## EARLY LIFE HISTORY DYNAMICS AND RECRUITMENT PROCESSES OF RAINBOW SMELT IN LAKE HURON

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#### ABSTRACT

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Rainbow smelt are an important prey species for native and introduced salmonines in the Great Lakes, as well as being a competitor and predator of native fish species. In Lake Huron, rainbow smelt populations have been characterized by variable recruitment and year class strength. To understand growth and survival dynamics during early life history, larval rainbow smelt populations were sampled during 2008 and 2009 in St. Martin Bay, Lake Huron. Growth rates of larval rainbow smelt and relative survival of stream cohorts was higher during 2009 than in 2008, a consequence of warmer water temperatures during June and cooler, more optimal temperatures during July. Early hatching stream cohorts experienced high mortality during 2008 and fish surviving experienced lower growth relative to cohorts during 2009. To investigate long term recruitment dynamics for these populations, Ricker stock-recruit models were developed for Lake Huron rainbow smelt sampled from 1976-2009. Ricker models were developed with the inclusion of four external variables that have been reported to affect rainbow smelt production: precipitation, water temperature, water levels, and lake trout abundance as measured by catch per unit effort (CPE). The best model describing rainbow smelt recruitment during 1976-2009 included lake trout CPE, Lake Huron water levels, and over basin precipitation. A separate model for the 1994-2009 time period identified lake trout CPE as an important regulator of rainbow smelt recruitment. These findings indicate that variability in growth and survival of rainbow smelt during early life history stages influences year class formation, but recruitment is strongly regulated by lake trout predation on adults or age-0 recruits.

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iv

LIST OF TABLES	vi
LIST OF FIGURES	vii
THESIS INTRODUCTION	1
CHAPTER 1	
ABUNDANCE, GROWTH, AND SURVIVAL OF LARVAL RAINBOW SMELT IN ST.	
MARTIN BAY, LAKE HURON	7
Introduction	7
Methods	9
Study area	9
Stream surveys	11
Ichthyoplankton surveys	12
Length frequency analysis of larval cohorts	13
Larval growth	14
Larval mortality	15
Results	16
Stream surveys	16
Ichthyoplankton surveys	19
Length frequency analysis of larval cohorts	22
Larval growth	27
Larval mortality	27
Discussion	31
CHAPTER 2	
EFFECTS OF STOCK SIZE, CLIMATE, AND PREDATION ON RAINBOW SMELT	
RECRUITMENT IN WESTERN LAKE HURON, 1976-2009	
Introduction	
Methods	42
Bottom trawl collections	42
Stock-recruit models	45
Integrated stock-recruit models	48
Model selection	49
Results	50
Stock-recruit models	53
Effects of stock size, climate, and predation	58
Discussion	62
REFERENCES	69

