**Distribution and Abundance of Larval Lake Whitefish
(*Coregonus clupeaformis*) in Stokes Bay, Lake Huron**

by

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ABSTRACT

DISTRIBUTION AND ABUNDANCE OF LARVAL LAKE WHITEFISH (*COREGONUS CLUPEAFORMIS*) IN STOKES BAY, LAKE HURON

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Lake whitefish (*Coregonus clupeaformis*) are an ecologically, culturally and economically important species throughout the Great Lakes. Studying the larval period of ontogeny is important to increasing knowledge of population dynamics and monitoring ecological changes in lake whitefish populations. Larval lake whitefish have been studied across the Great Lakes since the 1930's; however, there are major gaps in our understanding of the factors that affect distribution and abundance of larval lake whitefish. The goal of this study was to investigate the distribution and abundance of larval lake whitefish in a Great Lakes embayment, using Stokes Bay, Lake Huron as a case study. Plankton samples and environmental data were collected from mid-spring to early summer during 2011 and 2012. Plankton tows in 2011 (n=71, 21 April-03 June) revealed relatively high densities of larval lake whitefish as compared to other Great Lakes studies. Overall there was little relationship between environmental variables (temperature, dissolved oxygen, conductivity, depth) and larval lake whitefish distribution and abundance. Plankton tows in 2012 (n=25, 25 April-23 May) revealed a virtual absence of larval lake whitefish in Stokes Bay. The apparent 2012 year-class failure was concurrent with unseasonably warm temperatures and reduced ice coverage. Temperature-related hypotheses are evaluated in context with other possible explanations of a general year-class failure of lake whitefish during early life history.

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Introduction

Lake whitefish (*Coregonus clupeaformis*) are found in lakes of North America from the Laurentian Great Lakes region northward (Scott and Crossman 1973). In the Great Lakes, lake whitefish are an ecologically, culturally and economically significant species. Ecologically, lake whitefish direct energy from benthic to pelagic areas by feeding on a variety of benthic organisms (Brenden et al. 2010a). Culturally, First Nations communities have harvested lake whitefish for ceremony, food and commerce since ‘time immemorial’, and continue to rely on these fisheries as an important component of their survival (Cleland 1982; Crawford et al. 2001). Economically, lake whitefish are considered one of the most commercially valuable species in the Great Lakes, with millions of dollars contributed to Canada’s annual gross domestic product from commercial harvests (Mohr and Nalepa 2005).

Across the five Great Lakes, there are at least 56 hypothesized populations of lake whitefish separated by distances ranging from 5-100 km (Ebener et al. 2008). Over the past century, abundance of many of these lake whitefish populations has fluctuated dramatically in response to fishing pressure, food web changes, non-native species, and environmental change in the Great Lakes (Nalepa et al. 2005; Brenden et al. 2010b). In order to establish safe harvest limits, managers of lake whitefish commercial fisheries need to predict changes in population abundance on the basis of variable strengths of year-classes that will recruit into the fishery over time; although data available to support these predictions are often scarce (Taylor et al. 1987). It has been hypothesized that year-class strength of lake whitefish populations is determined during the first months after embryos hatch (Hoagman 1973; Freeberg et al. 1990; Holmes et al. 2002). One method of evaluating year-class strength in lake whitefish populations is to monitor relative abundance during the planktonic free embryonic and larval periods. Overwintering embryos

hatch from their egg envelopes and are transported by water currents from the spawning shoals to productive nearshore embayments where the larvae can begin feeding exogenously (Loftus 1978a; Freeberg et al. 1990; Claramunt et al. 2010). While the larval period could be critical for determining the abundance of lake whitefish year-classes, the actual mechanisms affecting distribution and abundance of larval lake whitefish remain largely unknown (Hoagman 1973; Cucin and Faber 1985; Claramunt et al. 2010).

Hart (1930) was among the first to conduct field investigations on the early life history of Great Lakes lake whitefish. Specifically at sites in the Bay of Quinte, Lake Ontario he found that larvae had a tendency to school and were concentrated in water ~0.5m deep, along gently sloping shorelines, rocky substrates and vegetative beds. Faber (1970) and Reckhan (1970) both studied the ecology of young whitefish in South Bay, Lake Huron; Faber observed larvae in greatest abundance at depths between 1-3m along steep shorelines of boulder, rock and cobble substrates. In contrast, Reckhan (1970) found larvae dispersed in waters less than 1m deep, adjacent to emergent vegetation. Hoagman (1973) and Frederick (1982) investigated larval lake whitefish distribution and abundance at Green Bay, Lake Michigan and observed that abundance was non-uniform across sites of similar depth; highest abundance was recorded at vegetated sites in waters between 1-3m, with few if any larvae in waters greater than 3m depth. Other studies in Lake Michigan and Ontario have investigated the relationships between embryonic/larval survival on later year class strength (Freeberg et al. 1990; Claramunt et al. 2010; Hoyle et al. 2011).

Great Lakes studies on larval lake whitefish have most commonly occurred in embayments, suggesting the importance of these areas as essential nursery habitat. Embayments are dynamic nearshore waters sheltered from open lake processes such as powerful winds and

water currents (Klumb et al. 2003). After over-wintering on Great Lakes spawning shoals, lake whitefish embryos hatch in early spring (late March-early April). At this time, open water temperatures in the Great Lakes are typically cold (2-4°C) and areas of warmer water (4-8°C) are located only at the surface and in nearshore embayments (Brown and Taylor 1992). Ice-free conditions, and the associated elevation of light and temperature levels, often lead to a spring pulse of primary productivity and planktonic prey for larval lake whitefish (Faber 1970). The availability of prey for lake whitefish larvae as they exhaust endogenous energy reserves (yolk) has been hypothesized to be a critical factor to their survival (Brown and Taylor 1992). Embayments also offer physical protection from offshore wind and water currents, increasing the probability of larval retention, and allowing for continued larval access to suitable prey resources for survival and growth (Holmes et al. 2002).

The goal of this thesis is to investigate the patterns of larval lake whitefish distribution and abundance in a Great Lakes embayment. In order to achieve this goal, it is necessary to satisfy the following specific objectives: 1) describe the patterns of distribution and abundance for sampled lake whitefish larvae in the embayment; 2) identify specific areas and/or habitat characteristics of the embayment that are strongly correlated with larval lake whitefish distribution and abundance; and 3) develop hypotheses regarding the possible cause-effect mechanisms affecting larval distribution and abundance.

