) $T_{pred,DOY} = (m \times DOY) - b$

where T_{pred} is the predicted water temperature in °C, m is the slope from the linear regression equation, DOY is the day of year, and b is the y-intercept from the linear regression equation. Linear regressions were estimated for each year between day 100 (April 10) and day 160 (June 09). Linear regressions were chosen because water temperatures in the Great Lakes typically exhibit a linear warming throughout the spring (Trumpickas et al. 2009).

For each larval fish sample, the cumulative GDD (cGDD) was estimated for every day between day 100 and day 160 in each sampling year:

(6) $cGDD_{DOY} = \sum T_{pred,\mathrm{DOY}} - T_{base}$

where T_{base} is the base temperature, set here to 5°C (Price 1940; Brooke 1975; Rennie et al. 2009), and $T_{pred,DOY}$ is a proxy for the average daily water temperature. In our study, the majority of larval hatching in both time periods (12/14 years) occurred at temperatures above 5°C and therefore temperatures below 5°C would not be expected to contribute substantially to growth. An analysis of covariance (ANCOVA) was conducted to test for a difference in larval growth rates from year-to-year within each time period. A separate ANCOVA was conducted to then determine if there was a difference in the overall larval growth rate between the historical and contemporary time periods at the same number of cGDD, $Growth = (length \sim cGDD) \times time\ period$. The data used for the second ANCOVA were truncated at 150 cGDD for both time periods, which represented the maximum number of cGDD in the contemporary time period.

RESULTS

Larval density

A total of 923 larval tows were conducted during the historical time period (1977-1986), with the majority of sampling occurring in May (Table 2.2). Larval fish were caught as early as April 06 and as late as June 09, although the duration and frequency of historical sampling varied from year-to-year. Historically, mean larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) tended to be higher in the later sampling years (1983-1986). In the contemporary time period (2017-2019), a total of 446 larval tows were conducted (Table 2.2). Contemporary larval sampling began as early as April 11 and continued as late as June 06. Contemporary sampling was consistent throughout the hatching period, with a similar number of tows conducted during the last two years of sampling. Mean contemporary larval densities were higher in the last two years of sampling and were generally similar to historical density estimates.

A total of 14 outliers were identified in the historical time period, with the majority of outliers occurring in 1986 (11/14 outliers; Table A2.1). Historical density outliers were from four sites: Irish Harbour (6 outliers), Pike Bay (4 outliers), Howdenvale (2 outliers), and Red Bay (2 outliers). In the contemporary time period, there were 6 outliers identified and no outliers were present in 2017 (Table A2.1).

Contemporary density outliers were from three sites: Pike Bay (2 outliers), Garden Island (2 outliers), and Irish Harbour (2 outliers). Pike Bay and Irish Harbour seemed to produce outliers more consistently than other sites across both time periods. Calculated mean larval densities with outliers included for the historical and contemporary time periods are in Table A2.2.

We found very strong evidence that larval lake whitefish densities have declined between the two time periods, with contemporary densities being lower than historically (ANOVA: $F_{1,\,1368} = 70.6$; $P < 0.001$; Fig. 2.5; Fig. A2.1). Mean larval density was three times lower in the contemporary time period (0.067 larval fish/m^3) compared to historically (0.215 larval fish/m^3). However, the overall decline in contemporary larval densities was not drastic, and there were both low- and high-density years during each time period. For example, calculated density estimates for the historical time period indicated that 1977 and 1982 were particularly low years, while estimates of larval density for the later sampling years gradually increased over time (i.e., 1983-1986; Fig. 2.5A). By deducting 10% of larval fish from each tow individually, we determined that contemporary larval densities remained significantly lower than historically (ANOVA: $F_{1,\,1368} = 64.4$; $P < 0.001$; Appendix 7). Results from the permutation test provided strong evidence that contemporary densities were lower than historically, both with and without density outliers included, and that the observed difference was unlikely due to chance (one-tailed permutation test; $P < 0.001$; Fig. A2.2; Fig. A2.3).

We determined that there were slight differences in larval density results when using contemporary data at various sampling diameters. Results from the nested ANOVAs conducted with the contemporary larval lake whitefish data indicated that there was a significant difference in larval densities among the years sampled at four of the five sampling diameters (2 km: $F_{2, 90} = 3.31$, $P < 0.05$; 3 km: $F_{2, 118} = 5.37$, $P < 0.05$; 4 km: $F_{2, 129} = 6.22$, $P < 0.05$; 5 km: $F_{2, 222} = 13.46$, $P < 0.05$; Appendix 2). A significant difference in larval densities was not found for data within 1 km of the sampling site (1 km: $F_{2, 43} = 1.56$, $P = 0.2212$; Appendix 2). In addition to variation across years sampled, we found significant variation in larval densities among weeks within years sampled and among sites within years sampled at four of the five diameters assessed (2-5 km dimeters; Appendix 2). Due to the fact that slight differences in density results were found at 1 km, contemporary trawl data collected at 5 km from each of the sampling sites was used to maximize the available data.

In addition to temporal variation, we found substantial annual spatial variation within each sampling time period (Fig. 2.6). Historical larval densities were consistent in Pike Bay, Garden Island, Irish Harbour, and Howdenvale (Fig. 2.6A). Earlier in the historical sampling period (1977-1979), larval whitefish were also abundant at Stokes Bay and the areas immediately surrounding Stokes Bay. Some sites (e.g., Chiefs Point) were exclusively sampled in 1976; however, data from this year was excluded due to the absence of flowmeter data that was required to estimate larval density. During the contemporary time period, larval lake whitefish were consistently present at Pike Bay, Stokes Bay, and Howdenvale (Fig. 2.6B). Larval densities were on average lower currently than historically when each of the four key sites were considered individually (Fig. 2.7); however, these differences were only statistically significant for Stokes Bay (ANOVAs; Howdenvale: $F_{1, 146} = 2.05$; $P = 0.1540$; Pike Bay: $F_{1, 278} = 2.91$; $P = 0.0892$; Red Bay: $F_{1, 115} = 0.80$; $P = 0.3740$; Stokes Bay: $F_{1, 417} = 6.69$; $P = 0.010$).

Larval growth

A subsample of 1462 larvae were measured from the larval lake whitefish sampled historically (Table 2.3). Mean larval lengths in the historical time period varied from year-to-year but tended to decrease over the duration of the sampling period. Larval lengths from earlier sampling years (1976-1980) displayed higher mean yearly lengths compared to the later sampling years (1981-1986). In the contemporary time period, a subsample of 2037 larval lake whitefish were measured and mean total lengths were similar across the three sampling years (Table 2.3).

Overall, larval lake whitefish growth was nearly two times faster in the historical time period ($F_{1, 1460} = 954.9$; $P < 0.001$; $R^2 = 0.40$; Fig. 2.8A) than in the contemporary time period ($F_{1, 2035} = 1433.0$; $P < 0.001$; $R^2 = 0.41$; Fig. 2.8B). Historical larval lake whitefish lengths increased linearly with day of year and growth rates varied from year-to-year (R^2 values; Fig. 2.9). Two years in particular, 1976 and 1979, had low growth rates, while the later sampling years had higher overall growth rates. Contemporary larval lengths also displayed a linear increase with day of year (Fig. 2.10). Larval growth rates tended to be similar across the three recent sampling years, particularly between 2018 and 2019. There was very strong evidence that larval growth rates varied from year-to-year in both the historical (ANCOVA; $F_{10, 1440} = 12.0$, $P < 0.001$) and contemporary (ANCOVA; $F_{2, 2034} = 4.0$, $P < 0.001$) time periods.

We found a difference in larval lake whitefish growth between the two time periods overall using data truncated at 150 cGDD, with contemporary growth being slower than historically (ANCOVA; $F_{1, 3046} = 7.5$, $P = 0.006$; Fig. 2.11). There were also a greater number of cGDD historically (ANOVA: $F_{1, 3048} = 718.6$; $P < 0.001$; Fig. 2.11;

Table 2.4). In the historical time period, the number of GDD that were greater than our set base temperature (5°C) varied from year-to-year, with a maximum of 427 cGDD in 1985 and a minimum of 237 cGDD in 1977 (Table 2.4). Overall, the contemporary time period had fewer GDD and cGDD that were above our base temperature (Table 2.4). In 2018 and 2019, predicted water temperatures were greater than 5°C on day 116 (April 26) and day 122 (May 02) respectively, which was considerably later compared to the historical sampling years.

DISCUSSION

Our results provide strong evidence of a significant decline in larval lake whitefish densities from the historical to the contemporary time period, indicating that recruitment is being limited at the larval life stage. We observed a high degree of year-to-year variation in larval density within each individual time period, which may be due to environmental factors. There was also substantial spatial variation in densities across the sites sampled and it appears as though some key sites, such as Pike Bay, are consistent producers of larval lake whitefish, regardless of time period. We further determined that larval lake whitefish growth was significantly slower in the contemporary time period after accounting for variation in spring water temperatures, which is consistent with the hypothesis that low food availability during the larval hatching period is limiting growth and survival of lake whitefish larvae.

Reductions in contemporary larval densities suggest that lake whitefish recruitment is being limited at the larval life stage and could be due to declines in larval production. Egg production has been linked to a number of parental traits including body condition, body size, and available energy (Kamler 2005; McBride et al. 2015). It may be that the observed declines in adult lake whitefish growth and body condition caused by the loss of *Diporeia* (Pothoven et al. 2001; Pothoven and Madenjian 2008) may have impacted the number of eggs produced per spawner or the amount of energy incorporated into each egg laid. Both of these factors are important determinants of lake whitefish year-class strength (Taylor et al. 1987; Brown and Taylor 1992). In a comparison of lake whitefish fecundity in the Upper Great Lakes before (1986-1987) and after (2003-2005) the loss of *Diporeia*, Kratzer et al. (2007) determined that fewer eggs were being produced in recent years. Additionally, statistical-catch-at-age (SCAA) modelling for the main basin of Lake Huron indicates dramatic declines in lake whitefish recruitment production in recent years (Fig. 2.3). The reductions in larval production over the past decade may be contributing to the contemporary declines in larval densities and lake whitefish recruitment.

In addition to reduced egg production, poor overwinter conditions during the incubation period may help explain the recent declines in larval lake whitefish densities. Specifically, ice coverage and the duration of ice cover during the winter months may be associated with greater survival of lake whitefish eggs. Taylor et al. (1987) observed a nearly fourfold increase in egg survival and greater larval densities following ice covered winters at sites in Lake Michigan. Similarly, Freeberg et al. (1990) reported poor hatching success and decreased larval lake whitefish survival in the mild winter of 1983 compared to the ice-covered winter of 1984. It has been hypothesized that greater ice cover may increase protection from wind-generated currents and therefore reduce mechanical destruction of eggs across the substrate (Taylor et al. 1987; Ryan and Crawford 2014). Ice cover may have played a similar role in our study, with the contemporary sampling years potentially experiencing poor ice cover and a greater number of ice-free days during the winter months. Reductions in ice cover could contribute to reduced egg survival and lower larval densities observed in the contemporary time period. Ice cover data obtained from the National Oceanic and Atmospheric Administration (NOAA) for Lake Huron indicates that the timing and duration of ice cover may, however, be similar between the two time periods, with maximum ice cover reached in either February or March. However, a more fine-scale analysis of the potential effect and role of ice cover on larval densities in the Fishing Islands region is needed.

Prey availability is one of the major drivers of larval lake whitefish survival and growth (Freeberg et al. 1990; Brown and Taylor 1992; Claramunt et al. 2010). We found a significant difference in larval growth rates between the historical and contemporary time periods (Fig. 2.10). Recent reductions in larval growth rates may be attributed to limited food availability due to the filter-feeding activity of dreissenid mussels. The rapid filtration rate of dreissenid mussels is known to play a substantial role in the circulation and movement of large quantities of water (Fanslow et al. 1995), as well as reductions in offshore primary productivity (Cha et al. 2011). Perhaps most importantly, the presence of dreissenid mussels can also alter the composition and abundance of copepod species present (Higgins and Vander Zanden 2010). Prior the dreissenid mussel invasion in the Great Lakes, cyclopoid and calanoid copepods were dominant in the spring zooplankton bloom and were the preferred prey item of larval lake whitefish (Reckahn 1970; Freeberg et al. 1990). However, since the arrival of dreissenid mussels, the abundance of copepods in the Great Lakes has decreased by 56-67% (Higgins and Vander Zanden 2010).

Additional studies have reported similar reductions in copepod abundances across the Great Lakes, with declines in Lake Huron beginning in 2003 (Barbiero et al. 2009; Barbiero et al. 2019). Declines in phytoplankton biomass have also been noted, which could contribute further to reductions in zooplankton abundance (Higgins and Vander Zanden 2010; Kissman et al. 2010). Reduced survival and poor larval growth rates could be due to changes in the abundance of key prey species in Lake Huron.

We observed substantial spatial variation in larval densities from year-to-year within each time period, which may be due to variation in the physical habitat. Lake whitefish are broadcast spawners that typically deposit their eggs across rocky substrates consisting of boulder, cobble, or gravel at depths <10 m (Scott and Crossman 1973; Goodyear et al. 1982; Lane et al. 1996). Spawning typically occurs between late October and early December in Lake Huron at water temperatures around 6ºC (Scott and Crossman 1973). It is likely that certain sites within the Fishing Islands spawning shoal provide ideal habitat for the development and incubation of lake whitefish eggs, leading to increased egg survival and higher larval densities. Two such sites may be Pike Bay and Stokes Bay. Both sites have previously been identified as key spawning areas for lake whitefish and have been studied in connection with larval lake whitefish (Loftus 1977; Goodyear et al. 1982; Ryan and Crawford 2014). Findings from our comparison of the key sites indicate that Pike Bay and Stokes Bay continue to produce high densities of larval lake whitefish and likely provide essential spawning habitat for lake whitefish. These key sites also appear to yield high densities during low-density years across the spawning shoal (e.g., 1982). However, a more fine-scale analysis of the nearshore areas and embayments throughout the Fishing Islands region is required to better understand these crucial spawning areas.

We determined that there were significantly fewer cGDD in the contemporary time period than historically, which was likely due to the rate of spring warming. In the historical time period, there were six years where water temperatures at day 100 (April 10) were above our base temperature of 5ºC (between 5.1-7.8ºC) and continued to increase throughout the larval hatching period. This led to a greater number of cGDD for years historically. Water temperatures in 2018 and 2019 warmed at a slower rate and reached our base temperature later in the hatching period, at day 116 (April 26) and day 122 (May 02) respectively. The slower warming water temperatures in the contemporary time period resulted in fewer days where temperatures were considered ideal for larval growth. The difference in larval growth rates between the time periods highlights the importance that other environmental variables have on larval growth, and ultimately recruitment. For example, spawning stock abundance and the number of days of ice cover were found to positively influence lake whitefish recruitment in areas of Lake Michigan (Brown et al. 1993). Claramunt et al. (2010) determined that variation in larval lake whitefish density was not directly regulated by water temperatures during spawning or hatching but was best explained by a combination of environmental variables, including larval length, spring winds, and adult stock density. Alternatively, Taylor et al. (1987) found that in addition to spawning stock biomass and ice cover, spring water temperatures were important during years of high larval density.

In our study, these biological changes that have occurred between time periods may have been influenced by differences in sampling methodology. For example, trawl speeds and the identification of larval lake whitefish. Tow speed is known to influence the catchability of larvae (Colton et al. 1980; Thayer et al. 1983). Colton et al. (1980) determined that trawls conducted at higher speeds (6.48 km/hr) did not yield higher catches compared to catches conducted at slower speeds (2.78 km/hr). In our study, we found that contemporary boat speeds were substantially faster than historically (ANOVA: $F_{1, 1598} = 53.94$; $P < 0.001$). Nevertheless, while contemporary boat speeds were faster it is unlikely that the number of larval lake whitefish caught was affected: as both the mean tow speed (3.85 km/hr) and the majority of tows conducted (895/904) did not exceed the high tow speed assessed in Colton et al. (1980). The visual identification of larval lake whitefish was another important difference in the sampling methodology. Our study made use of historical larval surveys that collected and visually identified a range of fish species, including larval cisco. Because larval cisco are frequently misidentified as lake whitefish through visual identification (Overdyk et al. 2016; George et al. 2018), the historical estimates of larval lake whitefish in our study may be higher. This conclusion lends further support to our findings that larval densities were higher historically.

In conclusion, our study determined that lake whitefish densities were lower in recent years in the Fishing Islands than in the 1970’s-1980’s, suggesting that recruitment is being limited at the larval life stage. Substantial year-to-year variability in both time periods in larval production was also observed, pointing to the possible role of environmental factors such as ice cover affecting larval dynamics. We furthermore found a lower larval growth rate in recent years after accounting for variation in growing degree days. These slower larval growth rates are consistent with the hypothesis that reduced food availability during the early life stages, potentially due to dreissenid mussel establishment, are contributing to reduced recruitment. Future research should focus on determining the role of overwinter conditions (i.e., ice cover, water temperature) on larval densities and whether larval density is a reliable determinant of lake whitefish year-class strength. Additional work is also needed to understand whether changes in zooplankton composition have occurred in the Fishing Islands and to examine the relationship between prey species and larval lake whitefish growth.

Table 2.1. Site names and GPS coordinates (latitude and longitude) for the sixteen sites sampled in the Fishing Islands region of Lake Huron in the historical (1976-1986) and contemporary (2017-2019) time periods.

Site name	GPS coordinates	
	Latitude (°)	Longitude (°)
Chiefs Point	44.6928	-81.30599
Cranberry Island	44.735978	-81.300364
Fishing Islands	44.740486	-81.313677
Garden Island	44.988522	-81.380681
Howdenvale	44.822511	-81.298494
Irish Harbour	44.9768889	-81.373306
Lonely Island	44.716447	-81.285489
McCallum Island	44.793225	-81.325033
Oliphant	44.733131	-81.282522
Pike Bay	44.873197	-81.323944
Red Bay	44.803436	-81.287436
Regatta Bay	44.714	-81.282047
Smokehouse Island	44.7271	-81.296858
Stokes Bay	44.995828	-81.374689
Tamarack	44.987361	-81.390594
Whitefish Island	44.71545	-81.308483

Table 2.2. Sampling effort and mean calculated larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) from larval tows conducted in the Fishing Islands region of Lake Huron during the historical (1977-1986; n=923 tows) and contemporary (2017-2019; n=446 tows) time periods. Mean larval densities displayed do not include outliers that were removed through z-score calculations, where outliers were identified as being values less than 3 standard deviations or more than 3 standard deviations from the mean. See Table A2.2 for mean larval densities with outliers included. Data collected in 1976 was not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted.