# **TABLE OF CONTENTS**

# LIST OF TABLES

Table 1. Parameter estimates for finite mixture distribution models fit to larval rainbow smelt length frequency distributions during 2009; $\pi$ = mixing proportions, $\mu$ = mean cohort length, $\sigma$ = standard error. Cohort 1 corresponds to the stream spawned larvae, cohort 2 corresponds to lake spawned larvae. Model degrees of freedom ( <i>Df</i> ) and Chi-square goodness-of-fit statistic ( <i>X</i> ^2) are presented for each model. All models were significant at $\alpha$ = 0.05. Modeled length distributions for 18-June and 8-Jul identified a third mode which was not included in this analysis due to low (i.e., < 10 larvae) sample sizes. Thus, mixing proportions for those sample dates do not add to 1
Table 2. Year specific YOY length cutoffs (mm) for rainbow smelt in Lake Huron, 1976-2009.Cutoffs were determined from length frequency analysis and applied to fishing power correctionsas determined by Adams et al. (2009)
Table 3. Original parameter estimates, approximate standard error, and 95% confidenceintervals for stock-recruit models of rainbow smelt recruitment (1976-2009, 1976-1991, and1994-2009)
Table 4. Mean, variance, and 95% confidence intervals of bootstrap parameter estimates for stock-recruit models of rainbow smelt recruitment (1976-2009, 1976-1991, and 1994-2009).Statistics are based on 1000 bootstrap samples
Table 5. Model selection results for rainbow smelt recruitment in Lake Huron, 1976-2009, based on Akaike weights $w_i$ and ranked top (best model) to bottom (least plausible model). Also shown are sums of squared errorr, AICc, $\Delta i$ (AICc differences), e <sup>(-1/2*\Delta i)</sup> (model likelihoods), and evidence ratios. All model combinations are shown with Ricker parameters ( $\alpha$ , $\beta$ ) and explanatory variables; LT = lake trout CPE, P = overbasin precipitation, W = Lake Huron-Michigan water levels, and T = mean lake temperature 0-20 meters
Table 6. Model selection results for rainbow smelt recruitment in Lake Huron, 1976-1991, based on Akaike weights $w_i$ and ranked top (best model) to bottom (least plausible model). Also shown are sum of squared errorr, AICc, $\Delta i$ (AICc differences), e <sup>(-1/2*\Delta i)</sup> (model likelihoods), and evidence ratios. All model combinations are shown with Ricker parameters ( $\alpha$ , $\beta$ ) and explanatory variables; LT = lake trout CPE, P = overbasin precipitation, W = Lake Huron-Michigan water levels, and T = mean lake temperature 0-20 meters
Table 7. Model selection results for rainbow smelt recruitment in Lake Huron, 1994-2009, based on Akaike weights $w_i$ and ranked top (best model) to bottom (least plausible model). Also shown are sum of squared errorr, AICc, $\Delta i$ (AICc differences), e <sup>(-1/2*\Delta i)</sup> (model likelihoods), and evidence ratios. All model combinations are shown with Ricker parameters ( $\alpha$ , $\beta$ ) and explanatory variables; LT = lake trout CPE, P = overbasin precipitation, W = Lake Huron-Michigan water levels, and T = mean lake temperature 0-20 meters

# LIST OF FIGURES

Figure 12. General linear model regressions (log (e) length (mm) v. estimated age) comparing growth of early stream spawned (circle) and late lake spawned (triangle) larval rainbow smelt cohorts during 2009 in St. Martin Bay, Lake Huron
Figure 13. Larval rainbow smelt catch curves (log (e) density v. estimated age) comparing instantaneous mortality rate of larval rainbow smelt during 2008 (triangle) and 2009 (circle), in St. Martin Bay, Lake Huron
Figure 14. Bottom trawl sampling locations in the main basin of Lake Huron, 1976-200944
Figure 15. Stock-recruit relationships for Lake Huron rainbow smelt modeled by the Ricker function for the years 1976-2009 (top panel), 1976-1991 (middle panel), and 1994-2009 (lower panel)
Figure 16. Frequency distributions of bootstrapped parameter estimates (log $\alpha$ , $\beta$ ) for the Ricker stock-recruit model for the 1976-2009 time series. Approximate location of "true" parameter estimates are indicated by arrows
Figure 17. Frequency distributions of bootstrapped parameter estimates (log $\alpha$ , $\beta$ ) for the Ricker stock-recruit model for the 1976-1991 time series. Approximate location of "true" parameter estimates are indicated by arrows
Figure 18. Frequency distributions of bootstrapped parameter estimates (log $\alpha$ , $\beta$ ) for the Ricker stock-recruit model for the 1994-2009 time series. Approximate location of "true" parameter estimates are indicated by arrows

#### THESIS INTRODUCTION

The rainbow smelt *Osmerus mordax* is indigenous to the Atlantic coastal drainage from Labrador to New Jersey, but has been widely introduced in North America (Scott and Crossman 1973). Rainbow smelt occur as a migratory marine species, but freshwater demes are indigenous to eastern North America where they inhabit lake systems in Maine, New Hampshire, and eastern and maritime provinces of Canada (Scott and Crossman 1973). Introduced as a prey species, rainbow smelt have become established in numerous North American lakes outside their native range, including the Laurentian Great Lakes and surrounding watersheds (Van Oosten 1937; Dymond 1944; Evans and Loftus 1987; Franzin et al. 1994).