Stokes Bay, Lake Huron was chosen as a case study for this investigation (Figure 1); it is the largest embayment on the western side of the Saugeen (Bruce) Peninsula, along the eastern shore of Lake Huron's Main Basin. This embayment is located in the middle of extensive lake whitefish spawning shoals extending 100km from Chief's Point, though the traditional Ojibway Geghetto (Fishing) Islands north to Cape Hurd at the tip of the peninsula (Loftus 1980). The

study area contains three sub-bays: Myles Bay, Stokes Bay and Gauley Bay, with complex bathymetric characteristics including many islands, shoals and channels. During the late 1970s Dave Loftus (Ontario Ministry of Natural Resources) reported high densities of larval fishes in Stokes Bay as a result of surveys undertaken to explore the determinants of year class strength for fisheries management (Loftus 1978a; 1978b; 1979). Soon thereafter, Loftus (1980) compiled interviews with many Lake Huron commercial fishermen, including several who specifically identified major lake whitefish spawning and nursery grounds along the Saugeen Peninsula generally, and the study region specifically. For these reasons, Stokes Bay was considered to be an ideal candidate to serve as a case study for this investigation of larval lake whitefish distribution and abundance.

Methods

In order to determine potential sampling locations, the Stokes Bay study area was divided into a set of cells (each cell ~300m x 320m), extending from the embayment shoreline to an offshore depth of approximately 15m (Figure 1). A total of 320 grid cells could have been randomly selected for sampling. Some cells were too shallow (<0.80m) for effective deployment of the plankton sampling gear and were removed from the sampling set.

In 2011, a total of $n=71$ grid cells were randomly selected (with replacement) for sampling of environmental conditions and plankton. The final decision to sample a given cell was made on the basis of prevailing weather conditions and requirements for safe boating in an open punt. The 2011 sampling season extended from ice-out on 21 April and continued for six weeks until 03 June. Environmental conditions were assessed at the mid-point location of the cell. A YSI PRO 2030 unit was used to measure environmental variables: water temperature ($^{\circ}\text{C}$), dissolved oxygen ($\%$, $\text{mg}\cdot\text{L}^{-1}$) and temperature-corrected specific conductivity ($\text{mS}\cdot\text{cm}^{-1}$) at

1 m intervals from the water surface to bottom; water depth and Secchi depth were also recorded at each sampling location. After environmental conditions had been recorded, a plankton net was towed at the side of the boat for 5 minutes along a transect through the mid point of the selected grid cell, proceeding at a speed ranging from 1.6-2.5 km hr⁻¹ into prevailing wind/waves at the time of sampling. The 500-micron nylon mesh plankton net was 2.3 m in length, with 0.75 m hoop diameter, and was equipped with a cod-end bucket. A flow meter (General Oceanics Model 2030R) was suspended in the mouth of the net, to allow calculation of sampled water volume for each tow. Weight was added to depress the net so that the top of the hoop net was level with the water surface, effectively sampling the top 0.75m of the water column. At the conclusion of each plankton tow, contents of the net were rinsed into the cod-end bucket, which was then emptied into a sealed plastic container until return to shore, then transferred into mason jars with 100 mL of 95% ethyl alcohol(10:1 ETOH:larvae). Larval specimens were visually identified using a dissecting microscope (Olympus SZ-CTV) and larval identification keys developed by Cucin and Faber (1985) and Auer (1982). Melanophore structure was used as the key feature for identification of larval lake whitefish and to distinguish between larval lake whitefish from other larval species, specifically lake herring (*Coregonus artedii*).

A variety of statistical techniques were used to explore the statistical relationships between larval lake whitefish density and environmental variables. The number of larval lake whitefish collected during a plankton tow was converted to a standard density using the number of rotor revolutions recorded from the flowmeter. The flowmeter manufacturer provided the appropriate rotor constants and equations for the flowmeter model for calculation of distance (m) (Difference in counts*rotor constant (26,873)/999999) and then volume of water sampled (m³) (3.14*net diameter (0.75)² * distance/4). The number of larval lake whitefish was then

converted to a density for each tow and then to a standard density per 1000m³. A test for spatial autocorrelation was performed for each environmental variable and larval lake whitefish density, using Moran's *I* statistic (Sokal and Thompson 1987; Roseman et al. 2005):

(1)

$$I = \frac{\sum \sum w_{ij}(d)(x_i - \mu)(x_j - \mu)}{\sum (x_i - \mu)^2 / (K-1)}$$

Where *i* and *j* index spatial location (*i,j*=1...number of cells [*K*]), *w_{ij}*(*d*) represents a spatial weight function related to distance *d*, *x_i* and *x_j* are the observed environmental covariates at location *i* and *j*, and *K* represents the total number of cells. A Box-Cox transformation function (Box and Cox 1964) was used to normalize lake whitefish density data; log transformation was identified as appropriate for normalization. A categorical regression analysis was performed to explore the relationship between week (1-6) and larval lake whitefish density. In the categorical regression analysis, the mean larval density for week 1 was used as the baseline value to which all other weeks (2-6) were compared. A univariate linear regression ($\log(\text{density}) = \beta_0 (\text{y-intercept}) + \beta_{\text{variable}} (\text{slope})$) of continuous data was used to explore relationships between larval lake whitefish density and the environmental variables. Secchi depth was not considered in the analysis because only 14 (19%) of observations did not detect the entire water depth. Statistical significance was indicated by a p-value of 0.05 or less for the univariate regression analyses and for Moran's *I* test. All analyses were performed using R (version 2.13.1, 2011-07-08).