Time period	Year	Sampling duration	Number of tows	Mean $CPUE_V$ (no. larval fish/m^3)
Historical	1977	May 11-June 08	37	0.042
	1978	April 26-May 26	96	0.073
	1979	April 23-May 29	103	0.162
	1980	April 23-May 15	92	0.217
	1981	April 16-May 29	115	0.157
	1982	April 19-June 01	67	0.042
	1983	April 06-May 24	117	0.230
	1984	April 18-May 23	97	0.316
	1985	April 16-May 22	108	0.313
	1986	April 21-June 05	91	0.456
Contemporary	2017	April 11-May 26	73	0.018
	2018	April 23-May 31	178	0.082
	2019	April 24-June 06	195	0.071

Table 2.3. Number of larval lake whitefish measured and mean total length (mm) of subsampled larvae obtained from tows conducted in the Fishing Islands region of Lake Huron during the historical (1976-1986; n=1462 larvae) and contemporary (2017-2019; n=2037 larvae) time periods.

Time period	Year	Sampling duration	Number of larvae	Mean total length (mm)
Historical	1976	April 29-May 10	51	14.1
	1977	April 26-June 09	108	15.7
	1978	April 27-May 26	90	14.4
	1979	April 23-May 29	221	14.5
	1980	April 23-May 15	166	15.8
	1981	April 16-May 29	179	14.6
	1982	April 19-June 01	78	14.2
	1983	April 12-May 24	148	14.1
	1984	April 18-May 23	137	13.9
	1985	April 16-May 22	142	13.9
	1986	April 21-June 05	142	14.5
Contemporary	2017	April 13-May 12	121	15.2
	2018	April 23-May 29	1252	15.3
	2019	April 24-June 04	664	15.0

Table 2.4. Total number of calculated cumulative growing degree days (cGDD) in the historical (1976-1986) and contemporary (2017-2019) time periods in the Fishing Islands region of Lake Huron. Numbers of cGDD were calculated by first estimating daily water temperatures between day 100 (April 10) and day 160 (June 09) for each year sampled in both time periods. The number of days above our base temperature of 5ºC were added up to provide an estimate of annual cGDD.

Time period	Year	Total number of cGDD at day 160 (June 09)
Historical	1976	326.5
	1977	237.3
	1978	380.8
	1979	396.5
	1980	298.9
	1981	235.4
	1982	344.4
	1983	311.1
	1984	262.2
	1985	427.0
	1986	359.9
Contemporary	2017	236.1
	2018	264.6
	2019	106.9

Fig. 2.1. (A) Lake whitefish spawning stock biomass (kg) in the central main basin of Lake Huron (1978-2021). (B) Number of age 4 lake whitefish in the central main basin of Lake Huron (1978-2021). Data were obtained from statistical catch-at-age (SCAA) models for Lake Huron developed by the Ontario Ministry of Northern Development, Mines, Resources and Forestry (OMNDMNRF).

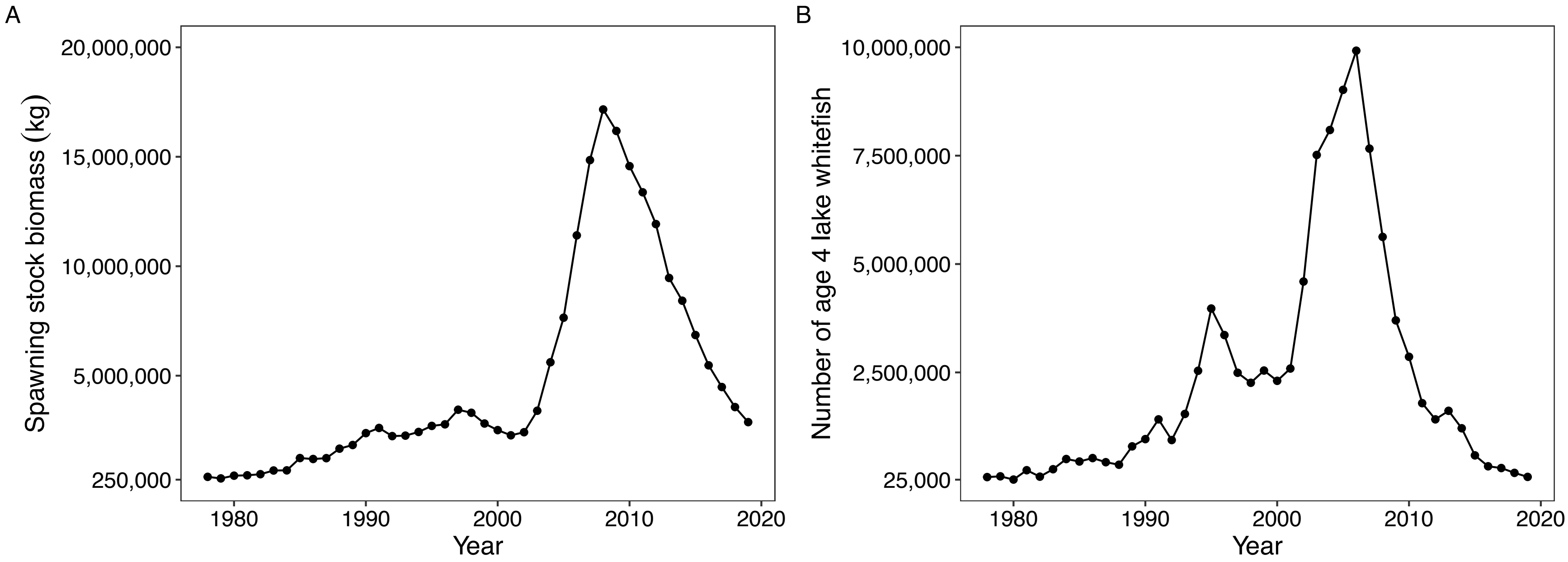


Fig. 2.2. Fishing Islands spawning shoal in the main basin of Lake Huron where larval fish surveys were conducted in 1976-1986 and 2017-2019.

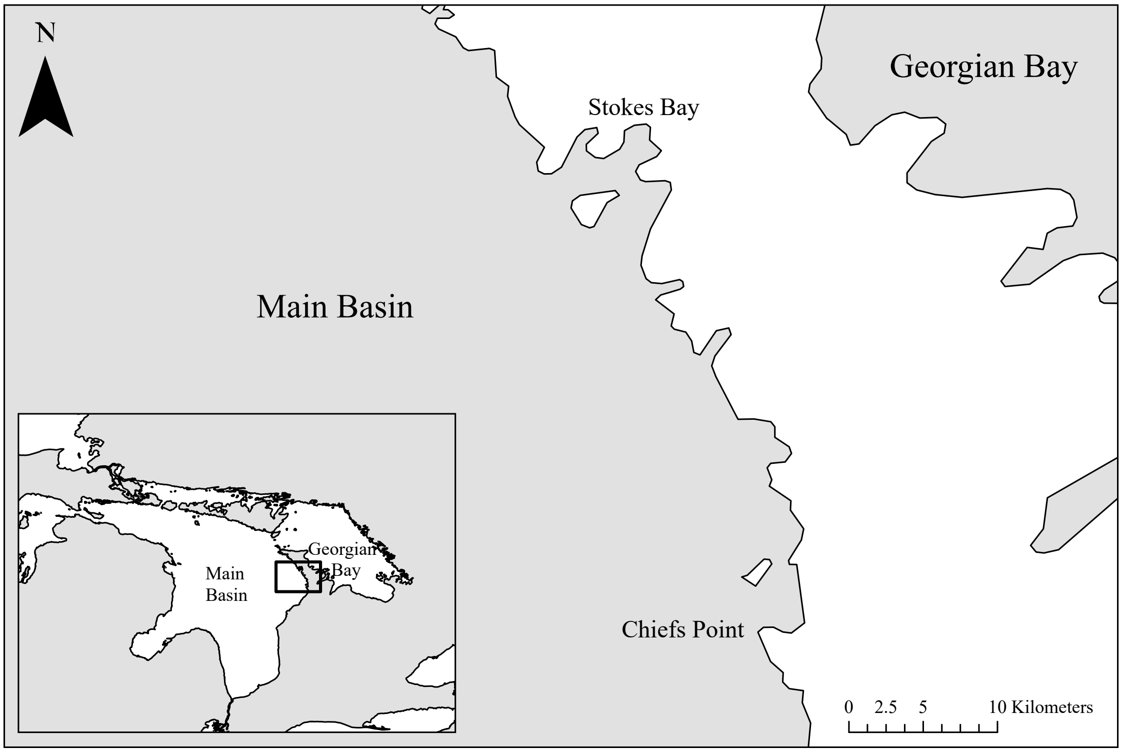


Fig. 2.3. Estimated larval lake whitefish production (density per kg) in the central main basin of Lake Huron. (A) Historical time period (1978-1986). (B) Contemporary time period (2017-2019). Larval production was calculated by dividing larval lake whitefish densities (no. larval fish/m^3) for years sampled in the Fishing Islands region by spawning stock biomass (SSB) in each time period using statistical catch-at-age (SCAA) modelling data for Lake Huron developed by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (OMNDMNRF).

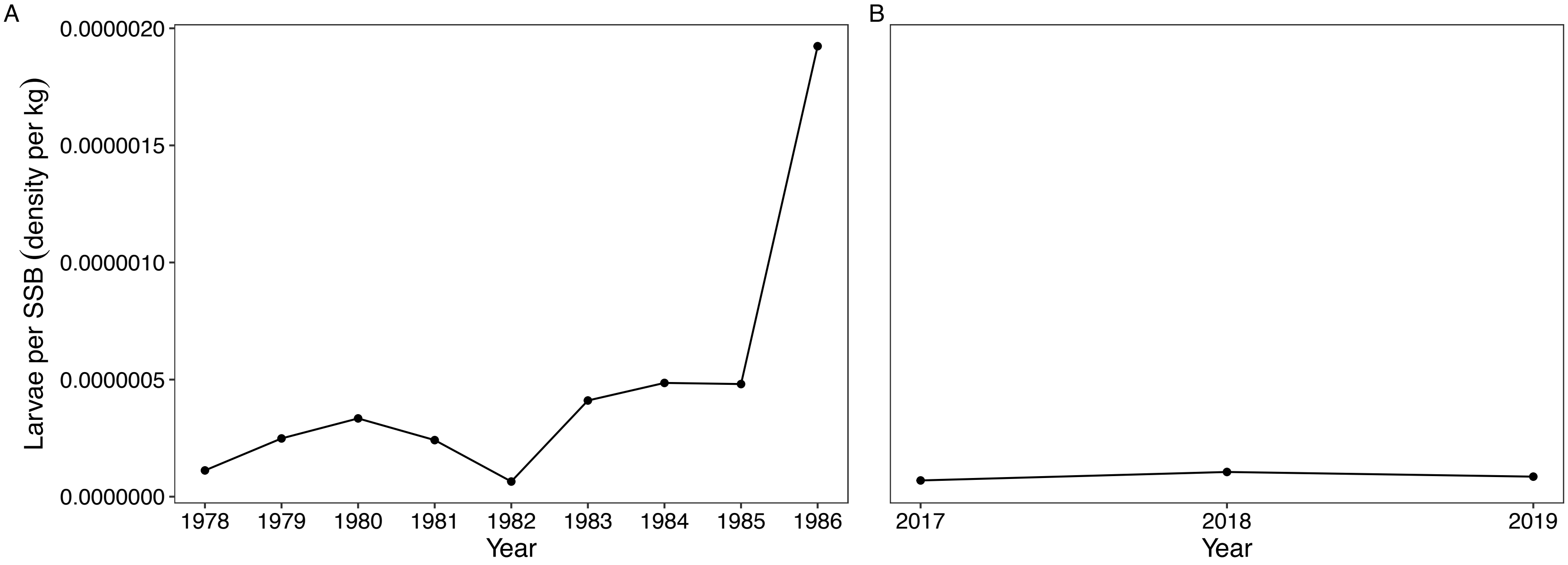


Fig. 2.4. Sixteen sites sampled in the Fishing Islands region of Lake Huron in the historical (1976-1986) and contemporary (2017-2019) time periods.

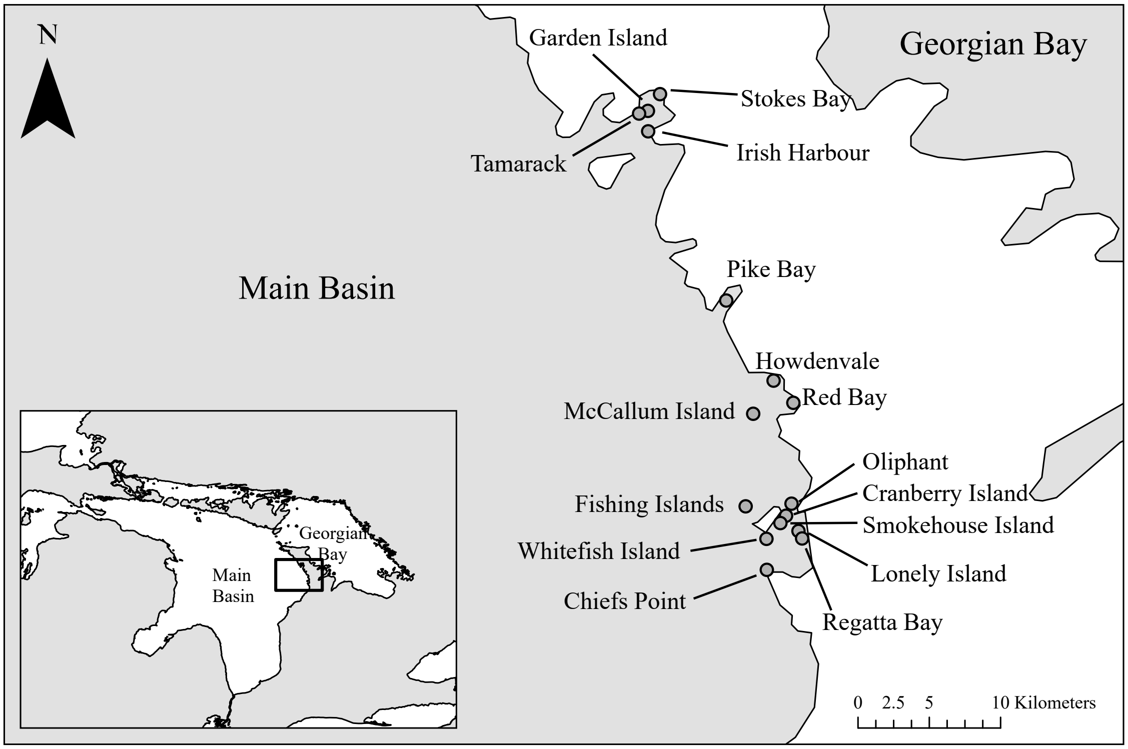


Fig. 2.5. Lake whitefish larval densities ($CPUE_V$; no. larval fish/m^3) in the Fishing Islands region of Lake Huron. (A) Historical time period (1977-1986; n=923 tows). (B) Contemporary time period (2017-2019; n=446 tows). Lower and upper box boundaries represent the 25th and 75th percentiles respectively, the dark line inside the box represents the median, and the whisker represents the maximum excluding any outliers. Dark open circles are considered outliers that are greater than the maximum. Larval densities displayed do not include outliers that were removed through z-score calculations, where outliers were identified as being values less than 3 standard deviations or more than 3 standard deviations from the mean. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted.

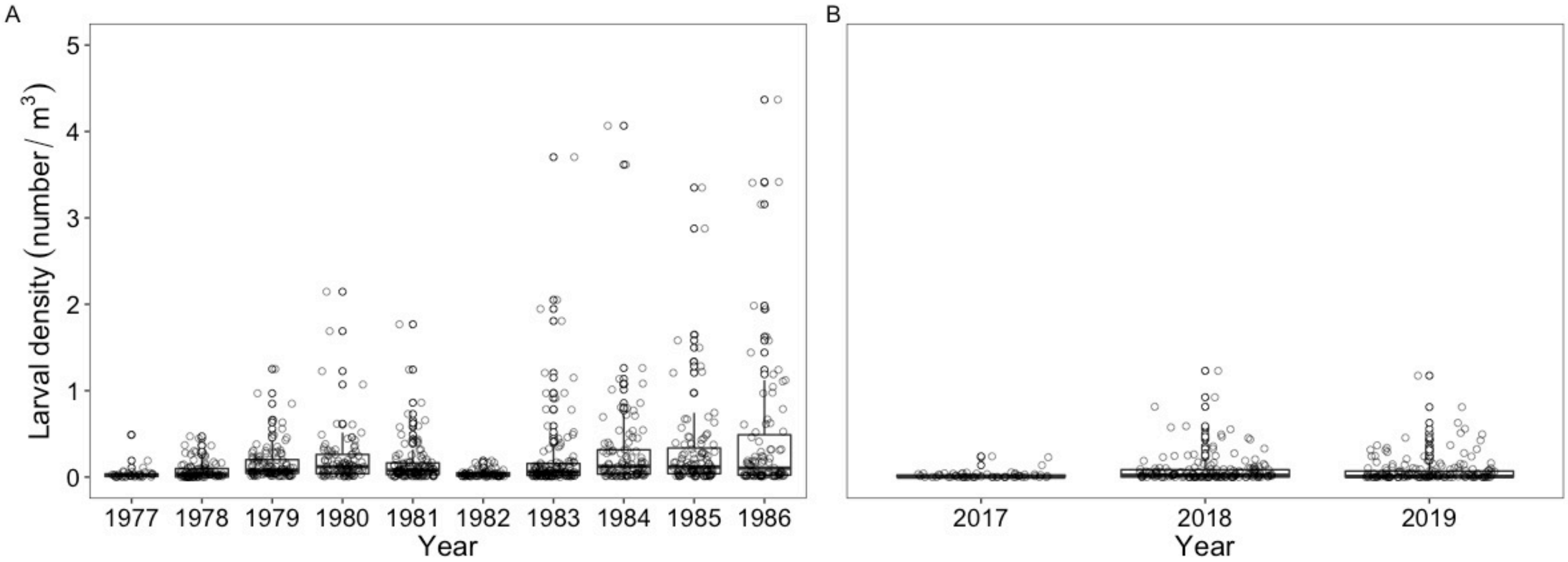


Fig. 2.6. Mean lake whitefish larval densities ($CPUE_V$; no. larval fish/m^3) for fish sampled in the Fishing Islands region of Lake Huron. (A) Historical time period (1977-1986). (B) Contemporary time period (2017-2019).