In the Great Lakes region, rainbow smelt became established following a large planting of eggs in Crystal Lake, Michigan in 1912 (Van Oosten 1937). Rainbow smelt populations that developed in lakes Michigan, Huron, Superior, and Erie during 1918-1940 are believed to have been a result of this single planting (Creaser 1926; Van Oosten 1937). In the Great Lakes, rainbow smelt were introduced as a prey species for native and stocked salmonines and their populations built up quickly, especially in lakes Michigan and Huron where the species became abundant by the late 1920s (Van Oosten 1937). Following their establishment in the Great Lakes, rainbow smelt became so abundant that commercial fisheries targeted the species for human consumption (Schneberger 1937), first in lakes Michigan and Huron by the early 1930s, and in lakes Erie, Superior, and Ontario by the early 1950s (Baldwin and Saalfeld 1962; Christie 1974; Baldwin et al. 2009; Figure 1). Commercial fishery yield of rainbow smelt continued to increase through the 1980s, but since the late 1990s harvest has been greatly reduced across the Great Lakes due to dramatic declines in abundance (Figure 1). Today, small scale commercial

fisheries for rainbow smelt operate in Canadian waters of lakes Erie and Huron, and in the Minnesota waters of Lake Superior (Baldwin et al. 2009).



Figure 1. Commercial harvest (1000s of pounds) of rainbow smelt for all five Great Lakes during 1931-2006, adapted from Baldwin et al. 2009.

As a naturalized exotic species, rainbow smelt have integrated into the pelagic food webs of the Great Lakes as both a prey species and predator. Accordingly, rainbow smelt are found in the diets of sundry salmonine predators in lakes Huron (Kocik and Taylor 1987; Diana 1990; Madenjian et al. 2006), Michigan (Stewart et al. 1981; Madenjian et al. 1998), Superior (Dryer et al. 1965; Conner et al. 1993; Ray et al. 2007), Erie (Henderson and Nepszy 1989), and Ontario (Brandt 1986). As a predator, rainbow smelt have been related to negative ecological interactions with other fish species as they consume the larvae of native fish or compete for zooplankton food resources, both of which inhibit young of the year recruitment in some species (Selgeby et al. 1978; Loftus and Hulsman 1986; Evans and Loftus 1987; Hrabik et al. 1998; Mercado-Silva et al. 2007; Myers et al. 2009). In Lake Huron, rainbow smelt are particularly important as a food source for salmonines and percids as they have been the dominant prey species following the collapse of alewife populations after 2004 (Riley et al. 2008).

Characteristic of small, pelagic fishes, rainbow smelt populations are typified by stochastic recruitment processes that result in variable year class formation (Nellbring 1989). Recruitment variability and population declines of rainbow smelt in the Great Lakes have been related to a combination of abiotic and biotic factors influencing growth and survival of young-of- the-year (YOY). Sources of direct mortality such as predation (He and LaBar 1994; Gorman 2007) and cannibalism (Henderson and Nepszy 1989; Lantry and Stewart 2000; Parker Stetter et al. 2007) have been shown to be important in structuring mean size and abundance of rainbow smelt populations. Alternatively, Hoff (2004) and Gorman (2007) found that when other prey species are available to lake trout (*Salvelinus namaycush*) and other large predators, rainbow smelt recruitment is positively affected through reduced predation. Mortality and growth during the egg or larval stage has also been demonstrated to impact overall year-class strength of

rainbow smelt. Factors reported to influence early life history stages include spring climate variables such as precipitation, mean air temperature, and solar intensity (Sluka 1991; Hoff 2004) all of which can modify the suitability of stream or nearshore habitats for egg or larval stages of rainbow smelt. For example, McKenzie (1964) found a significant negative association between larval production and rainfall occurring after spawning, likely due to displacement or stranding of eggs relating to stream flashiness.

In Lake Huron, rainbow smelt abundance has been monitored annually since 1973 by the U.S. Geological Survey (USGS) Great Lakes Science Center (GLSC), through an annual bottom trawl survey that effectively targets all prey species (Riley et al. 2010). Between 1976 and 1991, yearling and older (YAO) rainbow smelt were relatively abundant in this survey, but abundance of YOY rainbow smelt was generally lower than during 1994-2009 (Figure 2). However, from 1994 to 2009, YAO rainbow smelt abundance has been declining steadily, while abundance of YOY has oscillated dramatically with several large year classes forming during this period (Figure 2). Current abundance estimates of YAO rainbow smelt in Lake Huron are approximately 40% lower than during 1976-1994, a period of relatively high abundance (Riley et al. 2008; Figure 2). This steady recent decline of rainbow smelt over the past decade in this lake has been a concern for fishery managers tasked with matching stocking numbers of predators with available prey biomass.