In 2012, the focus of investigation was originally intended to address effects of water circulation (wind and water currents) on larval lake whitefish distribution and abundance in

Stokes Bay. However, preliminary plankton samples revealed a complete absence of fish larvae at sites that had yielded many larvae on similar dates in 2011. In response to this dramatic observation, the focus of 2012 sampling shifted to an evaluation of overall larval presence/absence in the study area. Based on a review of the 2011 plankton sampling results, the greater Stokes Bay study area was divided into four different regions (North vs. South, Outer vs. Inner). For each region, an extended 30 minute plankton tow transect (~1 km length) was established (Figure 2) to evaluate larval presence/absence with higher certainty. Shallow water of the South-Inner region prevented the execution of an extended transect; as a result an additional transect was added to the North-Inner region. Three reference sites were also selected based on observations of low, moderate and high larval density during the peak larval abundance period in 2011. These reference sites were sampled on 2012 field dates using the same 5-minute plankton sampling protocol used in 2011 (see above). The 2012 plankton tows were performed at Stokes Bay on a total of 5 days, beginning 25 April (four days later than in 2011) until 23 May 2012. Surface water temperatures were compiled from National Oceanic and Atmospheric Administration Great Lakes Coastal Forecasting System, Great Lakes Observing System (GLOS 2012; <http://glos.us/data-tools/point-query-tool-glcofs>). Seasonal ice-coverage summary data for Lake Huron were obtained from Environment Canada, Canadian Ice Services (<http://www.ec.gc.ca/glacesice/default.asp?lang=En&n=4BC7DB84-1>.)

Results

2011 Sampling Season

Environmental data for each sampled location (k=71) are presented on maps separated by week in Figures 3 through Figure 6. Water depths at sampled locations ranged from 1.8-11.0m

(mean=4.30, sd=2.68). Complex bathymetry within the embayment were not consistent with a simple depth gradient moving away from shore (Figure 3). With the exception of a few deeper sites, the southern region was generally shallower in contrast with the northern region that was characterized by a deeper channel extending into Stokes Bay proper. Figure 4 shows the weekly distribution of surface water temperatures ranging from 3.2-15.5°C over the sampling period (mean=10.80, sd=2.19). Temperatures increased gradually from weeks 1-6. Figure 5 shows the weekly distribution of surface water dissolved oxygen measurements ($\text{mg}\cdot\text{L}^{-1}$) for each of the sampled locations, ranging from 10.0-15.0 $\text{mg}\cdot\text{L}^{-1}$ (mean=12.50, sd=1.21). Dissolved oxygen (%) ranged from 90.0-126.0 % (mean=112.00, sd=8.66). Dissolved oxygen gradually decreased from weeks 1-6 and demonstrated variation across sampled locations, including initially high levels of dissolved oxygen in Stokes and Myles Bays. Figure 6 shows the weekly distribution of surface water specific conductance for each of the sampled locations, ranging from 0.174-0.349 specific $\text{mS}\cdot\text{cm}^{-1}$ (mean=0.2200, sd=0.0271). Specific conductance generally decreased from weeks 1-6. The highest levels of specific conductance were observed in nearshore waters of the sub-bays, while the lowest levels were consistently observed at the outer and exposed regions of the embayment.

Table 1 shows the results of Moran's *I* test for spatial autocorrelation between environmental variables and grid matrix row/column (i.e. sampling location). Specific conductance was the only variable that showed significant positive spatial autocorrelation, indicating that sites with similar conductivity values were situated in close spatial proximity.

Plankton were collected in k=71 plankton tows conducted from 21 April to 03 June 2011. Various species of fish larvae and plankton were collected during this sampling period, however for the purposes of this investigation only specimens identified as lake whitefish larvae will be

considered further (Figure 7). Over the entire six weeks of 2011 sampling a total of 1,419 larval lake whitefish were captured in k=71 tows. From 21 April until 19 May, all k=52 tows contained a minimum of one lake whitefish larva per sample. From the first day of sampling (21 April) until 04 May, yolk was observed on a small portion of larval lake whitefish collected in tows. Across the six-week sampling period (21 April-03 June), larval density showed considerable variation (Figures 8 and 9, Table 2). Larval lake whitefish densities ranged from 0 to $2,026 \cdot 1,000 \text{ m}^{-3}$, with an overall mean density of $140.1 \cdot 1,000 \text{ m}^{-3}$ (sd=387.4). The minimum, mean and maximum densities of larval lake whitefish for each of the six sampling weeks are shown in Table 2. Larval lake whitefish density peaked during week 2 (28 April-04 May) at $2,026 \text{ larvae} \cdot 1,000 \text{ m}^{-3}$ (n=160 larvae per tow) at a nearshore location in Myles Bay of 3m depth and surface water temperature of 9.2°C (Figure 9). The first 2011 sample with zero lake whitefish larvae occurred on 19 May at an exposed site near Lyal Island. After 03 June, multiple consecutive catches of zero whitefish larvae were observed. Figure 9 presents the weekly distribution of larval lake whitefish densities for each of the sampled locations, showing high densities scattered throughout open and nearshore waters in the northern half of the embayment. Larval densities were consistently lowest at exposed sites in the outer region of the embayment. Moran's *I* test showed no significant spatial autocorrelation between larval densities and locations ($I= 0.032$, $p=0.222$, Table 1), indicating that sites with similar densities were not typically in close spatial proximity.

The categorical regression analysis showed that inclusion of the categorical week variable was significant and had a strong relationship with larval density ($p<0.001$, $r^2=0.584$) (Table 3). Weeks 2-4 were not significantly different from the baseline week 1, although the

parameter estimates indicated a positive density response. Weeks 5 and 6 were significantly different from week 1, with negative parameter estimates indicating a negative density response.

The continuous univariate regression analysis showed that each environmental variable was statistically significant, but had weak relationships with larval density (Table 3). The relationship between water depth and larval density was significant ($p=0.021$), with a negative correlation; the r^2 value=0.061 was very low, indicating that variability in larval density was not explained well by water depth. Both measures of dissolved oxygen (% , $\text{mg}\cdot\text{L}^{-1}$) were positively and significantly related to larval densities in the regression analysis ($p= <0.001$, $p=<0.001$ respectively). The r^2 values for dissolved oxygen variables (%=0.160, $\text{mg}\cdot\text{L}^{-1}=0.278$) were both low, indicating that the relationship with larval density was weak, and variability in larval density was not well explained by this variable. Specific conductance (specific $\text{mS}\cdot\text{cm}^{-1}$) was significant ($p=0.015$) and positively related to larval density; the r^2 value for this variable was also very low ($r^2=0.068$). Temperature ($^{\circ}\text{C}$) was highly significant in a negative relationship with larval density ($p=<0.001$), however the r^2 value for this variable was also low ($r^2= 0.167$).