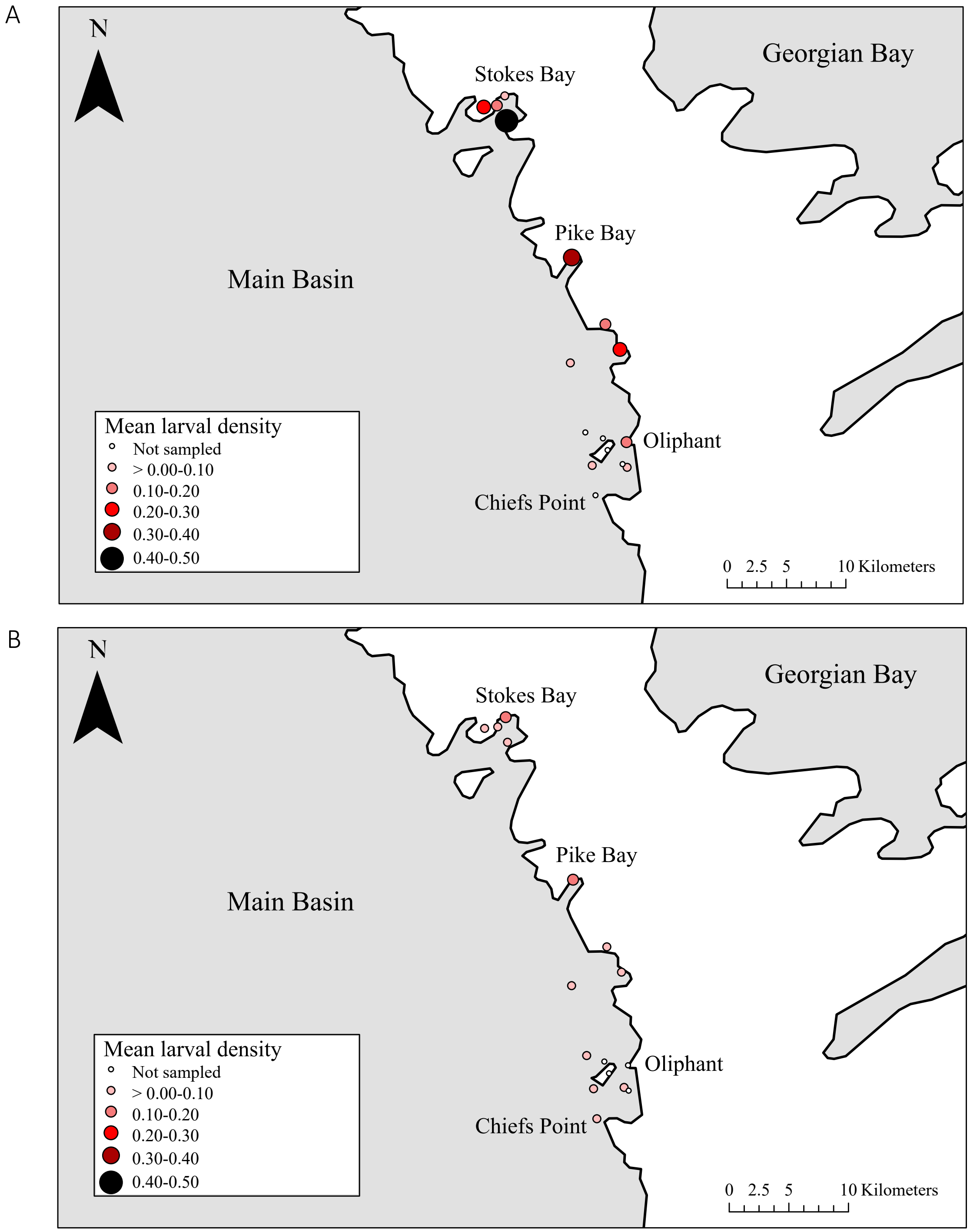


Fig. 2.7. Lake whitefish larval densities ($CPUE_V$; no. larval fish/m^3) at four key sites in the Fishing Islands region of Lake Huron in the historical (1977-1986) and contemporary (2017-2019) time periods. (A) Howdenvale. (B) Pike Bay. (C) Red Bay. (D) Stokes Bay.

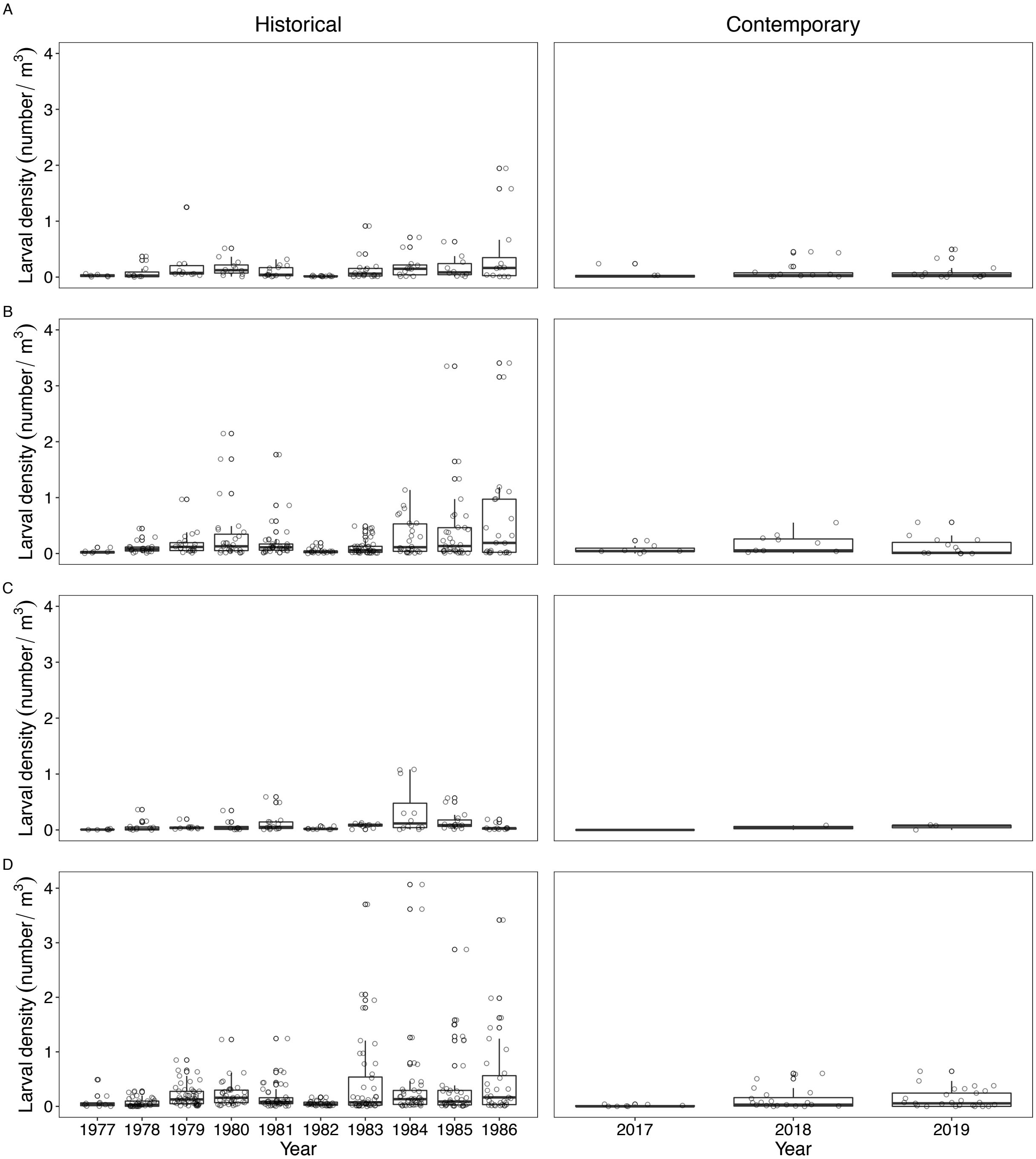


Fig. 2.8. Larval lake whitefish total length (mm) by day of year for a subsample of fish collected in the Fishing Islands region of Lake Huron. (A) Historical time period (1976-1986; n=1462 larvae). (B) Contemporary time period (2017-2019; n=2037 larvae). The linear regression equation ($y = mx + b$) and coefficient of determination (R^2) are displayed.

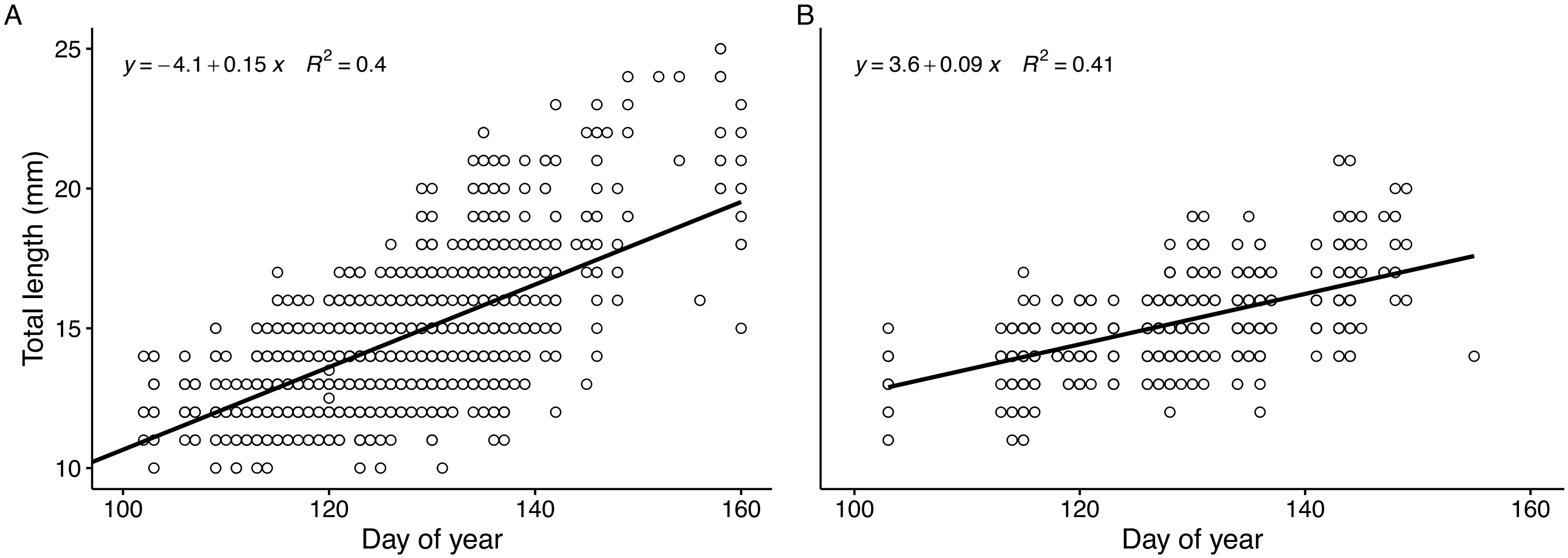


Fig. 2.9. Larval lake whitefish total length (mm) by day of year measured from a subsample of fish collected in the Fishing Islands region of Lake Huron in the historical time period (1976-1986; n=1462 larvae). The linear regression equation ($y = mx + b$) and coefficient of determination (R^2) are displayed for each year.

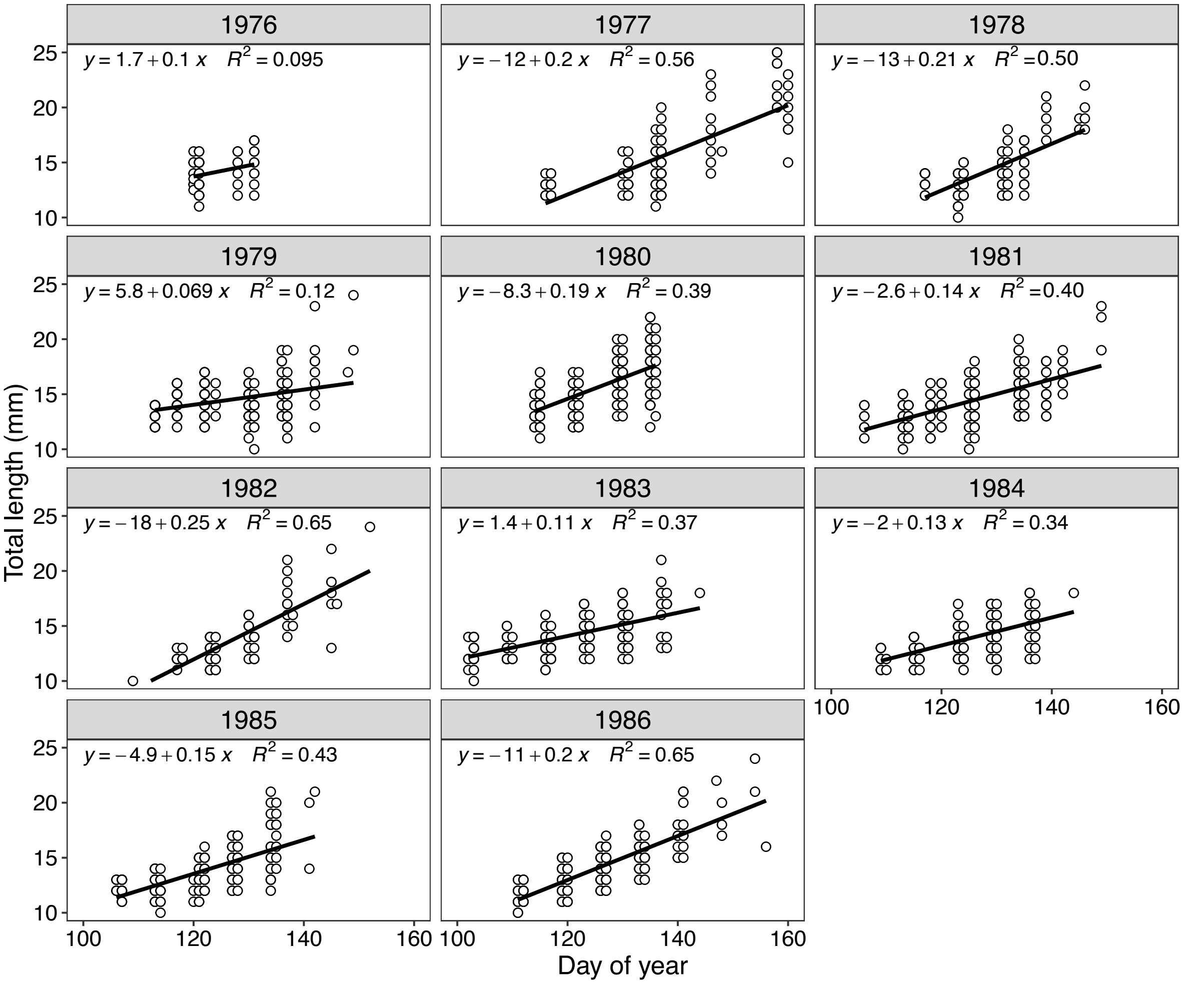


Fig. 2.10. Larval lake whitefish total length (mm) by day of year measured from a subsample of fish collected in the Fishing Islands region of Lake Huron in the contemporary time period (2017-2019; n=2037 larvae). The linear regression equation ($y = mx + b$) and coefficient of determination (R^2) are displayed for each year.

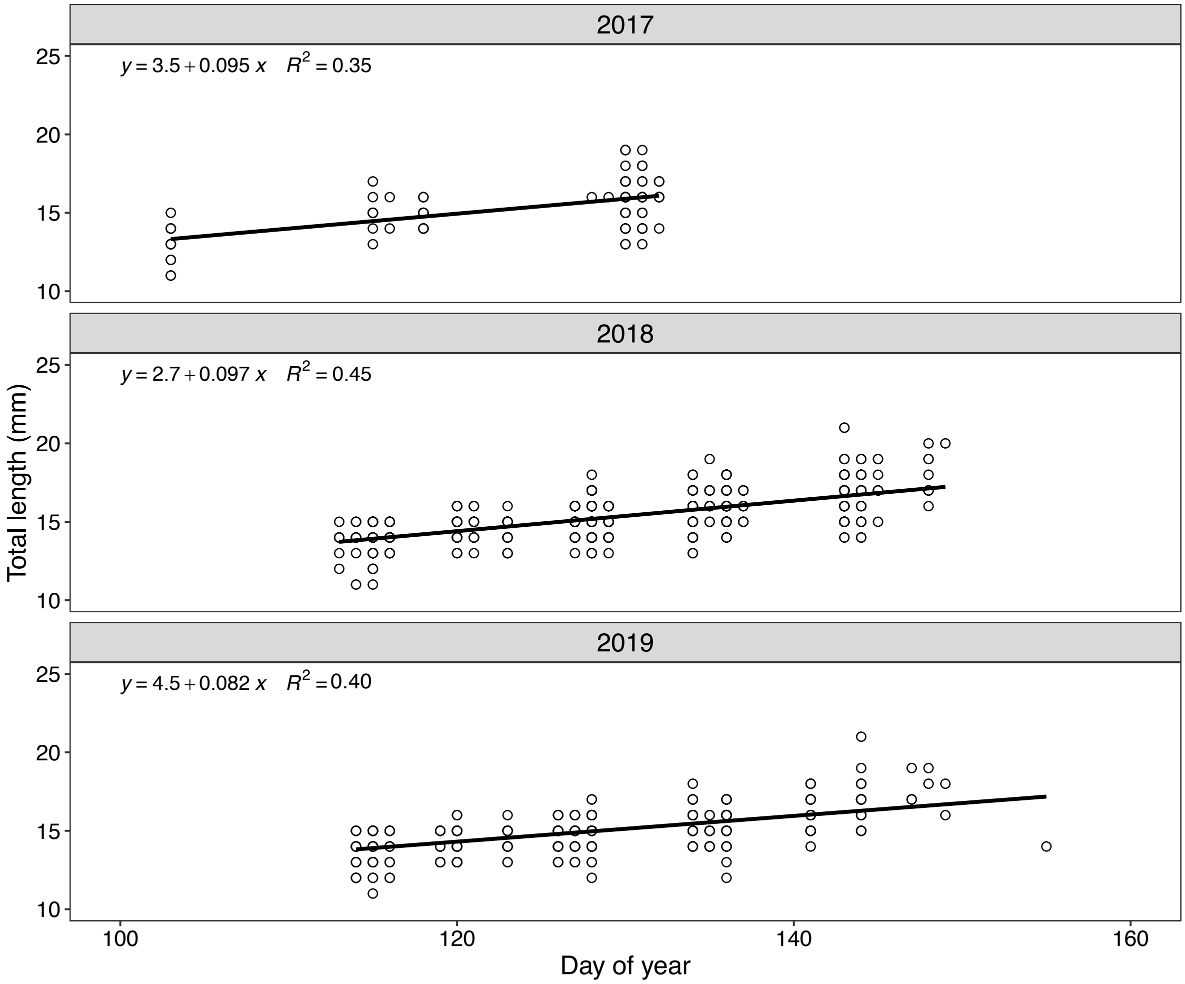


Fig. 2.11. Larval lake whitefish length by cumulative growing degree days (cGDD) for a subsample of fish collected in the Fishing Islands region of Lake Huron truncated at 150 cGDD. (A) Historical time period (1976-1986; n=1311 larvae). (B) Contemporary time period (2017-2019; n=1739 larvae). The linear regression equation ($y = mx + b$) and coefficient of determination (R^2) are displayed. For both time periods, water temperatures (°C) collected between day 100 (April 10) and day 160 (June 09) were included.