Figure 2. Density (No /ha., solid line, closed circle) and relative standard error (dotted line, open triangle) of YOY (top panel) and YAO (lower panel) rainbow smelt estimated from USGS bottom trawl surveys, 1976-2009, adapted from Riley et al. (2010).

The goal of this thesis was to evaluate the influence of selected abiotic and biotic factors on the growth, survival and recruitment dynamics of rainbow smelt in Lake Huron. This thesis is based on 2 years of field research in St. Martin Bay, northern Lake Huron (Chapter 1) combined with stock-recruit analysis of a thirty year time series of rainbow smelt abundance (chapter 2). The specific objective of research presented in Chapter 1 was to determine patterns in abundance, growth, and survival of larval rainbow smelt populations in St. Martin Bay, Lake Huron during 2008-2009, while the focus of Chapter 2 was on stock-recruit modeling using data from 1976-2009. This latter chapter further evaluated the role of water temperature, water levels, precipitation, and lake trout CPE in causing the noted variation in recruitment during this time period.

The research presented in this thesis increases our understanding of prey fish dynamics in Lake Huron by adding to our knowledge of environmental and biological factors influencing recruitment processes of rainbow smelt. For example, knowledge of rainbow smelt recruitment in relation to lake trout abundance emphasizes to fishery managers the important link between rainbow smelt as a prey resource and the restoration of lake trout populations in the Great Lakes. Factors such as precipitation and water temperature that are projected to increase in the Great Lakes basin given current climate change scenarios (Loftgren 2002) are important to consider in relation to future fish recruitment and restoration efforts. For example, increasing water temperatures in the Great Lakes are expected to have significant impacts on growth rates of fish populations with rainbow smelt and other coldwater species expected to have reductions in recruitment (Casselman 2002), further reducing the availability of this key prey species to our valuable salmonine and percid communities.

#### **CHAPTER ONE**

### ABUNDANCE, GROWTH, AND SURVIVAL OF LARVAL RAINBOW SMELT IN ST. MARTIN BAY, LAKE HURON, 2008-2009

#### Introduction

Rainbow smelt (*Osmerus mordax*) are indigenous to northeastern North America where they originally inhabited the Atlantic drainage from Labrador to coastal New Jersey (Scott and Crossman 1973). Rainbow smelt occur as a migratory marine species, and are also native to inland lake systems in Maine, New Hampshire, and the eastern and maritime provinces of Canada (Scott and Crossman 1973). Beyond their native range, rainbow smelt have been introduced widely as a prey species in North America, primarily in freshwater systems including the Laurentian Great Lakes and surrounding watersheds (Van Oosten 1937; Dymond 1944; Evans and Loftus 1987; Franzin et al. 1994).

The reproductive cycle of rainbow smelt is initiated during April, usually during the winter-spring transition period. Rainbow smelt spawn typically near ice out or when water temperatures reach 3-4 C (Creaser 1926; Rupp 1959). Adult rainbow smelt migrate into streams, typically at night, where females deposit eggs over a variety of substrates including sand, gravel, and sparse vegetation (McKenzie 1964). Smelt eggs sink rapidly and adhere readily to substrates where they are in turn fertilized by males (Rupp 1965). Incubation times vary according to water temperature and range from 32 days at 5 C to 9 days at 20 C (Cooper 1978; Ayer et al. 2005). After hatching, larvae are carried by currents into receiving waters where they transition to exogenous feeding and begin a pelagic larval phase as yolk reserves are expended.