2012 Sampling Season

In 2012, a total of $k=13$ extended 30-minute plankton tows were performed at four regional transects on 5 sampling dates between 25 April and 23 May (Figure 2, Table 4). An additional $k=12$ standard five minute tows were made at the low/moderate/high 2011 reference sites. For all of this sampling effort, only $n=3$ larval lake whitefish were captured, and all of these larvae were collected in a single extended plankton tow at the South-Inner transect on 13 May 2012. The 2011 transects covered a wide range of water depths, as extended tows covered large distances over complex bathymetry (1.5-11.0 m). Dissolved oxygen and specific

conductance measurements were similar to those obtained in 2011, though they showed less variability over time. Temperatures in 2012 ranged from 6.9°C-17.8°C and were markedly higher over a shorter time period compared to 3.2°C-15.5°C in 2011. Figure 10 shows the NOAA surface water temperatures for Stokes Bay, Lake Huron (N81.3956, W44.9706) for 2010-2011 and 2011-2012.

Discussion

The goal of this thesis was to investigate the distribution and abundance of larval lake whitefish in a Great Lakes embayment, using Stokes Bay, Lake Huron as a case study. The following discussion focuses on the patterns of distribution and abundance observed during the 2011 and 2012 sampling seasons for the respective lake whitefish year-classes, and the mechanisms that could have affected those patterns. Special attention will be paid to the possible lake whitefish year-class failure observed in 2012 and associated factors.

2011 Lake Whitefish Year-Class

Relatively high densities of Stokes Bay larval lake whitefish were observed in 2011, compared to other larval lake whitefish investigations in the Great Lakes - including previous studies at Stokes Bay. The maximum 2011 larval density of $2,026 \cdot 1,000\text{m}^{-3}$ exceeded the highest reported larval density for Great Lakes lake whitefish previously reported by Claramunt et al. (2010) for Rowley Bay, Lake Michigan ($2,000 \cdot 1,000\text{m}^{-3}$). The observation of high larval density at Stokes Bay supports the hypothesis that this embayment is an important nursery area for lake whitefish population(s) of Lake Huron. During the five weeks in 2011 that larvae were found, the mean weekly larval densities were consistently higher than those previously reported by

Loftus for Stokes Bay in 1978 (Table 5). It is possible that Loftus (1978b) pre-selected sites that were under-representative of larval lake whitefish in this embayment, however it is also possible that the difference in mean weekly densities indicates either that 2011 was a particularly strong year-class of lake whitefish, and/or that 1978 was a particularly weak year-class.

Larval lake whitefish density in Stokes Bay exhibited a distinct temporal pulse, reaching a peak density in early May (Table 2; Figures 8 and 9), in a manner consistent with previous observations for Great Lakes embayments (Faber 1970; Loftus 1978a; 1978b; Freeberg et al. 1990). Categorical regression analysis showed that week contributed significantly to explaining larval lake whitefish density ($p < 0.001$, $r^2 = 0.584$). Larval density increased from week 1-2, then progressively declined by week 6 to densities approaching zero (Table 2; Figures 8 and 9). It is important to note that larval lake whitefish were collected on the first effort deployed (21 April 2011), indicating that hatching of free embryos on the spawning shoals and transport into the embayment had already begun prior to commencement of sampling. The specific location(s) of source shoals for the sampled larvae is not known, but could include up-current spawning habitat south of Stokes Bay and/or spawning habitat within the embayment itself. In either case, the week 1 observation of lake whitefish with intact endogenous energy reserves is a strong indication that 2011 sampling overlapped with the period of hatching (Cucin and Faber 1985). Lake whitefish larvae typically exhaust their endogenous energy reserves between 12 and 25 days after hatching, depending on water temperature (Brown and Taylor 1992). Larval density was highest during week 2, and remained relatively high until week 4; this observation suggests that either the lake whitefish were surviving and being retained within the embayment during this time, or there was some balance between larvae being added to and those removed from the study area by physical mechanisms (e.g. water currents) or ecological mechanisms (e.g.

starvation/predation). Larval densities decreased dramatically over weeks 5 and 6, possibly due to emigration or mortality as discussed above, though it is also likely that many larger and morphologically advanced larvae/juveniles were able to actively avoid the sampling gear or had begun to leave the surface waters in preference for benthic prey items and/or deeper habitat (Loftus 1978a; Cucin and Faber 1985; McKenna and Johnson 2009).

Larval lake whitefish were widely distributed across the embayment, with a general pattern of high density in the inner region, and low density in the most outer region (Figure 9); however, due to the bathymetric complexity of the study area this pattern was not related simply to water depth. Sites located in the outer, more exposed region of the embayment consistently exhibited lower larval density and lower specific conductance. In the univariate regression model (Table 3), the relationship between specific conductance and larval density the relationship was weak ($r^2=0.068$) but statistically significant ($p=0.015$). The statistical significance of this relationship does not necessarily imply causation, however it may indicate the influence of one or more water masses (e.g. lake and river) in Stokes Bay during the spring sampling period. The lowest conductance values were associated with the outer regions of the embayment exposed to the offshore waters of Lake Huron; the highest values were associated with inner regions of the embayment subject to influence from river and groundwater discharge (Figure 6). Nearshore areas with high conductivity values diminished during the sampling period, possibly indicating the reduced loading of suspended solids from spring flooding in the tributaries and/or ongoing mixing of tributary discharge and embayment waters. Although primary and secondary production were not measured in this study, it could have been that the spring tributary discharge of nutrients into the bay caused localized pulses in prey for lake whitefish larvae, which in turn

led to higher survival and densities compared to nutrient-poor waters in the outer region (McKenna et al. 2008).