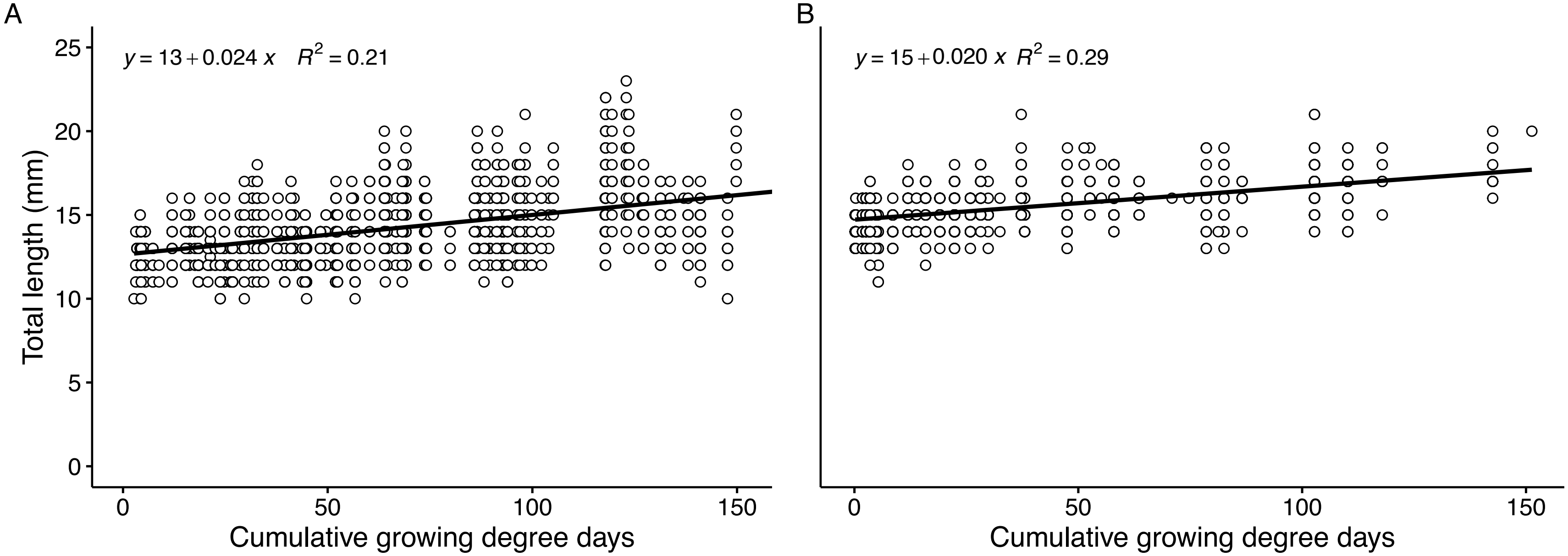


Table A2.1. Outliers identified through z-score calculations using estimated larval densities ($CPUE_V$; no. larval fish/m^3) of lake whitefish collected in the Fishing Islands region of Lake Huron for the historical (1977-1986; n=14 tows) and contemporary (2017-2019; n=6 tows) time periods. Calculated z-score values are displayed for each density outlier identified.

Time period	Year	Collection date	Site	Number of larvae	$CPUE_V$ (no. larval fish/m^3)	Z-score
Historical	1983	May 03	Stokes Bay (Irish Harbour)	424	4.684	+3.022
	1983	May 03	Stokes Bay (Irish Harbour)	1069	9.702	+6.536
	1984	May 02	Stokes Bay (Irish Harbour)	479	8.819	+5.918
	1986	May 06	Stokes Bay (Irish Harbour)	723	7.389	+4.916
	1986	May 06	Stokes Bay (Irish Harbour)	936	9.982	+6.732
	1986	May 06	Stokes Bay (Irish Harbour)	1699	19.165	+13.161
	1986	May 06	Pike Bay	623	6.249	+4.118
	1986	May 06	Pike Bay	635	6.739	+4.461
	1986	May 06	Pike Bay	1040	13.439	+9.153
	1986	May 06	Pike Bay	1838	16.592	+11.360
	1986	May 07	Howdenvale	710	8.182	+5.472
	1986	May 07	Howdenvale	2010	19.267	+13.233
	1986	May 07	Red Bay	825	7.404	+4.926
	1986	May 07	Red Bay	877	7.589	+5.057
Contemporary	2018	April 30	Pike Bay	286	1.944	+6.623
	2018	May 08	Pike Bay	220	1.319	+3.053
	2018	May 08	Stokes Bay (Irish Harbour)	326	2.058	+4.909
	2018	May 08	Stokes Bay (Garden Island)	522	3.252	+7.907
	2018	May 08	Stokes Bay (Garden Island)	962	6.271	+15.491
	2019	April 30	Stokes Bay (Irish Harbour)	226	2.238	+5.362

Table A2.2. Sampling effort, total number of larval lake whitefish identified, and mean calculated lake whitefish larval densities ($CPUE_V$; no. larval fish/m^3) for larval tows conducted in the Fishing Islands region of Lake Huron during the historical (1977-1986; n=938 tows) and contemporary (2017-2019; n=452 tows) time periods. Mean larval densities displayed include outliers identified through z-score calculations, where outliers were identified as being values less than 3 standard deviations or more than 3 standard deviations from the mean. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted.

Time period	Year	Sampling duration	Number of tows	Mean $CPUE_V$ (no. larval fish/m^3)
Historical	1977	May 11-June 08	37	0.042
	1978	April 26-May 26	96	0.073
	1979	April 23-May 29	104	0.162
	1980	April 23-May 15	92	0.218
	1981	April 16-May 29	115	0.157
	1982	April 19-June 01	67	0.042
	1983	April 06-May 24	119	0.346
	1984	April 18-May 23	98	0.402
	1985	April 16-May 22	108	0.313
	1986	April 21-June 05	102	1.603
Contemporary	2017	April 11-May 26	73	0.018
	2018	April 23-May 31	183	0.160
	2019	April 24-June 06	196	0.082

Fig. A2.1. Lake whitefish larval densities ($CPUE_V$; no. larval fish/m^3) in the Fishing Islands region of Lake Huron. (A) Historical time period (1977-1986; n=938 tows). (B) Contemporary time period (2017-2019; n=452 tows). Lower and upper box boundaries represent the 25th and 75th percentiles respectively, the dark line inside the box represents the median, and the whisker represents the maximum excluding any outliers. Dark open circles are considered outliers that are greater than the maximum. Larval densities displayed include outliers that were identified through z-score calculations, where outliers were identified as being values less than 3 standard deviations or more than 3 standard deviations from the mean. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted.

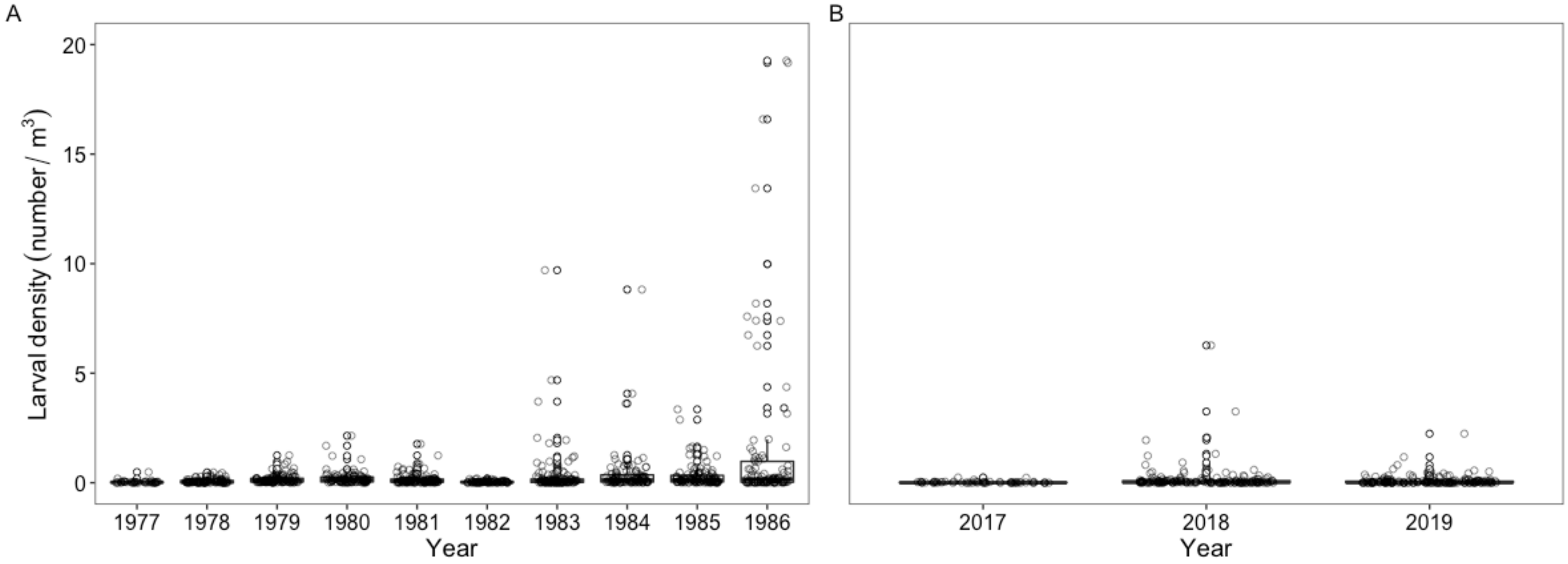


Fig. A2.2. Permutation distribution for the mean difference of the calculated and observed difference in larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) from 10,000 resamples between the historical (1977-1986) and contemporary (2017-2019) time periods. The dashed line indicates the observed difference in mean larval densities between the two time periods (0.0436 larval fish/m^3). Mean densities do not include outliers that were removed through z-score calculations, where outliers were identified as being values less than 3 standard deviations or more than 3 standard deviations from the mean.

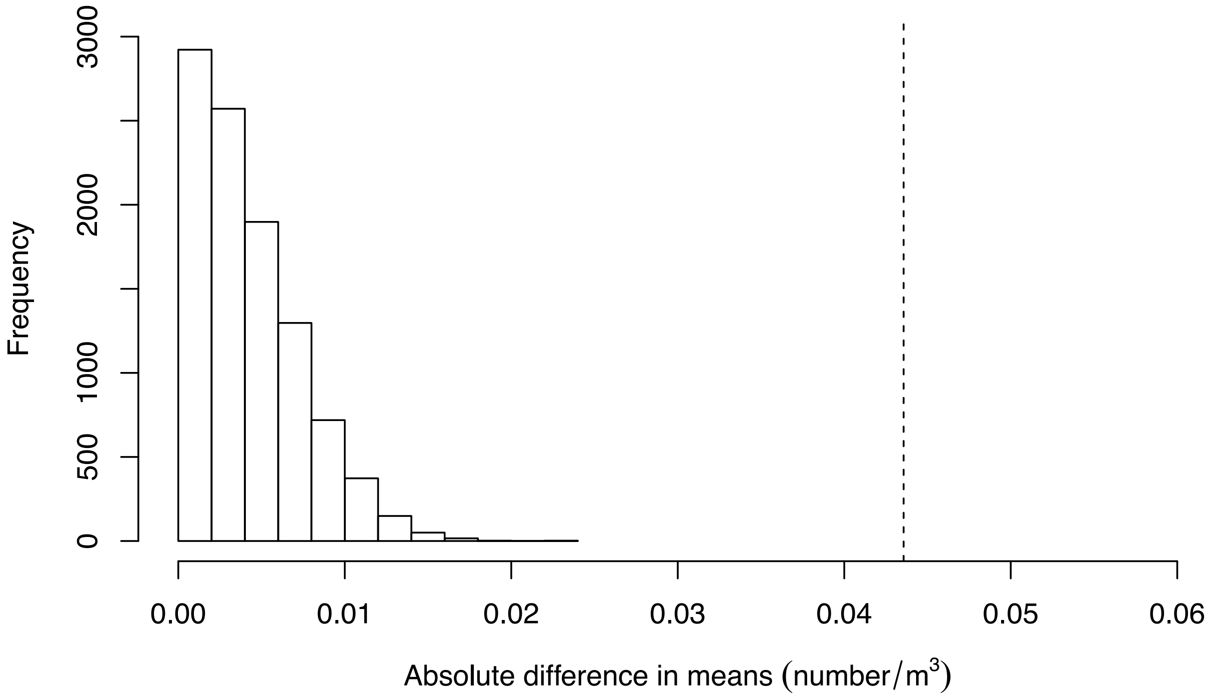
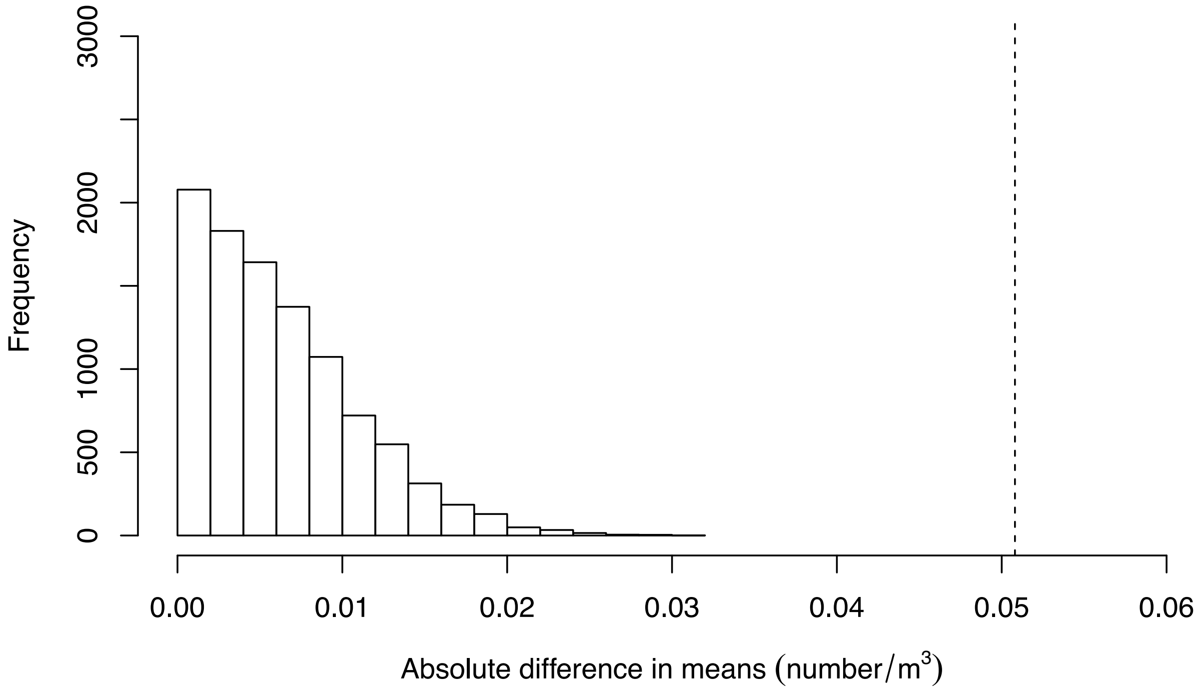


Fig. A2.3. Permutation distribution for the mean difference of the calculated and observed difference in larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) from 10,000 resamples between the historical (1977-1986) and contemporary (2017-2019) time periods. The dashed line indicates the observed difference in mean larval densities between the two time periods (0.0508 larval fish/m^3). Mean densities include outliers that were removed through z-score calculations, where outliers were identified as being values less than 3 standard deviations or more than 3 standard deviations from the mean.



CHAPTER 3: FACTORS AFFECTING ANNUAL VARIATION IN LARVAL LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*) DENSITY AND YEAR-CLASS STRENGTH IN LAKE HURON

ABSTRACT

Lake whitefish (*Coregonus clupeaformis*) are a cold-water species that comprise a significant proportion of the total Laurentian Great Lakes coregonine commercial catch, with the majority of lake whitefish harvested from Lake Huron. Over the past two decades, the abundance and commercial yield of lake whitefish has declined throughout Lake Huron. Reductions in yield have been largely attributed to drastic declines in population abundance and recruitment, but the causes are poorly understood. There is also a lack of knowledge regarding the variables affecting annual variation in larval recruitment and year-class strength. In this study, we determined the role of key environmental variables in influencing annual variation in larval lake whitefish recruitment and year-class strength in the Fishing Islands spawning shoal in Lake Huron. Larval fish were sampled in the Fishing Islands region during two time periods: a historical time period (1976-1986) and a contemporary time period (2017-2019). Lake whitefish showed an overall reduction in larval densities and growth between time periods, but a high degree of year-to-year variability in density and growth within both time periods. The annual variability of larval densities was best explained by a combination of biotic and abiotic variables, including spawning stock biomass, November water levels, and dreissenid mussel presence. We also found that larval density was a significant predictor of age 4 recruitment, suggesting that year-class strength may be partly established during the larval life stage.