Researchers previously studying larval rainbow smelt have recognized that many populations consist of early hatching cohorts originating from streams and late hatching cohorts that come from lake spawning sources. An intensive three year study conducted in St. Martin Bay, Lake Huron by Brown (1994) determined that larval contributions from lake spawning were moderate and less variable than larvae originating in streams. Further, the abundance of stream spawned larval populations was highly variable among years and as a result drove the variability in rainbow smelt year class formation in St. Martin Bay (Brown 1994). In eastern Lake Michigan, Tin and Jude (1983) found high densities of larvae in shallow water during May, and noted the presence of late June and July hatching cohorts originating in deeper, colder waters of the lake where incubation occurred more slowly. While the timing and location of lake spawning is not well understood, this reproductive strategy appears to be common among rainbow smelt populations (Rupp 1965; MacCallum and Regier 1970; Owens 1982), and the source of larval cohorts hatching during late June and July. Both stream and lake sources of larvae contribute to year class strength and form the basis of rainbow smelt populations in northern Lake Huron.

Rainbow smelt are both a pelagic prey species and predator across the Great Lakes and populations are characterized by highly variable recruitment and more recently, declining abundance across the region (Bronte et al. 2003; Mills et al. 2005; Bunnell et al. 2006; Riley et al. 2008). Reductions in the biomass of larger (>100 mm TL) rainbow smelt have been attributed to high levels of predation by salmonines (Bronte et al. 2003; Mills et al. 2003; Mills et al. 2005; Gorman 2007), leaving many stocks to rely on consistently strong year classes to sustain the population. Recruitment variation however and specifically, factors such as temperature that influence growth and survival during larval stages are not well understood.

The goal of this research was to evaluate the growth and survival dynamics of larval rainbow smelt in northern Lake Huron and to relate these findings to recruitment variability for this species in the Great Lakes. A model system to conduct this research, based on the work of Brown (1994), was St. Martin Bay, Lake Huron. The specific research objectives for this study were to (1) determine the influence of tributary water temperatures on the duration of rainbow smelt spawning during April and subsequent larval production during May, and (2) determine the abundances, growth rates, and mortality rates of larval rainbow smelt cohorts in St. Martin Bay, Lake Huron during May-July, 2008-2009. For objective (1) it was hypothesized that a longer spawning period would result in higher densities of larvae originating from streams in May.

#### Methods

### **Study Area**

St. Martin Bay is a large embayment in northwestern Lake Huron and borders the south shore of Michigan's eastern Upper Peninsula (Figure 3). The bay averages 8 m in depth and has a maximum depth of approximately 30 m. At its widest points, St. Martin Bay is approximately 12 km east to west, and 8.5 km north to south. Approximately 16 km of sand, boulder and cobble covered shoreline border the bay, most of which is undeveloped. St. Martin Bay is characteristically mesotrophic (Brown et al. 1995) with emergent vegetation in productive littoral areas near tributary mouths and clear waters offshore. Outside the littoral zone (>1 m) are typically sand or silt substrates with isolated aquatic macrophyte zones. St. Martin Bay is fed by three larger (3rd and 4th order) and four smaller (1st and 2nd order) tributaries that were historic spawning areas for migratory rainbow smelt (Goodyear et al. 1982). St. Martin Bay and the Les

Chenaux Islands area provide excellent nursery habitat for developing rainbow smelt larvae (Goodyear et al. 1982), which made this area ideal to investigate growth and survival dynamics.



Figure 3. St. Martin Bay, Lake Huron showing ichthyoplankton sampling transects (solid black lines) and spawning streams surveyed (Carp River, Nunns Creek, Spring Creek, and St. Martin Creek) during 2008-09.

#### Stream surveys

Rainbow smelt spawning occurs from mid-April to early May in the upper Great Lakes (Scott and Crossman 1973) and is initiated by a spring freshet and increasing water temperatures. To determine the influence of water temperature on spawning duration, streams were monitored for temperatures between early April and late June during both years of the study to estimate length of the spawning run and characterize warming patterns in spawning streams. The four streams studied in this bay had been identified as spawning habitats in St. Martin Bay (Goodyear et al. 1982; Brown 1994) including the Carp River, Nunns Creek, Spring Creek, and St. Martin Creek (Figure 3). In all four study streams HOBO Water Temp pro v2 temperature loggers (Onset Computer Corporation) were placed upstream from known spawning habitats in the lower reaches of rivers and streams, where rainbow smelt typically spawn (Bailey 1964). Data loggers collected water temperatures (degrees C) at 15 minute intervals before and during spawning and throughout the larval outmigration period.