There was little evidence in the 2011 Stokes Bay data of the inverse relationship between larval density and water depth commonly reported for Great Lakes embayments (Faber 1970; Reckhan 1970; Hoagman 1973). The univariate regression model for water depth and larval density showed a marginally significant, but weak negative relationship ($r^2=0.061$; $p=0.021$). During the first four weeks of sampling, moderate to high densities of lake whitefish were collected at sites ranging in water depth 1.8-11.0m (Figures 3 and 9). In previous field studies of larval lake whitefish, shallow waters between 1.0-3.0m depth have been associated with relatively high larval densities, compared to low densities observed in waters deeper than 3.0m (Faber 1970; Reckahn 1970; Hoagman 1973). Cucin and Faber (1985) observed larval lake whitefish in Lake Opeongo over water depths ranging from 1.5-10.0m; they reported that sampling efforts in deeper waters generally resulted in fewer larvae. However, in the Cucin and Faber (1985) study, many larval sampling locations were close to known lake whitefish spawning shoals, and this may have contributed to the observation of larvae over deeper waters. In western Lake Erie, Roseman et al. (2005) reported that shallow nearshore waters were generally associated with both warmer water temperature and higher abundance of plankton food sources for larval fishes. Availability of planktonic prey for larval lake whitefish has been hypothesized as a major determinant of individual and year-class strength (Freeberg et al. 19990; Brown and Taylor 1992). Higher survival of larval lake whitefish in shallow waters with favourable prey abundance may have contributed to the high densities observed in previous studies. Notwithstanding these causal explanations for previously observed inverse relationships between water depth and larval density, it is possible that previous investigators simply did not

expect to find larvae over deeper waters, and thus did not effectively sample both shallow and deeper waters. It would be worthwhile to revisit sampling designs for the previously investigated embayments to determine if larval lake whitefish are indeed widely distributed over varying water depths, as observed in 2011 for Stokes Bay. Since Great Lakes embayments may exhibit high variation in morphology and bathymetry, operational definitions of site-specific larval lake whitefish ‘nursery habitat’ would benefit greatly from empirical data gathered from well-balanced sampling design, rather than relying solely on sampling effort deployed in previous studies.

It is important to distinguish between patterns of distribution/abundance for larval lake whitefish, and the mechanisms that cause those patterns. While there were statistically significant relationships observed in the 2011 Stokes Bay data between each of the environmental variables measured in this study and larval density, none of these variables provided strong explanations for the (lack of) patterns of distribution/abundance of larval lake whitefish at different sites in this embayment. This observation suggests that there are other outstanding factors that significantly affect spatio-temporal dynamics of larval lake whitefish in nursery embayments – including one or more of the following distinct categories:

- 1) Spawning, overwintering survival and hatching success of embryos on the source shoals (Christie 1963; Lawler 1965; Taylor et al. 1987);
- 2) Water transport of free embryos/larvae into, around and out of the embayment (Frederick 1982; Hook et al. 2006; Claramunt et al. 2010);
- 3) Survival of larvae in the embayment associated with environmental conditions, food availability, predation, etc. (Taylor and Freeberg 1984; Loftus and Hulsman 1986; Hoyle et al. 2011).

As discussed in the Methods section above, the 2012 field program for this investigation was proceeding to focus on the role of surface water currents as a key uncertainty in larval transport, when it became obvious that the virtual absence of lake whitefish larvae in Stokes Bay would dominate the entire 2012 sampling season.

2012 Lake Whitefish Year-Class

Despite a 2012 sampling effort of 25 extended plankton tows distributed widely over Stokes Bay, lake whitefish larvae were virtually absent. Only $n=3$ larval lake whitefish were collected throughout the entire sampling period, in a single extended tow at the South Inner tow site (Figure 2). The sampling effort of 25 tows covered a large surface area of the embayment. The increase in tow duration in 2012 (from 5 to 30 minutes) resulted in a 2012 effort that was equivalent to 80 of the 5-minute tows used in 2011. There are several methodological and ecological hypotheses that could explain the lack of larvae sampled in Stokes Bay during 2012, and some of these hypotheses are explored in greater detail below.

From a methodological perspective, the perceived absence of lake whitefish larvae could have simply been an erroneous artifact of sampling error associated with spatio-temporal distribution of gear deployment. According to this explanation, the 2012 lake whitefish year-class would have been present in Stokes Bay, yet the extended tows were sampling at the wrong time, or at the wrong place, or with the wrong gear to capture the larvae. The probability that sampling error could have accounted for the absence of 2012 lake whitefish in Stokes Bay can be considered as low - for a variety of reasons. The sample gear (i.e. plankton net) was unchanged between the 2011 and 2012 field seasons. The 2012 tows were made at locations where 2011

tows had yielded larvae; the extended duration of tows should have at least detected the presence of, if not increased the likelihood of capturing larval lake whitefish at those locations. The 2011 sampling was deployed over roughly the same time period as in 2012, beginning on 21 and 25 April, respectively.

From an ecological perspective, the absence of lake whitefish larvae could have reflected a genuine year-class failure for lake whitefish larvae in Stokes Bay; a year-class failure that in turn could have been caused by one of more of the distinct categories of factors, as identified in the previous section: 1) Spawning, overwintering survival and hatching success of embryos on the source shoals; 2) Direction/velocity of water currents transporting free embryos/larvae into, around and out of the embayment; and 3) Survival of larvae in the embayment associated with environmental conditions, food availability, predation, etc. The remainder of this discussion will focus on the evidence associated with these ecological hypotheses that could account for the absence of lake whitefish larvae in Stokes Bay during the spring of 2012.

Absence of the 2012 lake whitefish year-class could have been caused by a failure of 2011 spawning and/or excessive mortality of overwintering embryos on shoals generating the larvae that were ultimately destined for Stokes Bay. It is possible that spawning/embryonic failure could have had very localized effects on larval recruitment to Stokes Bay only, with successful larval transport and survival in other nursery habitats within the population's range. While this investigation did not sample any of the other embayments along the western Saugeen Peninsula, it is difficult to imagine the proximate factors that could have had such a large yet confined effect on the source shoals for Stokes Bay, without having the same kind of effects on a regional scale. For these reasons, the probability that local failure could have accounted for the absence of the 2012 year-class is best described as low.

At a higher level, it is possible that a general population-level failure of spawning and/or embryonic incubation could explain the absence of the 2012 lake whitefish year-class in Stokes Bay. If this population-level failure did occur during the fall-winter of 2011/12, there are at least three factors that could have been involved: 1) body condition of spawning adults, 2) water temperature, and 3) ice formation and duration.