INTRODUCTION

Recruitment is a fundamental process that affects fish populations, productivity, and fisheries yield. Yet, for most fish stocks there are significant gaps in our understanding of the factors that affect recruitment. Recruitment generally refers to the process of young fish transitioning into a particular life stage (e.g., juvenile), size, or age. In fishery science, the term recruitment usually refers to the transition of young fish into the fishery, most often because those fish have reached a size at which they are vulnerable to capture. The recruitment of fish can be influenced by numerous interacting abiotic and biotic factors, including water temperature (Brown et al. 1993), spawning stock biomass (Ricker 1954), food availability during the larval period (Cushing 1990), and larval survival and growth (Anderson 1988; Pepin and Meyers 1991). Fish recruitment is often established during the egg and larval life stages, as natural mortality rates in the first year of life are extremely high (> 99% mortality; Ricker 1968). As a result, fish recruitment varies widely from year-to-year and can ultimately affect year-class strength, i.e., the number of fish in the population or fishery that were born in a given year (Pritt et al. 2014). For example, stronger year-classes of fish tend to be produced when larval survival and growth rates are higher (Christie 1963; Freeberg et al. 1990). Despite the importance of fish recruitment, there is a lack of understanding about the processes contributing to recruitment variation.

The Laurentian Great Lakes have undergone major ecological changes over the past century. The invasion of the parasitic sea lamprey (*Petromyzon marinus*), environmental shifts (e.g., habitat degradation), and overexploitation have led to variation in the recruitment of several native fish species in the Great Lakes (Christie 1974;

Bunnell et al. 2014). Additionally, the establishment of invasive zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*), collectively referred to as dreissenid mussels, further exacerbated the declines in recruitment (Bunnell et al. 2014). The proliferation of dreissenid mussels also coincided with dramatic declines in abundance of the benthic amphipod *Diporeia* spp. (hereafter *Diporeia*), a major prey item for many benthivorous fishes (Nalepa et al. 2005; Nalepa et al. 2007). These ecosystem changes were associated with reductions in the growth and body condition of several fish species throughout the Great Lakes (Pothoven and Madenjian 2008).

Lake Huron in particular has undergone significant changes in the structure of the fish community following the invasion of dreissenid mussels and subsequent loss of *Diporeia* (Mohr and Ebener 2005; Nalepa et al. 2005; Barbiero et al. 2011b). Most notably, the abundance and commercial yield of lake whitefish (*Coregonus clupeaformis*) has declined throughout the lake over the past two decades (Nalepa et al. 2005; Gobin et al. 2015; Ebener et al. 2021). Lake whitefish are a cold-water species that comprise a significant proportion of the total Great Lakes coregonine commercial catch, with the majority of lake whitefish harvested from Lake Huron (Ebener 2013; Cottrill et al. 2020). Reductions in lake whitefish yield have been largely attributed to drastic declines in recruitment, which are most pronounced in the northern and central regions of the main basin of Lake Huron (Cottrill et al. 2020; Ebener et al. 2021). In addition to declines in yield, significant declines in larval densities, larval growth, and juvenile recruitment (age 3+) have been observed throughout central Lake Huron, possibly linked to the establishment of dreissenid mussels (see Chapter 2). Interestingly, substantial year-to-year variations in larval densities occurred both before and after dreissenid mussel establishment (see Chapter 2), indicating that other variables are affecting annual recruitment variation.

While the leading hypothesis for the recent declines in lake whitefish recruitment is a lack of food availability during the early larval fish stage, previous research has shown that other biotic factors may also be important (Ebener et al. 2021). Egg composition plays a crucial role in the survival of eggs and the number of successfully hatched larvae (Miller et al. 1988; Brown and Taylor 1992). Lake whitefish eggs with greater lipid content are positively related to increased larval growth and survival, which provide developing larvae with increased endogenous energy reserves that allow for faster growth (Brown and Taylor 1992). Spawning stock biomass, which represents the total weight of spawning adult fish in a stock, also has the potential to impact larval densities. Moderate levels of spawning stock biomass tend to be associated with greater recruitment, while very high spawning stock biomass results in poorer recruitment (Henderson et al. 1983). This pattern of poor recruitment when spawning stock biomass is very high has been attributed to density-dependent mortality, likely resulting from competition for food among larval lake whitefish (Henderson et al. 1983).

In addition to biotic factors, environmental conditions can impact larval lake whitefish survival and recruitment. For example, overwinter conditions influence the survival of lake whitefish eggs, including ice cover and water temperatures (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993). Ice cover during the winter months has been suggested to provide protection to developing eggs from wind-generated currents, allowing the eggs to remain in optimal incubation habitats while developing (Freeberg et al. 1990). Ice cover can also be a significant predictor of lake whitefish recruitment, with increased ice coverage resulting in greater larval survival and stronger year-classes (Taylor et al. 1987; Brown et al. 1993). Water temperature also plays an important role in lake whitefish recruitment by potentially affecting the timing of egg development and consequently, the duration of ice cover (Price 1940; Smith 1991; Brown et al. 1993). For lake whitefish embryos, overwinter water temperatures between 0.5ºC and 2ºC are considered ideal and peak hatching occurs in the spring when water temperatures rise to around 6ºC (Price 1940). Lake whitefish eggs incubated at colder temperatures also result in greater survival and the larvae tend to be larger upon hatching (Price 1940; Brooke 1975).

The purpose of this study is to determine the role of key biotic and abiotic variables in influencing annual variation in larval recruitment and year-class strength in Lake Huron. Determining the factors that affects recruitment will help shed light on the role any of these factors may have had in the recent declines of lake whitefish densities in Lake Huron. Understanding the link between larval density and year-class strength will allow us to determine whether recruitment is being limited at the larval life stage and whether that affect juvenile recruitment. Specifically, we: 1) determined the effect that ice cover, spawning stock biomass, water levels, and dreissenid mussel presence/absence has on year-to-year variability in lake whitefish larval density and 2) assessed whether larval density and larval growth were accurate predictors of juvenile recruitment (age 4+) in the central main basin of Lake Huron. Larval fish samples were collected in the Fishing Islands region of Lake Huron, a historically significant spawning shoal for lake whitefish and an area of the lake where recruitment declines have been observed (Ebener et al. 2021).

METHODS

Study area

This study focused on the Fishing Islands spawning shoal that is located in the main basin of Lake Huron along the eastern shore (Fig. 2.4). This historically important spawning shoal spans from near Stokes Bay down to Chiefs Point and encompasses a number of key nursery habitats for lake whitefish, including Pike Bay and Stokes Bay (Loftus 1977; Loftus 1980; Goodyear et al. 1982). In recent years, the Fishing Islands is a region where there have been significant declines in juvenile lake whitefish recruitment (age 3+; Ebener et al. 2021), as well as larval density (see Chapter 2).

Larval fish sampling

Our study utilized larval lake whitefish samples that were collected during two time periods: a historical time period (1976-1986) and a contemporary time period (2017-2019). In the historical time period, larval fish surveys were conducted by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (OMNDMNRF) at sixteen sites in the Fishing Islands region (Fig. 2.4; Table 2.1). Fish surveys were conducted throughout the spring larval hatching period (mid-April until early June) on a weekly basis (Table 2.2). Larval trawls were conducted using circular fish nets (80 cm diameter; 300 cm long) that were towed approximately 1.0 m below the surface from the side of a vessel. The frequency of tows conducted varied from year-to-year, with tows conducted for 5-20 minutes. Tows were replicated by making a second tow immediately following the first, and a maximum of two replicate tows were performed at each site. Tow velocities were measured with a General Oceanics flowmeter that was mounted in the net opening. After each tow, larval fish were preserved in 5-10%

formalin. Larval samples were then visually identified with a microscope with the aid of reference keys (Fish 1932; May and Gasaway 1967). Fish were then enumerated and total body lengths were measured to the nearest 0.05 mm.

In the contemporary time period, the sampling region covered the same area as the historical Fishing Islands larval survey (Fig. 2.4). We sampled a combination of random and fixed sites throughout the larval hatching period, with the fixed sites (11 in total) sampled at least once a week (Table 2.2). Random sites were selected weekly using the quantum geographic information system (QGIS) random points tool. Trawls were conducted using a circular net (500 μm mesh; 50 cm diameter; 150 cm long) towed approximately 1.0 m below the surface of the water between 15-30 cm from the side of the vessel for 10 minutes. Larval samples were preserved in ethanol (95%) following each trawl. In the laboratory, samples were enumerated and total body lengths were measured to the nearest 0.01 mm using a microscope and digital camera. A subsample of larval fish were genetically identified to species through DNA barcoding using a portion of the caudal fin (Appendix 1).

Larval density data

Catch-per-unit effort ($CPUE$) was used as the measure of larval lake whitefish density. We calculated larval catches per volume (no. larval fish/m^3), denoted as $CPUE_V$. To do this, we first calculated the tow volume for each individual trawl by multiplying the tow distance (m) by the net area (m^2). For the historical time period, we calculated tow distance based on flowmeter data and these data were used to calculate tow volume. Distance travelled (m) using flowmeter data was calculated as follows:

(1) $$Distance = \frac{C_{Diff} \times R_{Const}}{999{,}999}$$

where C_{Diff} is the difference in counts (calculated by subtracting the initial count from the final count) and R_{Const} is the standard speed rotor constant, which is 26, 873 (General Oceanics 2018). For the contemporary time period, the start (Lat0 and Lon0) and end (Lat1 and Lon1) GPS coordinates were used to calculate tow distance (m). For a more in-depth description of density calculations performed using the historical and contemporary larval data, see the Methods section in Chapter 2.

Environmental data

Daily ice cover (%) for Lake Huron was obtained from the National Oceanic and Atmospheric Administration (NOAA) in the historical (1979-1986) and contemporary (2017-2019) time periods. Ice cover was chosen as a measure of overwinter conditions and has been shown to impact lake whitefish egg survival (Taylor et al. 1987; Freeberg et al. 1990). We extracted the annual maximum ice cover values during both sampling time periods and used these data for our analyses.

Water levels (m) for Lake Huron were obtained from Fisheries and Oceans Canada (DFO) in the historical (1979-1986) and contemporary (2017-2019) time periods. These data were in the form of monthly average water levels that were calculated for lakes Michigan/Huron combined using a network of gauging stations at the following locations: Thessalon, Tobermory, Mackinaw City, and Harbour Beach. Water levels during the lake whitefish spawning period (November) were chosen because variation in water level can affect access to spawning grounds (hereafter November water levels; Gertzen et al. 2012). This may in turn potentially impact the number of eggs that are successfully laid. Additionally, water levels during the lake whitefish hatching period (May) were selected as variation in water level may affect hatching success and the survival of larvae (hereafter May water levels; Bégout Anras et al. 1999). Initially, water levels during the lake whitefish spawning period (November) and during the larval hatching period (May) were chosen. However, results from a Spearman Rank correlation test determined that there was a significant correlation between the two variables ($P = 0.0043$; $R^2 = 0.78$). Based on these findings, May water level data were removed from our analyses.

Dreissenid mussel presence or absence were also included in our analyses. Zebra mussels first invaded Lake Huron in 1989 and quagga mussels then invaded the lake in 1997 (Griffiths et al. 1991; Mills et al. 1999). Dreissenid mussels quickly became established throughout the lake (Griffiths et al. 1991; Nalepa et al. 1995). In our dataset, 1979-1986 represents a pre-dreissenid time period, whereas 2017-2019 represent years where dreissenids were present.

Lake whitefish population data

Lake whitefish spawning stock biomass (kg) estimates were derived from statistical-catch-at-age (SCAA) models developed for the central main basin of Lake Huron developed by the OMNDMNRF in the historical (1979-1986) and contemporary (2017-2019) time periods for 1979-2019. Spawning stock biomass was estimated by summing up all the abundances for each mature age class and then multiplying by the mean weight of fish in each age class. Mature age classes were assumed to be age 4 and older, based on the estimated age at 50% maturity. Typically, moderate levels of spawning stock biomass are associated with the greatest levels of recruitment as density-dependent effects are minimized (Henderson et al. 1983; Taylor et al. 1987; Brown et al. 1993). Age 4 lake whitefish abundances were also derived from the SCAA models for

1979-1986 and 2017-2019. Abundance data were used as a measure of year-class strength.

We also estimated larval lake whitefish growth rates in order to look at their influence on year-class strength. Growth rates were estimated by performing linear regressions of larval size at capture and day of capture (see Chapter 2). Linear regressions were estimated for each sampling year between day 100 (April 10) and day 160 (June 09), as these dates represent the earliest and latest samples of fish collected that were measured. The slopes from the linear regressions were used as the estimate of larval growth for that year.

Statistical analyses: larval density

Generalized linear models (GLMs) were used to examine the potential relationship between larval lake whitefish density and the aforementioned predictor variables with a Gaussian distribution (glm function). Data in the historical time period spanned from 1979-1986 and in the contemporary time period from 2017-2019. The full GLM used was as follows:

$$(2) \qquad \overline{CPUE_V} \sim (\log(Ice)) + (\log(SSB)) + \overline{Water} + Mussels$$

where $\overline{CPUE_V}$ is the annual mean larval lake whitefish density, $\log(Ice)$ is the log-transformed maximum ice cover, $\log(SSB)$ is the log-transformed spawning stock biomass, $\overline{Water}$ is the mean November water level for the previous spawning season (e.g., 1979 water levels for the 1980 year-class), and $Mussels$ is the absence or presence of dreissenid mussels. We evaluated the full model and all potential combinations of reduced models. Models were ranked using the Akaike Information Criterion (AIC). For all statistical analyses we used R version 3.5.2.

Statistical analyses: year-class strength

GLMs were conducted to determine whether larval density and larval growth were significant predictors of lake whitefish year-class strength with a Gaussian distribution (glm function). Data in the historical time period spanned from 1977-1986. The full GLM used to examine the role of larval density was as follows:

(3) $N4 \sim (\overline{CPUE_V})$

where $N4$ is the number of age 4 lake whitefish from four years later (e.g., 1979 larval density for 1983 age 4 abundance) and $\overline{CPUE_V}$ is the mean annual larval lake whitefish densities (log-transformed). The full GLM used to examine the role of larval growth was as follows:

(4) $N4 \sim (growth)$

where $N4$ is the number of age 4 lake whitefish from four years later and $growth$ is the annual larval lake whitefish growth rate (slope). The full GLM used to examine the role of both larval density and larval growth as follows:

(5) $N4 \sim (\overline{CPUE_V} + growth)$

where N4 is the number of age 4 lake whitefish from four years later, $\overline{CPUE_V}$ is the mean annual larval lake whitefish density (log-transformed), and $growth$ is the annual larval lake whitefish growth rate (slope).

RESULTS

Annual mean larval density tended to increase throughout the historical sampling period, with the highest mean densities in the later sampling years (i.e., 1983-1986; Fig. 3.1). In the contemporary time period, mean larval densities remained similar across the three years sampled and there was less annual variation in density observed (Fig. 3.1).

There was a general decline in the overall maximum ice cover from the historical (mean = 78.9%) to the contemporary (mean = 70.8%) time period (Fig. 3.2). Historical maximum ice cover varied from year-to-year, with almost half the years sampled reaching greater than 90% ice cover (5/11 years; Fig. 3.2). In the contemporary time period, there was a general increase in annual maximum ice cover and ice cover was particularly low in 2017 (35.4%; Fig. 3.2).

Mean November water levels are variable through time, showing an increasing trend from 1975 to 1986, before showing a gradual decreasing trend until 2012, after which time water levels rose again until the end of the time series (Fig. 3.3). When comparing the historical to contemporary time period, it appears that water levels are overall fairly similar (Fig. 3.3).

Lake whitefish spawning stock biomass gradually increased between 1979 and about 2000, after which it rapidly increased until reaching a peak (17,161,340 kg) in 2008 (Fig. 3.4). Following the peak, there was a steep decline until 2020. Interestingly, we see that spawning stock biomass is higher in the contemporary time period than in the historical period (Fig. 3.4).

GLMs conducted using mean larval density as the dependent variable revealed that the top tanked model included spawning stock biomass, mean November water levels, and dreissenid mussel presence/absence (AIC = -24.63; Table 3.1). The full model was ranked second according to AIC values (AIC = -23.50; Table 3.1) and the only significant variable was dreissenid mussels. When comparing the full model against reduced models, all models tested were significant (before the Bonferroni correction) and models were ranked lower with fewer predictor variables included (Table 3.1). We found that mean November water levels and dreissenid mussel presence/absence were included in each of the top five ranked models, while maximum ice cover and spawning stock biomass tended to be included in the models ranked lower (Table 3.1). Results from GLMs indicated the impact of maximum ice cover (Fig. 3.5A) and spawning stock biomass (Fig. 3.5B) on larval whitefish density varied depending on the model. For example, in model 2 maximum ice cover has a negative overall effect but in model 11, a positive effect. Mean November water levels consistently had a positive impact on larval lake whitefish density (Fig. 3.5C), whereas dreissenid mussels negatively influenced densities (Fig. 3.5D). After a Bonferroni correction was applied, all models assessed remained significant (Table 3.1).

We found that larval lake whitefish density was a significant predictor of year-class strength ($P = 0.0152$; $R^2 = 0.57$; Table 3.2), with higher age 4 recruitment being associated with higher larval densities (Fig. 3.6). However, there was no evidence that larval lake whitefish growth was associated with year-class strength ($P = 0.6800$; $R^2 = 0.02$; Table 3.3; Fig. 3.7). In the combined GLM, there was an association between larval density and year-class strength ($P = 0.0053$; Table 3.4), but only weak evidence for such a relationship with larval growth was observed ($P = 0.0951$; Table 3.4).

DISCUSSION

Lake whitefish show a high degree of year-to-year variability in the density of hatching larvae at the Fishing Islands spawning shoal. We determined that a combination of biotic and abiotic variables, including spawning stock biomass, November water levels, and dreissenid mussel presence, best explained the annual variability of larval lake whitefish densities in our study. Larval density was positively correlated with November water levels and negatively correlated with dreissenid mussel presence in all models tested. The influence of ice cover and spawning stock biomass on larval densities varied between models. Thus, we provide evidence that the year-to-year variability in the density of larval lake whitefish hatching at the Fishing Islands spawning shoal is potentially driven by a number of factors, with the highest larval densities associated with the absence of dreissenid mussels and high water levels.