Rainbow smelt spawning in study tributaries was evaluated by conducting stream dip-net surveys during April of 2008 and 2009. Spawning rainbow smelt were sampled in all four study streams that were monitored with temperature loggers. Each stream was sampled twice nightly for spawning rainbow smelt (between 2200-0100 hrs and 0100-0400 hrs). Rainbow smelt were sampled with wire mesh dip-nets (10 mm mesh) in spawning locations in each stream that were verified by visual observation. Each site was sampled for approximately 45 minutes, or until 100 fish were collected. Dip-net surveys were important for verifying that fish were spawning in area streams, and when combined with temperature data allowed for estimation of the length of the spawning run.

#### Ichthyoplankton surveys

To sample St. Martin Bay for larval rainbow smelt, fixed site icthyolplankton surveys were conducted between May and August during 2008-2009, using a study design similar to Brown (1994). All larval fish sampling was conducted in the surface waters (0.5-1 m) of St. Martin Bay. From May through early July 2008, larval rainbow smelt were sampled with 0.5 m diameter, 500 micron conical plankton net with a metal frame, modified from a design by Nester (1987), with a 22 kg brass depressor suspended below the frame. Flow meters were attached to all larval fish gear to determine volume of water filtered. In order to increase sample sizes of larval fish, rainbow smelt were sampled with a 1x2x4 m neuston net with 500 micron mesh for the remainder of the 2008 sampling season and all of 2009. This mesh size has been shown to be effective at catching larval rainbow smelt (O'Gorman 1984), and has been used in previous rainbow smelt research in St. Martin Bay (Brown 1994). To adequately sample depth strata and surface area within St. Martin Bay, 12 larval transects were selected over 2.5, 5, and 10 m contours and distributed around the bay to representatively sample available nearshore and offshore habitats (Figure 3). All ichthyoplankton sampling occurred at night (McKenzie 1964); sampling typically occurred between 2200-0300 hrs. Tows were conducted for 5 minutes at a speed of approximately 4 km/hr. Transects were sampled weekly during May and June, and bimonthly during July and August in both years. Survey dates were from 12 May – 19 August during 2008 and 21 May – 24 August during 2009. In 2008, 136 larval fish samples were collected while 105 samples were collected during 2009. Water temperatures were recorded at the start of all larval fish tows.

Once collected, all larval fish samples were rinsed into 1 liter bottles and stored in 90% EtOH until analyzed. In the laboratory, all larval fish were identified to species (Auer 1982) and

enumerated. Catches of larval rainbow smelt were converted to density and expressed as numbers per 1000 m<sup>3</sup> of water. Rainbow smelt larvae were measured to the nearest 0.1 mm through a stereoscopic microscope interfaced with a digital image analysis system.

#### Length frequency analysis of larval cohorts

Length frequency analysis was used to determine if early and late spawned cohorts were present in the population (i.e., more than one mode or age class) and to determine mean length of surviving larval cohorts for the computation of mean population growth rates (Ricker 1975). For each year, composite length frequency plots were created by grouping all larvae caught by month. Length frequency distributions showing distinct modal separation indicate multiple age groups are present in the population being sampled (Macdonald 1987). If multiple modes were present in composite distributions, length frequency distributions were computed by sampling date. When clear separation of length groups was still evident during individual sampling events, mixed probability density functions (mixture models) were fit to each distribution to identify changes in mean length of each group through time (Ricker 1975). The mixed probability during in the general form is a weighted sum of k component probability density function in the general form is a weighted sum of k component probability densities:

$$g(x|\boldsymbol{\pi},\boldsymbol{\mu},\boldsymbol{\sigma}) = \pi_1 f(x|\mu_1,\sigma_1) + \dots + \pi_k f(x|\mu_k,\sigma_k)$$