Concern regarding growth and body condition of adult lake whitefish in the Great Lakes has been expressed since the early 1990's, along with the decline of *Diporeia spp.* - an energy rich benthic invertebrate that has historically been a dominant component of adult lake whitefish diets (Nalepa et al. 2005). Fishery managers for Lake Ontario have reported some years with virtually no lake whitefish reproduction, as well as extended periods without the kind of occasional 'boom' year-classes considered typical for this species (Christie 1963; Clark 1984). Hoyle (2005) reported that a strong year-class of lake whitefish had not been produced since 1995, and that lake whitefish had experienced reproductive failures since 1998. In Lake Huron, similar occurrences of poor condition have also been reported and attributed to the loss of *Diporeia*; however, these observations were largely confined to the southern Main Basin, and the effects have not been nearly as severe as the effects seen in Lake Ontario (Mohr and Ebener 2005). Brown and Taylor (1992) found that lake whitefish larvae produced from eggs with higher levels of endogenous energy could survive longer before beginning to feed exogenously. However, Muir et al. (2010) evaluated new data for Great Lakes lake whitefish and concluded that parental effects (i.e., age, body size, body condition) were probably not as important as extrinsic site-related effects and/or density-dependent effects in determining physiological condition of juveniles. Although specific 2010/11 data are not available for body condition of adult lake whitefish spawning along the Saugeen Peninsula, the Saugeen Ojibway fishermen/

fisheries biologist did not observe any remarkable differences in the body size, girth or firmness of lake whitefish collected during the fall of those two years (R. Lauzon, Chippewas of Nawash Fisheries Assessment Program, pers.comm.). For these reasons, it is unlikely that changes in adult body condition accounted for the apparent 2012 year-class failure of lake whitefish in Stokes Bay.

The diverse effects of water temperature on spawning time, embryonic incubation and hatching success represents another complex of sub-factors that could explain the observed absence of larval lake whitefish at Stokes Bay in 2012. Christie (1963) reported that strong year-classes of Great Lakes lake whitefish often occurred after a cool fall and a warm spring. Casselman (2002) compiled water temperatures for lake whitefish spawning reported in the literature, and suggested that a water temperature of 5.7°C could be reasonably considered as a preferred condition. In this study, the NOAA temperature data for Stokes Bay indicate that water temperature first dropped below 6°C in 2010 on 02 December and in 2011 on 23 November (Figure 10). Similarly, water temperatures experienced by lake whitefish embryos overwintering on the shoals hovered around 0°C during both 2010/11 and 2011/12. Water temperatures were comparable between 2010/11 and 2011/12 for the fall spawning duration and into the overwintering period for embryonic lake whitefish.

It is important to note that water temperature increased much more rapidly in the spring of 2012, compared to 2011. By mid-March 2011, water temperature had increased to 2-3°C; by mid-March 2012, water temperature had already reached 9-11°C. Brooke (1975) reported laboratory incubation periods of 182, 152, 82 and 42 days for lake whitefish embryos incubated at a constant 0.5, 2.0, 5.9 and 10.0°C, respectively. Brooke (1975) also observed peak hatching success (70.9-73.3%) in the 4-7°C range, with substantial reductions in success rates at

temperatures below 4°C and above 7°C. Based on the available data, it is quite possible that elevated 2012 water temperatures reduced both embryonic incubation time and hatching success by a considerable amount. For those embryos that did hatch successfully, the elevated 2012 water temperatures could also have increased metabolic rates compared to 2011 - ultimately increasing the rate at which endogenous energy reserves would be used, and reducing the time to starvation before encountering exogenous food sources. It is important to recall the possibility of sampling error identified above; a situation in which 2012 sampling effort was deployed too late to detect the accelerated embryonic/larval schedule. While this could still be a factor, it seems highly unlikely that the 2012 schedule would have been accelerated by the 3-5 weeks required for larvae to get in, develop and emigrate from Stokes Bay before the first deployment of sampling gear on 25 April 2012.

Water temperature could also have had indirect effects on formation and duration of ice cover over the lake whitefish embryos incubating on source shoals (Christie 1963; Lawler 1965), and these effects could also explain the absence of larval lake whitefish at Stokes Bay in 2012. Freeberg et al. (1990) investigated the effects of ice conditions in Grand Traverse Bay, Lake Michigan on lake whitefish embryonic survival. The winter of 1982-1983 was unseasonably warm in the Great Lakes region, with temperatures high enough to completely prevent ice-formation in the bay. As a result, lake whitefish spawning grounds were exposed to elevated wind, wave and associated water currents throughout the winter. For 1982-83, Freeberg et al. (1990) reported that lake whitefish embryos exhibited relatively low survival rates (0.6%) across all sampled depth ranges. The winter of 1983-84 was much colder, with ice coverage over Grand Traverse Bay spawning shoals during most of the incubation period. For 1983-84, Freeberg et al. (1990) reported that the embryonic survival rate was much higher (5.6%) at all sampled depth

ranges during the ice-covered year, compared to the warmer open water year. These observations support the hypothesis that colder temperature and ice-formation serve to protect the embryos from physical disruption, relocation and associated mortality. Brown et al. (1993) investigated the effect of abiotic and biotic factors on population dynamics of lake whitefish in Lake Michigan, and found that ice cover, winter wind velocity and spring water temperature were statistically significant sources of annual variation in abundance and mortality rates.

Environment Canada ice-coverage data indicate that a) ice surface area for winter 2010/11 was consistently above annual norms, and b) the ice cleared from nearshore waters during the second week of April. This trend is consistent with observations made in this study during the 2011 field program at Stokes Bay. In stark contrast, the ice surface area for winter 2011/12 was the lowest recorded since winter 1972/73, with nearshore ice breakup was complete by early April - three weeks earlier than usual.

Taken together, there is substantial evidence to suspect that the various direct and indirect hypothesized effects of water temperature on lake whitefish embryonic/larval survival collectively played an important role in determining the fate of both the 2011 and 2012 year-classes of lake whitefish in Stokes Bay. By themselves, the diverse effects of water temperature on spawning time, embryonic incubation and hatching success could explain much of an apparent 2012 recruitment failure for larval lake whitefish at Stokes Bay. When evidence regarding the indirect effects via ice conditions is also considered, water temperature emerges as a major determinant in lake whitefish larval ecology.