Furthermore, we found an association between larval density and age 4 recruitment, which suggests that year-class strength may be partly established during the larval life stage. In other words, we find evidence that high larval densities translate into higher juvenile lake whitefish densities. However, while contemporary larval lake whitefish growth rates were lower than historically (see Chapter 2), we did not find a relationship between larval growth and year-class strength. This suggests that larval growth rates on their own do not have a large effect on whether larval fish survival to the juvenile life stage.

Increased ice cover may enhance lake whitefish recruitment in the Great Lakes. In our study, ice cover was included in our full model that was ranked second ($\Delta AIC < 2.0$; Table 3.1; Fig. 3.5A). It is hypothesized that greater ice cover results in increased larval survival, potentially by protecting developing eggs and larvae from being shifted off important nursery habitats by strong winds and currents (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993). Previous research on lake whitefish has found a possible association between ice cover characteristics and fish egg and larval survival (Taylor et al. 1987; Freeberg et al. 1990). For example, Taylor et al. (1987) observed in their two-year study that the winter with the earliest ice cover formation in the winter of 1983-1984 resulted in a nearly fourfold increase in lake whitefish egg survival compared to the ice-free winter of the previous year in Lake Michigan. Similar findings were observed with larval lake whitefish survival; increasing hatching and greater larval survival occurred following the winter of 1983-1984 after the milder winter of 1982-1983 (Freeberg et al. 1990). In contrast, Claramunt et al. (2010) found that larval densities were 20 times higher following the winter of 2005-2006 than the previous year where there was less ice coverage. However, these previous studies only looked at associations between ice cover and early survival over two years, whereas our study includes larval densities observed over a much longer period of time. With that in mind, our study interestingly did not find a consistent effect of ice cover, with some models showing a positive relationship between larval densities and other models showing a negative relationship. In the full model, reduced ice cover was associated with higher larval densities, the opposite to what might be expected. This demonstrates the importance of considering multiple environmental variables that combine to determine whether ecosystems are conducive to producing strong year-classes of larval fish.

Lake whitefish spawning grounds and nursery habitats may be susceptible to changes in water levels. We found that November water levels were a significant predictor of larval lake whitefish density and had a consistently positive effect on densities in our GLMs (Table 3.1; Fig. 3.5C). While we could find little evidence in the literature that water levels affect lake whitefish recruitment, we hypothesize that water levels could affect recruitment through their influence on access to spawning grounds. In the Great Lakes, water levels can fluctuate on an annual basis due to changes in precipitation and air temperatures (Quinn 2002), but do not show general trends through time (Fig. 3.4). Declines in Lake Huron water levels have been recorded over the past century, likely due to dredging, which have permanently lowered lake levels by 0.27 m (Derecki 1985). Concerns were also raised around Lake Huron when water levels were dropping between the 1980's and 2012 (Fig. 3.4; Sellinger et al. 2008; Canadian Hydrographic Service 2020). At low water levels, suitable spawning habitat may be reduced and some habitats may no longer be accessible (Gertzen et al. 2012). Water levels may also impact the survival of lake whitefish eggs and larvae. By experimentally lowering overwinter water levels in a lake located in the IISD Experimental Lakes Area, Mills et al. (2002) examined the changes in a lake whitefish population. The lake was lowered by 2-3 m over the span of three winters (Mills et al. 2002). Lake whitefish abundance declined by over 80% following the winter drawdown, likely due to poor larval survival and recruitment failure (Mills et al. 2002). Water levels also appear to impact lake whitefish growth, with trends in the mean weight of adult lake whitefish being significantly correlated with cycles in water level in South Bay, Lake Huron (Reckahn 1986). In South Bay, lake whitefish growth increased with higher water levels and this trend was observed over the span of 32 years (Reckahn 1986).

Prey availability may play a crucial role in the survival of larval lake whitefish and recruitment. It may be that prey availability during the larval life stage is contributing to the observed variability in larval densities in our study. Early research conducted by Hjort (1914) hypothesized that variability in recruitment between years is a result of variation in food availability following the transition from endogenous to exogenous feeding. This concept, referred to as the critical period hypothesis, states that limited food during this critical transition would result in high larval mortality and poor recruitment

(Hjort 1914). Similarly, Cushing (1990) proposed that variation in the timing of the spring plankton bloom leads to variable larval survival. High overlap between the timing of plankton production and larval emergence may then result in greater recruitment, a concept referred to as the match/mismatch hypothesis (Cushing 1974; Cushing 1990). Lake whitefish are opportunistic feeders that exhibit considerable variation in prey selection during their first year of life (Freeberg et al. 1990; Pothoven et al. 2014; Pothoven and Olds 2020). Following hatching in the spring, larvae begin to exogenously feed on cyclopoid copepods and switch to consuming Daphniidae, Bosminidae, and Chironomidae as the spring progresses (Reckahn 1970; Freeberg et al. 1990; Pothoven 2014). Zooplankton species abundance is known to vary both spatially and temporally in the Great Lakes, which may influence prey availability for larval lake whitefish following hatching (Barbiero et al. 2019). Additionally, the establishment of dreissenid mussels across the Great Lakes has altered the abundance of several key prey items of larval lake whitefish, including copepods whose abundance declined by 56-67% (Higgins and Vander Zanden 2010). Fluctuations in both zooplankton species composition and abundance may be contributing to the survival of larval lake whitefish and the abundance of young of year lake whitefish in Lake Huron.

Larval density may be useful in predicting future year-class strength for lake whitefish. We found evidence that mean larval lake whitefish density was positively associated with age 4 abundance ($P = 0.0152$), with higher densities resulting in greater juvenile recruitment ($R^2 = 0.57$; Fig. 3.6). Year-class strength generally refers to the number of fish born in a given year that survive to be recruitable into the fishery (or some specific later stage, for example the juvenile stage). Year-class strength is typically thought to be established during the early life history stages (e.g., egg and larval stages) and can be affected by several variables including water temperature and spawning stock factors (Hjort 1914; Houde 2008; Pritt et al. 2014). In the Great Lakes, previous research studies have identified some of the main environmental drivers of lake whitefish year-class strength. For example, both Christie (1963) and Lawler (1965) observed that cold water temperatures during the spawning period (November) followed by warm spring temperatures produced large year-classes in lakes Huron and Erie. While there have been no previous studies that we know of directly linking larval density and lake whitefish year-class strength in the Great Lakes, this link has been observed in other freshwater fish species, including alewife (Hatcher et al. 1991; Sammons and Bettoli 1998; Jackson and Noble 2000).

There were fewer years sampled in the contemporary time period and included in our GLM models assessing the effect of several key variables on larval density. The lack of recent density data included may have provided a limited view of long-term density patterns compared to the historical time period; however, our study is one of few that has aimed to disentangle the major environmental drivers of larval lake whitefish recruitment using an extensive dataset. Assessing the relationship between larval density and year-class strength using data exclusively from the historical time period was another potential limitation. Lake whitefish age 4 abundance from the SCAA modelling data for Lake Huron were available only until 2019. Consequently, we were unable to examine the relationship between larval densities and growth and age 4 abundances for the 2017-2019 year classes because we need a few more years before those fish are sampled in the fishery. Broad-scale ecosystem changes have occurred throughout Lake Huron following the establishment of dreissenid mussels, between the historical to the contemporary time periods defined in our study (Bunnell et al. 2014). Determining whether the relationship between larval density and year-class strength also exists in the contemporary time period will be informative because it will reveal whether dreissenids have changed this potential relationship.

In conclusion, our results indicate that annual variability in lake whitefish larval density in Lake Huron is primarily influenced by spawning stock biomass, water levels, and dreissenid mussels. We observed that there were no large reductions in any of the environmental variables examined between the two time periods that were correlated with declines in larval density. We found that larval densities were a significant predictor of lake whitefish year-class strength. The relationship between larval density and age 4 abundance may be used to predict year-class strength of lake whitefish populations in Lake Huron. Future research should focus on determining the direct effects of prey availability and species composition on larval densities in the Fishing Islands.

Table 3.1. Generalized linear models (GLM) examining the effect of four predictor variables on annual larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) in the central main basin of Lake Huron during two time periods: a historical time period (1979-1986) and a contemporary time period (2017-2019). Annual mean larval lake whitefish density was the dependent variable used in the models. The four predictor variables were: annual maximum ice cover (%), spawning stock biomass (SSB; kg), mean November water levels (m), and dreissenid mussel presence/absence. Maximum ice cover data and spawning stock biomass data were log-transformed. Models were ranked according to Akaike Information Criterion (AIC) values, with lower AIC values indicating a better-fit model.

Rank	Model specifics	Log-likelihood	Deviance	P value	Bonferroni adjusted p value	AIC	ΔAIC
1	$Density \sim SSB\ (\uparrow) + Water\ (\uparrow) + Mussels\ (\downarrow)$	17.31	0.0276	2.64e-08	3.96e-07	-24.63	0.00
2	$Density \sim Ice\ (\downarrow) + SSB\ (\uparrow) + Water\ (\uparrow) + Mussels\ (\downarrow)$	17.72	0.0257	3.49e-07	5.23e-06	-23.50	1.13
3	$Density \sim Ice\ (\downarrow) + Water\ (\uparrow) + Mussels\ (\downarrow)$	16.37	0.0328	4.82e-08	7.23e-07	-22.74	1.89
4	$Density \sim Water\ (\uparrow) + Mussels\ (\downarrow)$	15.24	0.0430	6.78e-09	1.02e-07	-22.48	2.15
5	$Density \sim SSB\ (\uparrow) + Mussels\ (\downarrow)$	14.03	0.0503	1.63e-08	2.45e-07	-20.05	4.58
6	$Density \sim SSB\ (\downarrow) + Water\ (\uparrow)$	13.07	0.0598	3.25e-08	4.87e-07	-18.14	6.49
7	$Density \sim Ice\ (\downarrow) + SSB\ (\uparrow) + Mussels\ (\downarrow)$	14.03	0.0503	2.12e-07	3.18e-06	-18.05	6.58
8	$Density \sim Ice\ (\downarrow) + SSB\ (\downarrow) + Water\ (\uparrow)$	13.86	0.0518	2.35e-07	3.52e-06	-17.73	6.90
9	$Density \sim Water\ (\uparrow)$	10.13	0.1020	2.80e-08	4.20e-07	-14.27	10.36
10	$Density \sim Mussels\ (\downarrow)$	9.58	0.1128	4.39e-08	6.58e-07	-13.16	11.47
11	$Density \sim Ice\ (\uparrow) + Water\ (\uparrow)$	10.20	0.1001	2.59e-07	3.89e-06	-12.40	12.23
12	$Density \sim Ice\ (\downarrow) + Mussels\ (\downarrow)$	9.92	0.1060	3.15e-07	4.73e-06	-11.85	12.78
13	$Density \sim SSB\ (\downarrow)$	7.74	0.1576	1.94e-07	2.91e-06	-9.48	15.15
14	$Density \sim Ice\ (\uparrow)$	6.98	0.1811	3.59e-07	5.38e-06	-7.95	16.67
15	$Density \sim Ice\ (\downarrow) + SSB\ (\downarrow)$	7.81	0.1557	1.44e-06	-2.16e-05	-7.62	17.01

Table 3.2. Results of the generalized linear model (GLM) examining the effect of mean annual log-transformed larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) on lake whitefish year-class strength in the central main basin of Lake Huron in the historical time period (1977-1986; n=10). Annual mean larval lake whitefish density was the dependent variable used in the model. Larval densities were calculated on a per volume basis for sites sampled in the Fishing Islands region. Year-class strength data (measured as age 4 abundance) was obtained from statistical catch-at-age (SCAA) models for Lake Huron developed by the Ontario Ministry of Northern Development, Mines, Northern Resources and Forestry (OMNDMNRF). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Parameters	Estimate	Standard error	t value	P value
Intercept	157,916	114,992	1.37	0.2069
Mean larval density	3,955,460	1,285,449	3.01	0.0152*

Table 3.3. Results of the generalized linear model (GLM) examining the effect of annual larval growth (represented by slope) on lake whitefish year-class strength in the central main basin of Lake Huron in the historical time period (1977-1986; n=10). Larval lake whitefish growth was the dependent variable used in the models. Growth rates were obtained from linear regression equations estimated for each sampling year. Year-class strength data (measured as age 4 abundance) was obtained from statistical catch-at-age (SCAA) models for Lake Huron developed by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (OMNDMNRF). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Parameters	Estimate	Standard error	t value	P value
Intercept	346,112	285,495	1.21	0.2600
Larval growth	707,527	16,552,272	0.43	0.6800

Table 3.4. Results of the generalized linear model (GLM) examining the effect of mean annual log-transformed larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) and annual larval growth (represented by slope) on lake whitefish year-class strength in the central main basin of Lake Huron in the historical time period (1977-1986; n=10). Larval lake whitefish growth was the dependent variable used in the models. Growth rates were obtained from linear regression equations estimated for each sampling year. Year-class strength data (measured as age 4 abundance) was obtained from statistical catch-at-age (SCAA) models for Lake Huron developed by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (OMNDMNRF). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Parameters	Estimate	Standard error	t value	P value
Intercept	-223,088	221,122	-1.01	0.3466
Mean larval density	4,656,884	1,168,517	3.98	0.0053**
Larval growth	1,982,661	1,028,014	1.93	0.0951

Fig. 3.1. Annual mean lake whitefish larval densities ($\overline{CPUE_V}$ ± SE; no. larval fish/m^3) in the Fishing Islands region of Lake Huron. (A) Historical time period (1977-1986). (B) Contemporary time period (2017-2019). Mean larval densities displayed do not include outliers that were removed through z-score calculations, where outliers were identified as being values less than 3 standard deviations or more than 3 standard deviations from the mean. Data collected in 1976 was not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted.

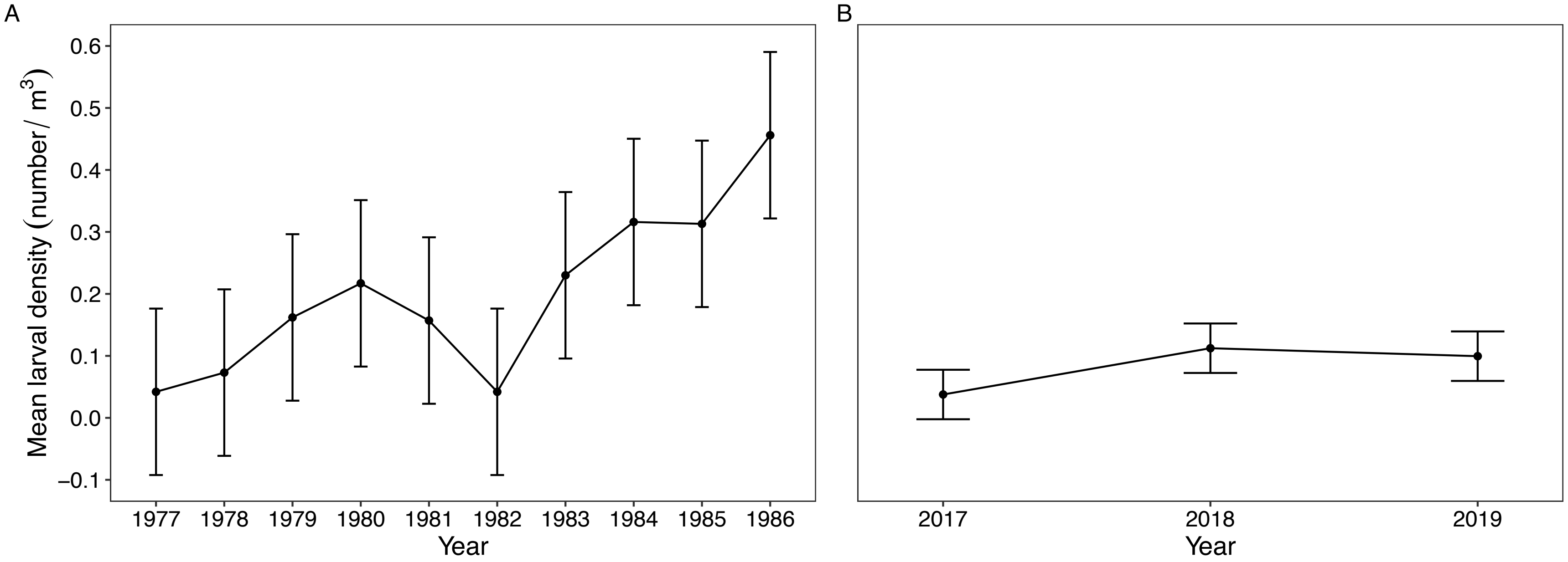


Fig. 3.2. Annual maximum ice cover (%) in Lake Huron. Historical time period: 1976-1986. Contemporary time period: 2017-2019. The grey shaded regions represent each of the two time periods. The maximum (1996; 98.2%) and minimum (2012; 23.1%) ice cover years in the time series are indicated. Ice cover data from the National Oceanic and Atmospheric Administration (NOAA) Great Lakes Environmental Research Laboratory.