Even if lake whitefish fall spawning and/or overwintering embryonic incubation were all normal during 2011/12, absence of the 2012 lake whitefish year-class in Stokes Bay could also be explained by variability in water currents that the free embryos/larvae depend on for transport

and retention in the nursery embayment. Wind-induced surface currents could play a major role in moving planktonic lake whitefish (embryos/larvae) from spawning shoals to nearshore embayments, as well as influencing the type and productivity of nursery habitat into which the embryos/larvae are transported (Frederick 1982; Hook et al. 2006; Claramunt et al. 2010). Hook et al. (2006) studied the effects of water currents on transport of larval yellow perch in Lake Michigan. Through collection of both lab and field data Hook et al. (2006) found that typically, current velocities were much stronger than potential larval swimming speeds, suggesting the important role of water currents in transporting planktonic embryos/larvae from spawning to nursery areas. Frederick (1982) investigated the effect of water currents on transport of larval lake whitefish from spawning shoals into embayment nursery areas by deploying 500 apples as larval proxies under different wind conditions. The distribution and abundance of proxies in the embayment was highly variable across the wind directions, however Frederick (1982) did report spatial clustering - suggesting that cyclic properties of the water currents could serve to retain some larvae in the nursery habitat over a longer time period. Unfortunately, our knowledge of Stokes Bay hydrodynamics is sparse. Several factors can exert dramatic effects on water flow in Saugeen Peninsula Bays and on Stokes Bay specifically, including: longshore currents (J.Jones Sr., Chippewas of Nawash First Nation, pers. comm.), thermal bars and seiches (D.Loftus, Ontario Ministry of Natural Resources Biologist (Retired), pers. comm.). However, at this point it is not possible to even qualitatively evaluate the probability that water currents could account for the observed absence of larval lake whitefish at Stokes Bay in 2012.

Finally, the observed absence of larval lake whitefish at Stokes Bay in 2012 could have been caused by a failure associated with larval food availability, competition and/or predation. Freeberg et al. (1990) found that larval lake whitefish growth was markedly altered by changes

in zooplankton density, and that body growth was an effective indicator of the energy available to larvae in their immediate environment, especially during the transition between endogenous and exogenous feeding. Brown and Taylor (1992) found that quantity and quality of planktonic prey, especially copepods, significantly affected the survival of larval lake whitefish. Few larval fishes have spatio-temporal overlap with lake whitefish larvae and their need for zooplanktonic prey in the nursery habitat. Lake herring (*Coregonus artedii*) are one of the few species that are consistently found as larvae in the same waters as lake whitefish larvae. However, Todd and Davis (1998) concluded on the basis of laboratory experiments that larval lake whitefish hold a significant competitive feeding advantage over lake herring. Loftus and Hulsman (1986) investigated predation on larval lake whitefish by rainbow smelt (*Osmerus mordax*) in Twelve Mile Lake, Ontario. They found that larval lake whitefish suffered intense predation by adult rainbow smelt, and that predation could have been an important factor in historical recruitment failure experienced by this lake whitefish population. Loftus and Hulsman (1986) hypothesized that predation of larval lake whitefish would be less intense in large water bodies such as the Great Lakes because the larvae would be distributed over a larger area and less susceptible to searching predators. However, Frederick (1982) suggested that larval lake whitefish 'clustering' increases predation vulnerability. Once again, without additional information regarding ecological dynamics in the study region, it is not possible to evaluate the probability that larval mortality could account for the observed absence of larval lake whitefish at Stokes Bay in 2012.

There is substantial uncertainty about the ultimate consequences of a year-class failure in a Great Lakes population of lake whitefish. Numerous biologists have claimed that 'boom-and-bust' episodes are characteristic of this species, its life history and ecology (Davidoff et al. 1973, Loftus 1980, Clark 1984). Others have suggested that these extreme episodes are exaggerated in

response to human-caused stressors on lake whitefish population dynamics (Lawler 1965, Ebener 1997, Mohr and Ebener 2005). Either way, it would be fair to say that responsible fisheries managers should be strongly motivated to address this key ecological uncertainty, using the eastern Lake Huron population(s) of lake whitefish as a most suitable ongoing case study.

General Conclusions

The goal of this thesis was to investigate the distribution and abundance of larval lake whitefish in a Great Lakes embayment, using Stokes Bay, Lake Huron as a case study. The initial field investigations during 2011 documented relatively high densities of larval lake whitefish, possibly the highest yet recorded in the Great Lakes. These observations strongly support the hypothesized importance of Stokes Bay as a nursery area for lake whitefish along the western shore of the Saugeen Peninsula (Loftus 1978b; 1980). The follow-up field investigations during 2012 revealed a surprising and dramatic absence of larval lake whitefish from Stokes Bay. Taken together, these observations highlight the complexity and inter-relatedness of ecological factors that could account for such a perceived absence of an entire year-class.

Obviously, there are several key uncertainties that have been raised by this study. Were the embryonic/larval schedules simply advanced in 2012 to the point where sampling effort missed them? Did the elevated temperatures of winter 2011/12 trigger mortality effects that combined cumulatively to wipe out the entire 2012 year-class of lake whitefish in Stokes Bay and possibly the eastern Main Basin of Lake Huron? If so, was this recruitment failure simply part of a typical ‘boom-and-bust’ lake whitefish population dynamic that has enabled this species to survive in oligotrophic ecosystems for millennia? Or was this the first of a series of major recruitment failures in the face of a rapidly warming world; a series that leads ultimately to the

local extinction of Great Lakes lake whitefish at the most southerly margin of their species' distribution. We would be well advised to keep a close eye on the Stokes Bay ecosystem over the next few decades in order to answer some of these important questions that emerged from this investigation.

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Figure 1. Map of the study area Stokes Bay, Lake Huron (Ontario) (N 44 59 51.14, W 81 22 30.23) with grid cells used for the random selection of 2011 larval lake whitefish (*Coregonus clupeaformis*) sampling locations. Triangles indicate grid cells in which k=71 surface plankton tows were conducted.

Figure 2. Map of Stokes Bay, Lake Huron (Ontario) with larval lake whitefish (*Coregonus clupeaformis*) sampling locations for 2012. Solid lines indicate location of extended regional plankton tows (South Inner/Outer: SI, SO and North Inner/Outer: NI, NO) filled triangles indicate locations of 2011 reference plankton tows (L=low, M=moderate, H=high).

Figure 3. Water depths (m) at 2011 Stokes Bay, Lake Huron sampling locations (21 April-03 June 2011). Depth categories are based on the 20th, 40th, 60th, 80th and 100th percentiles of the 2011 data (k=71).

Figure 4. Temperature ($^{\circ}\text{C}$) at Stokes Bay, Lake Huron sampling locations by week (1-6) (21 April-03 June 2011). Temperature categories are based on the 20th, 40th, 60th, 80th and 100th percentiles of the 2011 data (k=71).

Figure 5. Dissolved oxygen concentrations ($\text{mg}\cdot\text{L}^{-1}$) at Stokes Bay, Lake Huron sampling locations by week (1-6) (21 April-03 June 2011). Dissolved oxygen concentration categories are based on the 20th, 40th, 60th, 80th and 100th percentiles of the 2011 data ($k=71$).

Figure 6. Specific conductance (mS·cm⁻¹) at Stokes Bay, Lake Huron sampling locations by week (1-6) (21 April-03 June 2011). Specific conductance categories are based on the 20th, 40th, 60th, 80th and 100th percentiles of the 2011 data (k=71).

a.

b.

c.

Figure 7. Images of example lake whitefish (*Coregonus clupeaformis*) larva (a-dorsal, b-lateral, c-ventral) collected on 05 May 2011 (week 2) in Stokes Bay, Lake Huron on the south side of Stokes Bay proper; total length =16.53mm.

Figure 8. Boxplot of 2011 lake whitefish (*Coregonus clupeaformis*) larval density (No•1000m⁻³) from weekly plankton tows performed at Stokes Bay, Lake Huron (21 April-03 June). Boxes depict 1st and 3rd quartiles, thick line indicates median, and open circles indicate potential outliers.

Figure 9. Densities ($\text{No} \cdot 1000\text{m}^{-3}$) of larval lake whitefish (*Coregonus clupeaformis*) by week (1-6) from plankton tows performed at Stokes Bay, Lake Huron (21 April-03 June). Density categories are based on the 20th, 40th, 60th, 80th and 100th percentiles of the 2011 data ($k=71$).

Figure 10. Surface water temperatures (°C) estimates for Stokes Bay, Lake Huron during the periods of 1 October to 30 June 2010-2011 and 2011-2012. Data obtained from NOAA Great Lakes Coastal Forecasting System. Source: <http://glos.us/data-tools/point-query-tool-glcfc>, accessed on 24 July 2012.

Table 1. Moran's I index of spatial autocorrelation for 2011 lake whitefish (*Coregonus clupeaformis*) larval density and environmental variables recorded in Stokes Bay, Lake Huron (21 April-03 June, n=71). Asterisk indicates statistical significance at p=0.05.

Parameter	Moran's I	p-value
Dissolved Oxygen (mg•L ⁻¹)	0.029	0.260
Specific Conductance (mS•cm ⁻¹)	0.265	<0.001*
Water temperature (°C)	0.059	0.144
Depth (m)	0.069	0.115
Larval Density (No•1000m ⁻³)	0.032	0.222

Table 2. Weekly summary of 2011 sampling effort and lake whitefish (*Coregonus clupeaformis*) larval density from plankton tows in Stokes Bay, Lake Huron (21 April-03 June, k=71).

Period	Lake Whitefish Larval Density (No•1,000m⁻³)				
	# Tows	Min	Mean	Max	SD
Week 1 (21 Apr-27 Apr)	3	64	220.5	321	110.0
Week 2 (28 Apr-04 May)	13	14	270.7	2026	637.9
Week 3 (05 May-11 May)	17	21	249.5	1168	356.5
Week 4 (12 May-18 May)	17	6	232.3	892	221.0
Week 5 (19 May-25 May)	16	0	37.8	83	26.3
Week 6 (26 May-03 Jun)	5	0	12.0	18	7.9

Table 3. Results of univariate linear regression analyses to test relationships between environmental variables and log larval lake whitefish (*Coregonus clupeaformis*) density at Stokes Bay, Lake Huron (21 April-03 June, k=71). The number in parentheses under slope and y-intercept headings is the associated standard error for parameter estimates. Asterisk indicates statistical significance at p=0.05.

Variable	slope	y-intercept	p-value	r² (adjusted)
Week (1-6)			<0.001*	0.584
1 (baseline)		5.055 (1.405)	<0.001*	
2		0.731(1.559)	0.640	
3		0.636(1.524)	0.678	
4		0.318(1.524)	0.835	
5		-5.554(1.531)	<0.001*	
6		-6.889(1.777)	<0.001*	
Water Depth (m)	-0.385(0.163)	5.617(0.927)	0.021*	0.061
Water Temperature (°C)	-0.727(0.187)	11.609(2.084)	<0.001*	0.167
Dissolved Oxygen (%)	0.181(0.047)	-16.142(5.248)	0.015*	0.160
Dissolved Oxygen (mg•l ⁻¹)	1.678(0.317)	-16.731(3.875)	<0.001*	0.278
Specific Conductance (mS•cm ⁻¹)	38.651(15.585)	-5.144(3.584)	0.015*	0.068

Table 4. Summary of 2012 sampling effort and lake whitefish (*Coregonus clupeaformis*) larval frequency from plankton tows at reference sites and reference sites in Stokes Bay, Lake Huron (25 April-23 May, k=25).

Sample date	Transect/Site	Frequency of larvae
25 April 2012	Reference L	0
	Reference M	0
	Reference H	0
01 May 2012	Reference L	0
	Reference M	0
	Reference H	0
	South Inner	0
	North Inner	0
13 May 2012	North Inner	0
	South Inner	0
	North Outer	0
	South Outer	0
18 May 2012	Reference L	0
	Reference M	0
	Reference H	0
	North Inner	0
	South Inner	3
	South Outer	0
23 May 2012	Reference L	0
	Reference M	0
	Reference H	0
	North Inner	0
	South Inner	0
	North Outer	0
	South Outer	0

Table 5. Mean weekly density (No•1000m⁻³) of larval lake whitefish (*Coregonus clupeaformis*) at Stokes Bay, Lake Huron in 2011 compared to 1978 (study performed by Loftus 1978b). Time period (1-6) represent weeks of sampling (Loftus 1978b: April 23-June 3, Ryan 2011: April 21-June 3)

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	Mean Weekly Larval Lake Whitefish Density (No•1000m⁻³) at Stokes Bay, Lake Huron	
Time Period (Week)	Loftus 1978	2011
1	25	220
2	48	271
3	128	249
4	7	232
5	0	38
6	0	12