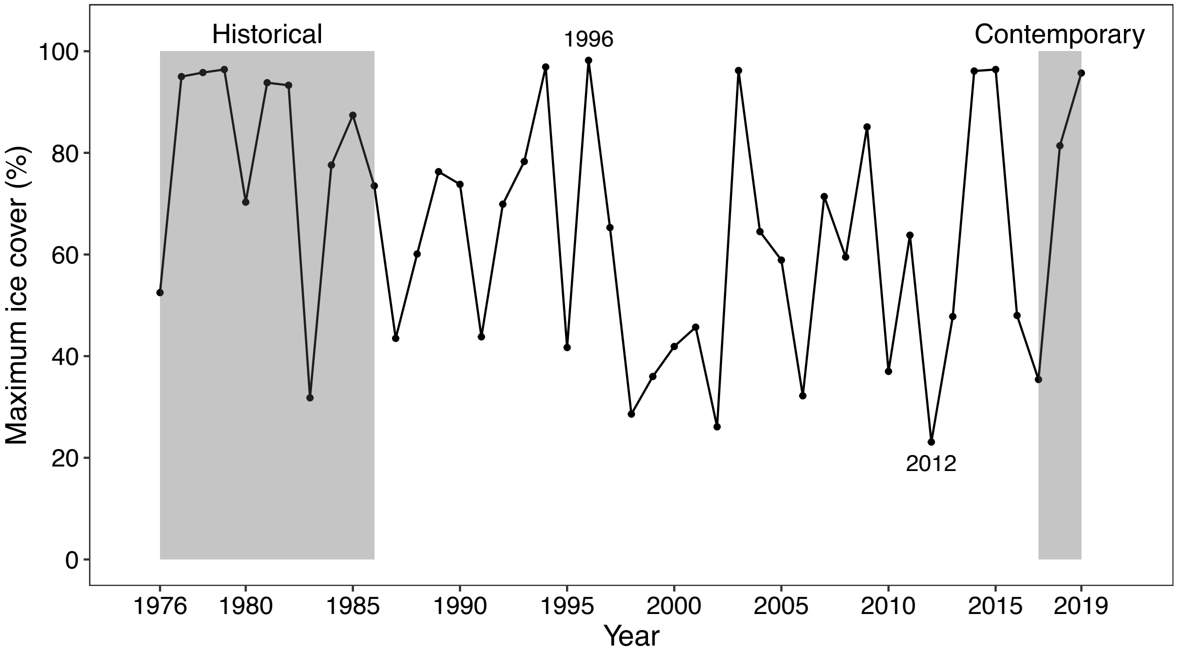


Fig. 3.3. Mean November water levels (m) in Lake Huron. Historical time period: 1976-1986. Contemporary time period: 2017-2019. The grey shaded regions represent each of the two time periods. The maximum (1986; 177.4 m) and minimum (2012; 175.7 m) November water levels in the time series are indicated. Mean November water level data from Fisheries and Oceans Canada (DFO).

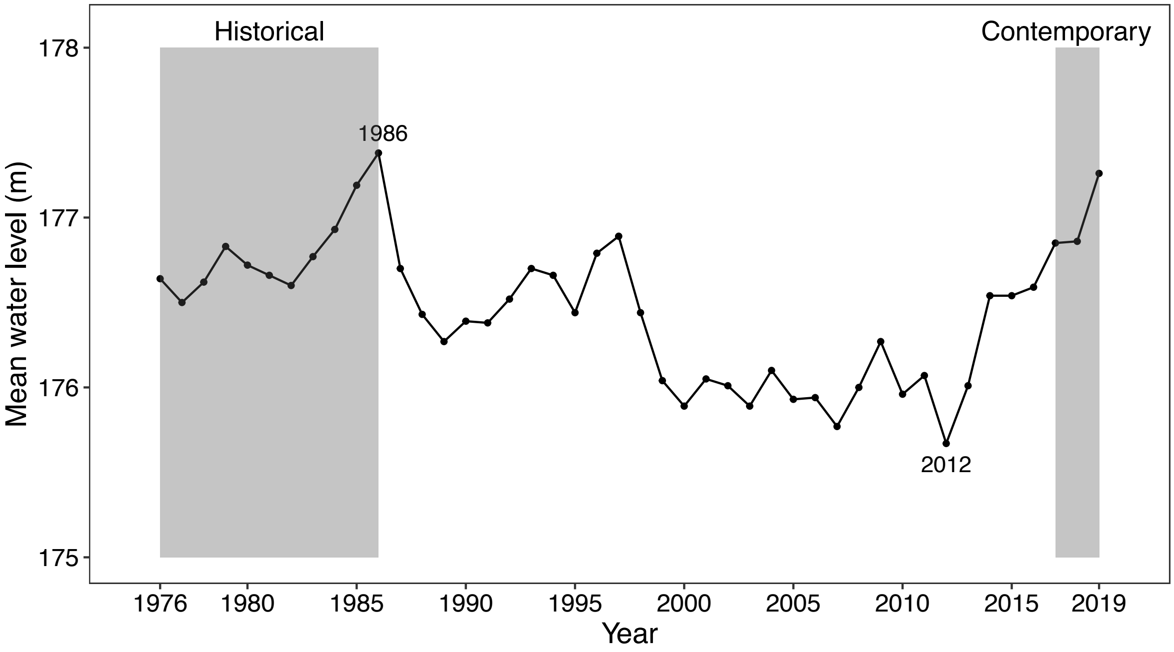


Fig. 3.4. Lake whitefish spawning stock biomass (kg) in the central main basin of Lake Huron. Historical time period: 1978-1986. Contemporary time period: 2017-2019. The maximum (2008; 17,161,340 kg) and minimum (1979; 308,353 kg) spawning stock biomass values in the time series are indicated. Lake whitefish spawning stock biomass data from statistical catch-at-age (SCAA) models for Lake Huron developed by the Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry (OMNDMNRF).

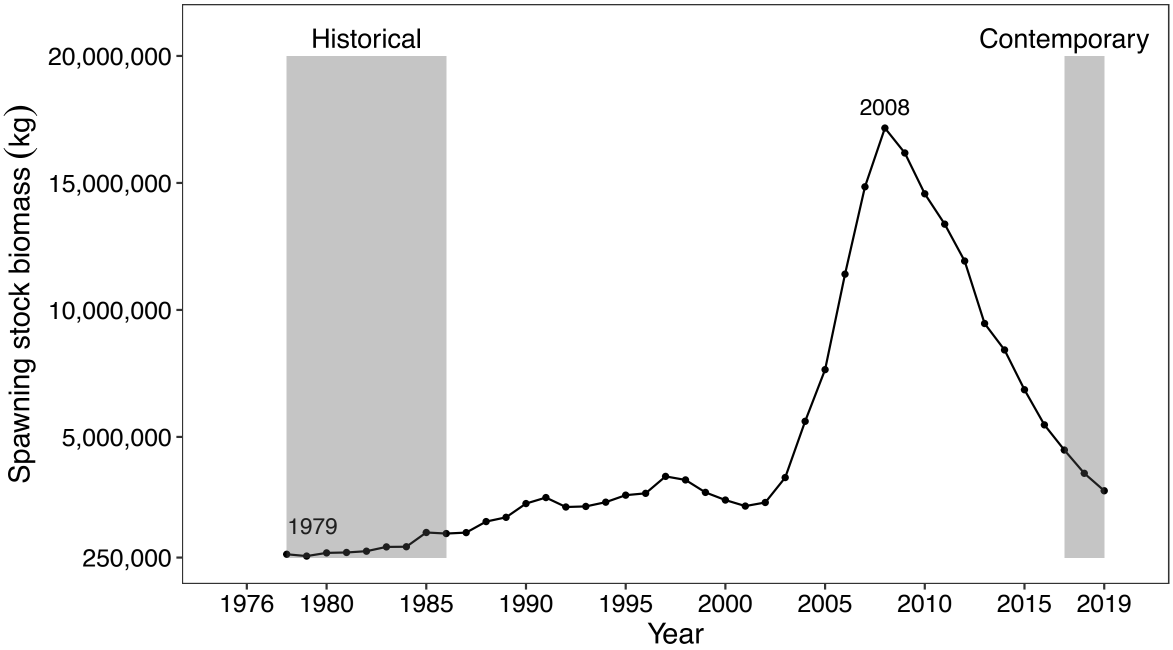


Fig. 3.5. Estimate values of four predictor variables from the generalized linear models conducted to examine their effect on larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) in the central main basin of Lake Huron during the historical (1979-1986) and contemporary (2017-2019) time periods. Models were ranked based on Akaike Information Criterion (AIC) values. (A) Maximum ice cover (%). (B) Spawning stock biomass (kg). (C) Mean November water levels (m). (D) Dreissenid mussel presence/absence.

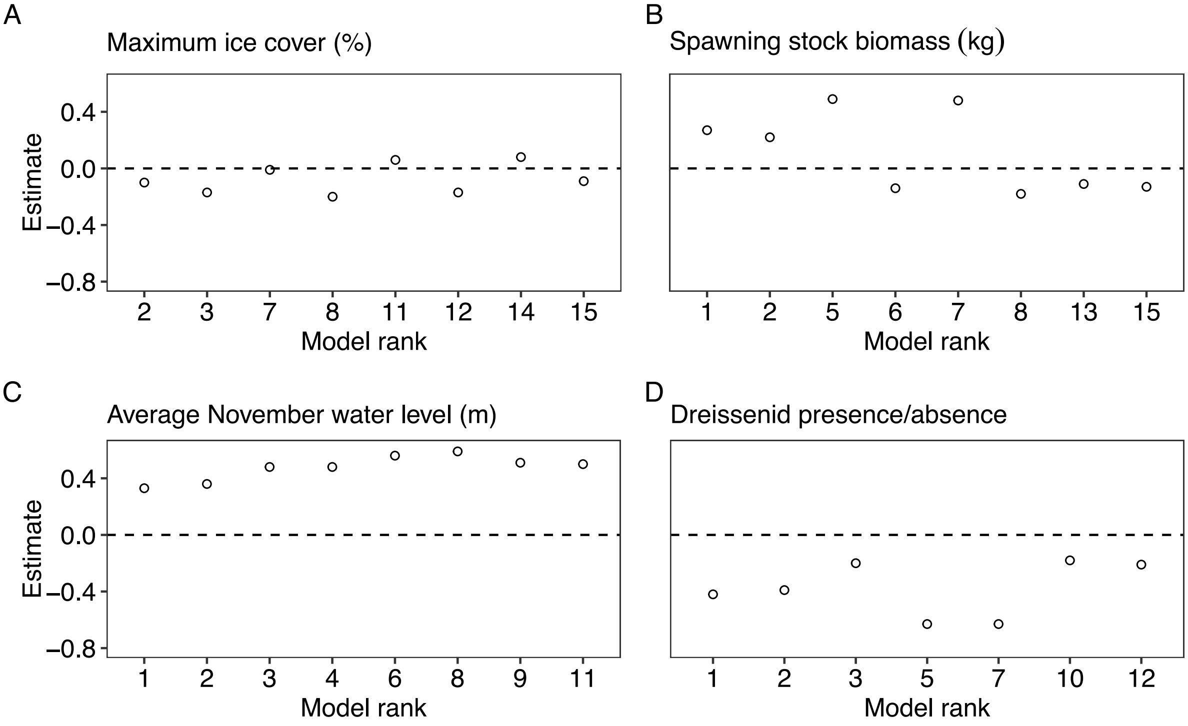


Fig. 3.6. Abundance of age 4 lake whitefish and mean larval lake whitefish density ($CPUE_V$; no. larval fish/m^3) in Lake Huron from 1977-1986 (n=10). Age 4 abundance data was obtained from statistical catch-at-age (SCAA) modelling data for the central main basin of Lake Huron. Larval lake whitefish densities were calculated using larval data collected throughout the larval hatching period (mid-April to end of May) in the Fishing Islands region of Lake Huron. Annual mean densities were then calculated for each sampling year.

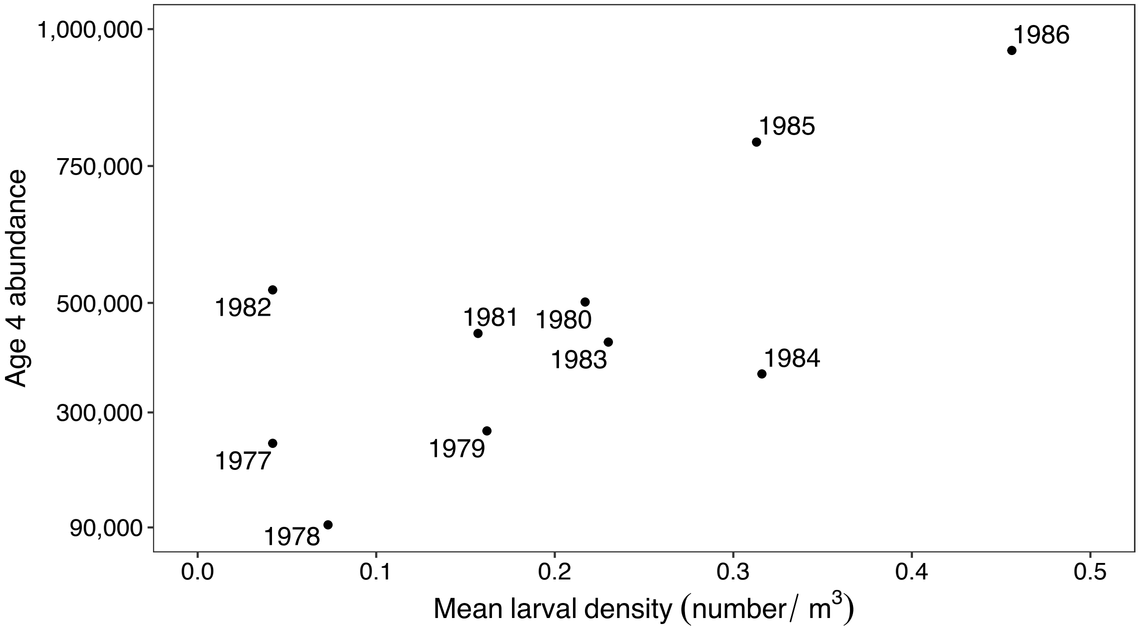
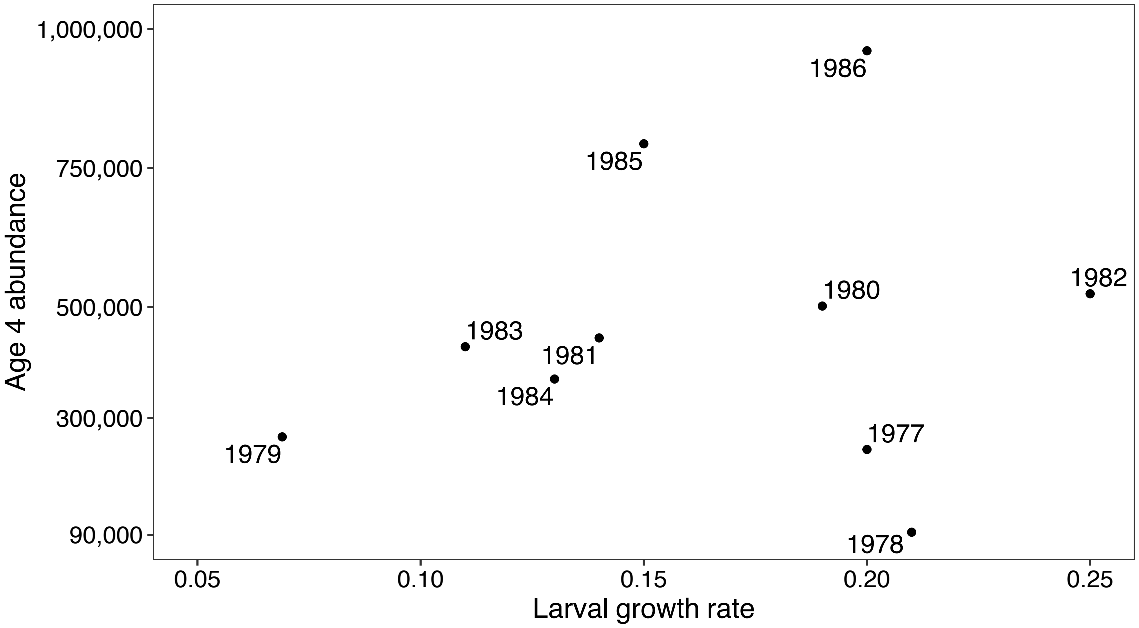


Fig. 3.7. Lake whitefish age 4 lake whitefish abundance and annual larval lake whitefish growth rates in Lake Huron from 1977-1986 (n=10). Age 4 abundance data was obtained from statistical catch-at-age (SCAA) modelling data for the central main basin of Lake Huron. Growth rates were obtained from linear regression equations estimated for each sampling year.



CHAPTER 4: GENERAL DISCUSSION

Lake whitefish support one of the largest commercial fisheries in the Great Lakes, with the majority of lake whitefish harvested from Lake Huron (Mohr and Nalepa 2005; Ebener et al. 2008; Cottrill et al. 2020). Following the invasion of dreissenid mussels and the subsequent loss of *Diporeia*, lake whitefish abundance and growth began to decline (Mohr and Nalepa 2005; Nalepa et al. 2005). Since commercial yields peaked in the late 1990's, lake whitefish recruitment has declined dramatically over the past two decades (Gobin et al. 2015; Ebener et al. 2021). In Lake Huron, recent declines in larval density and larval growth have also been observed (Ebener et al. 2021; see Chapter 2). Despite being one of the most valued commercial fish species in the Great Lakes, there remains a knowledge gap in the early life history and dynamics of lake whitefish. Most research on lake whitefish has focused primarily on the juvenile and adult life stages because these are the ages when fish become susceptible to capture by sampling gear. Presently, it is unclear at what life stage the recruitment bottleneck is occurring and what factors are influencing larval survival.

The overall objective of my thesis was to examine lake whitefish dynamics at the larval life stage in an effort to provide insights into the recent declines in juvenile recruitment (age 4+) in Lake Huron. Specifically, I aimed to determine: 1) whether declines in larval density and growth have occurred between a historical time period (pre-dreissenid mussels) and a contemporary time period (post-dreissenid mussels) and 2) what factors contribute to the year-to-year variation in larval densities in the Fishing Islands spawning shoal. In Chapter 2, I determined that larval lake whitefish density has declined between the two time periods, with contemporary densities being three times lower than historically overall. Larval lake whitefish growth was nearly two times slower in recent years and there was strong evidence that larval growth rates varied from year-to-year. After accounting for the effects of water temperature on growth, I observed that larval growth remained slower in the contemporary time period. Declines in contemporary larval densities indicate that at least a proportion of the recruitment bottleneck is occurring sometime between the egg and larval stages. Additionally, slower contemporary growth rates are consistent with the hypothesis that reduced food availability during the early life stages are contributing to poor survival of larval fish and potentially contributing to reduced juvenile (age 4+) recruitment. In Chapter 3, I determined that spawning stock biomass, November water levels, and dreissenid mussel presence best explained the annual variation in larval lake whitefish densities, although the direction of the effect of spawning stock biomass was not consistent among models. I found evidence for a relationship between larval density and year-class strength, with greater age 4 abundance occurring at higher larval densities. These findings indicate that larval lake whitefish recruitment may be influenced by a combination of biotic and abiotic variables.

I observed significant spatial and temporal variation in larval lake whitefish density throughout the Fishing Islands region. These findings are consistent with previous research studies aimed at determining the distribution patterns of larval lake whitefish in the Great Lakes (Taylor et al. 1987; Freeberg et al. 1990; Brown et al. 1993; McKenna and Johnson 2009; Claramunt et al. 2010). For example, larval lake whitefish densities in Chaumont Bay, Lake Ontario were consistently greatest near the northern sections and mouth of the bay during a four year sampling period, but densities varied significantly from year-to-year (McKenna Jr. and Johnson 2009). In Lake Huron, similar findings have been observed at certain sites within the lake including Stokes Bay, Thunder Bay, and Saginaw Bay (Ryan and Crawford 2014; Pothoven and Olds 2020). While previous research studies have shown that larval densities vary greatly over space and time, our study is unique because we examined larval lake whitefish density patterns over the course of several years and among two distinct time periods. This allowed me to compare larval densities within and between the time periods, and to determine whether density had changed following the invasion of dreissenid mussels and resulting ecosystem changes.

Water currents may play an important role in the survival and distribution of larval lake whitefish, a variable that was not assessed in our study. The relationship between larval fish dispersal and currents in marine environments is well known, with harsher water currents moving fish larvae out of favourable nursery habitats that results in greater larval mortality (Houde 2009; Ludsin et al. 2014). In the Great Lakes, only a handful of studies have aimed at understanding the effects of water currents on larval fish abundances. Heufelder et al. (1982) observed that water currents transported larval alewives (*Alosa pseudoharengus*) away from nursery habitats in Lake Michigan, which ultimately may have affected recruitment success. Similar findings were found for other freshwater fish species including larval cisco (*Coregonus artedi*) and larval walleye (*Sander vitreus*) in lakes Superior and Erie respectively (Hoff 2004; Oyadomari and Auer 2008; Humphrey et al. 2012). While no research studies to date have attempted to disentangle the effects of water currents on lake whitefish in the Great Lakes, a major unresolved question is the potential role of water currents on larval lake whitefish dispersal, survival, and recruitment.

There was a positive association between larval densities and the abundance of juvenile (age 4+) lake whitefish. Lake whitefish recruitment can be affected by numerous factors including physical habitat, spawning stock, overwinter conditions (e.g., ice cover), and food availability (Brooke 1975; Taylor et al. 1987; Cushing 1990; Freeberg et al. 1990); however, the link between larval lake whitefish density and recruitment remains unclear. My findings suggest that larval densities may play a role in influencing juvenile lake whitefish recruitment, as greater age 4 abundance was correlated with higher larval density. Previous research studies have attempted to determine whether a relationship exists between larval density and year-class strength for lake whitefish (Freeberg et al. 1990; Claramunt et al. 2010), but the exact mechanism affecting larval lake whitefish densities still remains unclear. Future research studies should focus on evaluating whether larval density is a reliable early predictor of future year-class strength for lake whitefish.

The findings of my study provide valuable information that could be useful in informing management decisions of lake whitefish populations in Lake Huron. Two management recommendations that have been put forth following the reduced lake whitefish recruitment in Lake Huron include protecting spawning and nursery habitats to reduce larval mortality and altering commercial harvest levels (Great Lakes Fishery Commission 2018). By determining recent, fine-scale variations in larval abundance across the Fishing Islands spawning shoal, I identified that Howdenvale, Pike Bay, Red Bay, and Stokes Bay are key larval production sites. I also determined that the Fishing

Islands region remains an important spawning shoal for lake whitefish as it is producing viable larval lake whitefish. Such knowledge should be used to inform and direct conservation efforts for lake whitefish in Lake Huron. More specifically, protection of the Fishing Islands region during the lake whitefish spawning period and larval hatching could help increase recruitment to the later juvenile stage. I also identified numerous information gaps in relation to larval lake whitefish recruitment specifically, one of which is that there is a general lack of current information on larval densities and growth rates in each of the Great Lakes. I was able to provide annual estimates of larval densities and growth rates in the central main basin of Lake Huron. I also provided evidence that both density and growth have declined since the establishment of dreissenid mussels, which has likely reduced recruitment. With such drastic declines occurring in larval production and growth, harvest levels could be reduced to support recruitment and to encourage the future sustainability of this valuable fish population.

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APPENDICES

Appendix 1: Larval fish identification through DNA barcoding.

DNA barcoding that was used to determine the species of larval fish obtained from samples in the Fishing Islands region of Lake Huron during the contemporary time period (2017-2019).

DNA extraction

Place individual fish into each well of a large label tray. Add 25 mL of 1X lysis buffering solution and 1 vial of Pro K solution into a beaker. Add 250 µl of lysis into each well and incubate overnight. Then, add 10 µl of NaCl and 500 µl of 80% isopropanol to each well and centrifuge for 45 minutes at 4600 RPM. Add 1000 µl of 70% ethanol (ETOH) and centrifuge for 45 minutes at 4600 RPM. Leave label tray to dry or place in oven (68°C) for 45 minutes. Once completely dry, add 150 µL of 1 X TE buffer to each well and refrigerate for 12 hours. Transfer solution to smaller working label tray and run gels to observe DNA samples.

DNA amplification

Create a diluted working solution using 58 µl ddH_20, centrifuge the pure DNA sample, and add 2 µl of DNA from original label tray into a new label tray. Make a solution for the amplification process to determine if either Song CytB or Fish CO1 is being used. The amplification solution contains: 429 µl of ddH_20, 220 µl 5X buffer, 110 µl BSA, 22 µl MgCl, 22 µl dNTP's, 33 µl forward primer (either Fish CO1 F or Song CytB F), 33 µl reverse primer (either Fish CO1 R or Song CytB In R), and 11 µl Go Taq. In a new label tray, add 8 µl of amplification solution with 2 µl of working solution to each well. Centrifuge label tray at 1000 RPM. Run label tray in PCR machine under

CytB54 if amplifying Fish CO1 for 2 hours and DLOOP 50 if amplifying Song CytB for 2.75 hours.

Sequencing

Create a sequencing solution using 935 µl ddH$_2$0, 55 µl Terminator mix, 110 µl 5X sequencing buffer, and 110µl forward primer (Fish CO1 F or Song CytB F). In a new label tray, add 11 µl of sequencing solution and 1.3 µl of DNA sample into each well. Then, make a positive PGEM solution using 7 µl ddH$_2$0, 0.5 µl Terminator mix, 1 µl 5X sequencing bugger, 1.5 µl DNA PGEM, and 2 µl primer M13. Centrifuge and run in the PRC machine under Big Dye 3 (3 hours).

Ethanol cleanse

Take label tray and add 1.2 µl of sodium acetate and 37 µl of 90% ethanol to each well. Seal and centrifuge at 4600 RPM for 45 minutes. Dump out sample in sink. Add 150 µl of 70% ethanol to each well. Seal and centrifuge at 4600 RPM for 25 minutes. Dump out sample in sink and dry in oven. Under the fume hood, add 10 µl of HIDI to each well and centrifuge. Transfer 10 µl of DNA solution into a new label tray. Load trap map into the ABI machine and load label tray (3 hours).

Scrubbing the data

Load data into Sequencher 5.1 and sort by type. Remove DNA fragment files, duplicates, and low-quality data (ex < 15%) from the database. If there are several differences in the individual base pairs, adjust the minimum match percentage parameters. Select sections of sequences and run through BLAST (NCBI). Similar species will group together and will need to be evaluated individually to clearly define differences between species. Non-similar species will group separately and need to be run through BLAST individually to identify.

Appendix 2: Effect of varying sampling diameter with contemporary larval densities ($CPUE_A$).

Nested analysis of variance (ANOVA) results conducted using log-transformed larval lake whitefish densities ($CPUE_A$; no. larval fish/m^2/min) collected in the contemporary time period (2017-2019). Five separate nested ANOVAs were used to explore effect of varying the sampling diameter at each site (ranging from 1-5 km) on our results, while controlling for the random variation of year, week, and site on larval densities. The statistical model used in the nested ANOVA was as follows:

(3) $aov(\log(CPUE_V) \sim Year + Year|Week + Year|Site + Year|Week|Site)$

Table A2.1. Results from nested ANOVA using log-transformed larval lake whitefish densities ($CPUE_A$; no. larval fish/m^2/min) at 1 km diameter from each site sampled in the Fishing Islands region of Lake Huron during the contemporary time period (2017-2019; n=74 tows). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Year	2	4.54	2.27	1.56	0.2212
Year:week	3	17.59	5.86	4.04	0.0129*
Year:site	17	34.76	2.05	1.41	0.1801
Year:week:site	8	5.84	0.73	0.50	0.8474
Residuals	43	62.45	1.45		

Table A2.2. Results from nested ANOVA using log-transformed larval lake whitefish densities ($CPUE_A$; no. larval fish/m^2/min) at 2 km diameter from each site sampled in the Fishing Islands region of Lake Huron during the contemporary time period (2017-2019; n=145 tows). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Year	2	8.99	4.49	3.31	0.0412*

Year:week	3	26.14	8.71	6.41	0.0006***
Year:site	29	43.20	1.49	1.10	0.3613
Year:week:site	20	21.40	1.07	0.79	0.7223
Residuals	90	122.38	1.36		

Table A2.3. Results from nested ANOVA using log-transformed larval lake whitefish densities ($CPUE_A$; no. larval fish/m^2/min) at 3 km diameter from each site sampled in the Fishing Islands region of Lake Huron during the contemporary time period (2017-2019; n=177 tows). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	P value
Year	2	13.17	6.58	5.37	0.0059**
Year:week	3	36.69	12.23	9.98	6.55e-06***
Year:site	31	64.31	2.08	1.70	0.0238*
Year:week:site	22	23.30	1.06	0.86	0.6412
Residuals	118	144.70	1.23		

Table A2.4. Results from nested ANOVA using log-transformed larval lake whitefish densities ($CPUE_A$; no. larval fish/m^2/min) at 4 km diameter from each site sampled in the Fishing Islands region of Lake Huron during the contemporary time period (2017-2019; n=188 tows). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	P value
Year	2	12.44	6.22	4.73	0.0104*
Year:week	3	31.48	10.50	7.99	6.3e-05***
Year:site	31	65.54	2.11	1.61	0.0348*
Year:week:site	22	17.32	0.79	0.60	0.9180
Residuals	129	169.40	1.31		

Table A2.5. Results from nested ANOVA using log-transformed larval lake whitefish densities ($CPUE_A$; no. larval fish/m^2/min) at 5 km diameter from each site sampled in the

Fishing Islands region of Lake Huron during the contemporary time period (2017-2019; n=287 tows). Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Year	2	5.88	13.46	13.46	3.04e-06***
Year:week	3	25.70	39.22	39.22	<2e-16***
Year:site	30	11.14	0.37	1.70	0.0167*
Year:week:site	28	4.64	0.17	0.76	0.8106
Residuals	222	48.49	0.22		

Appendix 3: Calculating larval densities by area ($CPUE_A$).

Methods used to calculate larval density per unit area per tow minute (no. larval fish/m^2/min), denoted $CPUE_A$, using data collected from the Fishing Islands region of Lake Huron during the historical (1976-1986) and contemporary (2017-2019) time periods. Larval lake whitefish density data collected in 1979 were not used due to the absence of tow duration values.

To calculate catch-per-unit effort per unit area per tow minute ($CPUE_A$), the number of larval fish per trawl was divided by the tow duration as follows:

(1) $$CPUE_A = C_{Cnt} \div T_{Dur}$$

where C_{Cnt} is the number of larval fish and T_{Dur} is the tow duration (minutes). $CPUE_A$ values were then standardized to account for the difference in net diameters used. Each $CPUE_A$ value was divided by the following standard conversion factor:

(2) $$CPUE_A\ conversion = \pi \times (d \div 2)^2$$

where net diameter d is 80 cm historically and 50 cm currently.

Appendix 4: Comparison of larval densities ($CPUE_V$) including outliers identified through z-score calculations.

Nested analysis of variance (ANOVA) and ANOVA results conducted using log-transformed larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) collected in the historical (1977-1986) and contemporary time period (2017-2019) with outliers identified through z-score calculations included. Nested ANOVAs were conducted to examine the effect of year, week, and site on lake whitefish densities in both time periods (Table A4.1; Table A4.2). The statistical model used in the nested ANOVA was as follows:

$$(3) \qquad aov(\log(CPUE_V) \sim Year + Year|Week + Year|Site + Year|Week|Site)$$

An ANOVA was also performed to test for a difference in larval CPUE between the historical and contemporary time periods, $aov(\log(CPUE_V) \sim Time\ period)$ (Table A4.3).

Table A4.1. Results from nested ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=938 tows) with outliers included. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Year	9	2.91	0.32	15.95	< 2e-16***
Year:week	10	0.15	0.01	0.72	0.7030
Year:site	63	2.87	0.05	2.24	3.65e-07***
Year:week:site	57	0.81	0.01	0.70	0.9520
Residuals	798	16.19	0.02		

Table A4.2. Results from nested ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected in the Fishing Islands region of Lake Huron in the contemporary time period (2017-2019; n=394 tows) with outliers included. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Year	2	0.07	0.04	5.79	0.0034**
Year:week	3	0.22	0.07	11.60	3.09e-07***
Year:site	36	0.41	0.01	1.81	0.0041**
Year:week:site	34	0.14	0.04	0.67	0.9212
Residuals	318	2.01	0.06		

Table A4.3. Results from ANOVA using log-transformed larval lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected in the Fishing Islands region of Lake Huron in the historical (1977-1986; n=938) and contemporary time period (2017-2019; n=452) with outliers included. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Time period	1	0.79	0.79	42.33	1.07e-10***
Residuals	1388	25.81	0.02		

Appendix 5: Comparison of larval densities ($CPUE_V$) including outliers identified through z-score calculations and 10% of larval fish per trawl deducted from historical tows.

Nested analysis of variance (ANOVA) and ANOVA results conducted using log-transformed larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) collected in the historical (1977-1986) time period, with outliers identified through z-score calculations included and 10% of larval whitefish removed from each individual tow historically (see Discussion section). A nested ANOVA was conducted to examine the effect of year, week, and site on lake whitefish densities in the historical time period (Table A5.1). The statistical model used in the nested ANOVA was as follows:

(3) $aov(\log(CPUE_V) \sim Year + Year|Week + Year|Site + Year|Week|Site)$

An ANOVA was also performed to test for a difference in larval $CPUE$ between the historical and contemporary time periods, $aov(\log(CPUE_V) \sim Time\ period)$ (Table A5.2).

Table A5.1. Results from nested ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=938 tows) with outliers included and 10% of larval whitefish removed from each individual tow historically. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Year	9	2.62	0.29	15.87	2.00e-16***
Year:week	10	0.14	0.01	0.75	0.6760

Year:site	63	2.57	0.04	2.23	4.80e-07***
Year:week:site	57	0.73	0.01	0.70	0.9520
Residuals	798	14.61	0.02		

Table A5.2. Results from ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=938 tows) and contemporary time period (2017-2019; n=452 tows). Outliers were included and 10% of larval whitefish removed from each individual tow historically. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Time period	1	0.20	0.20	3.08	0.0794
Residuals	1388	92.16	0.07		

Appendix 6: Comparison of larval densities ($CPUE_V$) including outliers identified through z-score calculations at four key sites.

Analysis of variance (ANOVA) results conducted using log-transformed larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) collected in the historical (1977-1986) and contemporary (2017-2019) time periods with outliers identified through z-score calculations included. ANOVAs were conducted to test for potential differences in larval density between the two time periods at four key sites. Annual $CPUE_V$ values were examined at Howdenvale (Table A6.1), Pike Bay (Table A6.2), Red Bay (Table A6.3), and Stokes Bay (Table A6.4). The site of Stokes Bay encompassed larval densities from Garden Island, Irish Harbour, and Tamarack. The model used was, $aov(\log(CPUE_V) \sim site)$.

Table A6.1. Results from ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected at Howdenvale in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=117 tows) and contemporary (2017-2019; n=33 tows) time period with outliers included. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	P value
Time period	1	0.04	0.04	1.89	0.1710
Residuals	148	3.17	0.02		

Table A6.2. Results from ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected at Pike Bay in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=251 tows) and contemporary (2017-2019;

n=35 tows) time period with outliers included. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	P value
Time period	1	0.02	0.02	0.93	0.3660
Residuals	284	7.11	0.03		

Table A6.3. Results from ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected at Red Bay in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=113 tows) and contemporary (2017-2019; n=6 tows) time period with outliers included. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	P value
Time period	1	0.01	0.01	0.50	0.4820
Residuals	117	1.97	0.02		

Table A6.4. Results from ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected at Stokes Bay in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=362 tows) and contemporary (2017-2019; n=67 tows) time period with outliers included. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	P value
Time period	1	0.02	0.02	0.80	0.3720
Residuals	427	11.65	0.03		

Appendix 7: Comparison of larval densities ($CPUE_V$) not including outliers identified through z-score calculations and 10% of larval fish per trawl deducted from historical tows.

Nested analysis of variance (ANOVA) and ANOVA resulted conducted using log-transformed larval lake whitefish densities ($CPUE_V$; no. larval fish/m^3) collected in the historical (1977-1986) time period, with outliers identified through z-score calculations not included and 10% of larval whitefish removed from each individual tow historically. A nested ANOVA was conducted to examine the effect of year, week, and site on lake whitefish densities in the historical time period (Table A7.1). The statistical model used in the nested ANOVA was as follows:

(3) $aov(\log(CPUE_V) \sim Year + Year|Week + Year|Site + Year|Week|Site)$

An ANOVA was also performed to test for a difference in larval $CPUE$ between the historical and contemporary time periods, $aov(\log(CPUE_V) \sim Time\ period)$ (Table A7.2).

Table A7.1. Results from nested ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=923 tows) with outliers not included and 10% of larval whitefish removed from each individual tow historically. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	*P* value
Year	9	0.75	0.08	10.14	7.36e-15***
Year:week	10	0.12	0.01	1.50	0.1365

Year:site	63	0.96	0.02	1.84	0.0001***
Year:week:site	57	0.36	0.01	0.76	0.9017
Residuals	784	6.47	0.01		

Table A7.2. Results from ANOVA using log-transformed lake whitefish density ($CPUE_V$; no. larval fish/m^3) data collected in the Fishing Islands region of Lake Huron in the historical time period (1977-1986; n=923 tows) and contemporary time period (2017-2019; n=446 tows). Outliers were not included and 10% of larval whitefish removed from each individual tow historically. Data collected in 1976 were not included due to the absence of flowmeter data that was used to calculate distance travelled for each tow conducted. Significant codes: * = 0.05, ** = 0.005, *** = 0.001.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F-value	P value
Time period	1	0.46	0.46	64.35	2.22e-15***
Residuals	1368	9.74	0.01		