Where  $\mu$  corresponds to the means of component length distributions,  $\sigma$  is standard deviations of component distributions, and  $\pi$  is the corresponding mixing proportions of components (Everitt and Hand 1981). To fit mixture models to observed frequency distributions, R statistical programming software (R Development Core Team 2009) was used with the Mixdist package

for fitting finite mixture distribution models (Peter Macdonald with contributions from Juan Du 2008). All length frequency distributions were developed using 1 mm bins. The R package Mixdist fits finite mixture models using maximum likelihood and Newton-type and EM algorithms. All mixture models were fit using normal distributions and constant coefficient of variation (CCV). For each model, a goodness of fit test based on the chi-square likelihood ratio statistic (Rao 1965) was used to determine how well mixture distributions g(x) fit observed length frequency histograms (Du 2008). This test statistic is expressed as:

$$x^2 = -2\ln\frac{L(\beta_1)}{L(\beta)}$$

Where  $L(\beta)$  is the maximum value of the likelihood function for the full model and  $L(\beta 1)$  is the maximum value for the likelihood function for the reduced model (Montgomery et al. 2001). All Chi-square tests were evaluated with  $\alpha = 0.05$ .

#### Larval growth

Growth rates of rainbow smelt from late May through July were estimated using changes in larval lengths throughout the sampling period (Hackney and Webb 1978, DeAngelis et al. 1980, Zigler and Jennings 1993). For each length group of larvae (1mm bins), a plot of density (No./1000m^3) through time yielded an estimated age for each length group by determining the mean day that an individual larvae attained a given size (Hackney and Webb 1978; Zigler and Jennings 1993). This method allows growth to be estimated empirically under existing environmental conditions and allows for variable growth without a "fixed" rate (Hackney and Webb 1978). Length was then plotted against calculated mean day of capture and modeled using the exponential function:

$$L = a e^{Gt}$$

Where L = larval length following the growth period, a = the initial larval length or the length axis intercept, G = the instantaneous growth coefficient, and t = time in days. This derived growth curve estimates average growth rates for larvae over the sampling period (Hatch and Underhill 1988).

Growth between years and between 2009 early and late hatching cohorts was compared using ANCOVA (Proc GLM, SAS Institute 1999). For general linear models, all length data were log transformed to meet the assumption of normality. Larval growth was compared between years by regressing natural log transformed length against estimated age. The slope of each regression was compared with an *F*-test to test the assumption of parallel slopes (Neter et al. 1996). During 2009, mean population growth rate was compared between early and late hatching cohorts by tracking the progression of mean length of cohorts through time (Ricker 1975). Linear regression (i.e., log (e) mean length via mixture models vs. date of capture) was then employed to determine if average growth rate was different between cohorts in the same year. Each regression slope was tested for equality with an *F*-test, as in the cross-year comparison. All statistical tests were evaluated with  $\alpha = 0.05$ .

#### **Larval Mortality**

Mortality rates of larval rainbow smelt were estimated by plotting age against abundance through time (No/1000 m^3) for each 1 mm length group. Mortality was then modeled using the exponential decay function:

$$N_t = N_0 e^{-Zt}$$

Where Nt = abundance at time t, No = initial abundance, Z = the instantaneous mortality rate, and t = time in days (DeAngelis et al. 1980). This relationship describes average mortality rates for larval rainbow smelt cohorts over the growing season. Larval rainbow smelt densities (No/1000 m^3) were natural log transformed (Log (e) (x+1), Brown and Guy 2007) for linearity and regressed against age to yield a catch curve, from which instantaneous mortality could be estimated (Ricker 1975). Differences in mortality were compared among years using ANCOVA (Proc GLM, SAS Institute) and all statistical tests were evaluated with  $\alpha$  = 0.05.

#### Results

#### Stream surveys

Patterns in stream temperatures and warming rates varied considerably between years during the early spring spawning period in the St. Martin Bay region. During 2008, temperature loggers were placed in streams at the onset of spawning on April 17th. During the first week of documented spawning, water temperatures increased quickly on all St. Martin Bay tributaries due to warmer than average air temperatures in the region. Nunns Creek, Spring Creek, and St. Martin Creek were between 3-4 C when water temperature sampling began, but increased to between 9 and 11 C the following week (Figure 4). The Carp River, the warmest and largest tributary, was approximately 6 C when temperature sampling began and increased to near 12 C by the following week (Figure 4). This period of rapid warming during 2008, resulted in a spawning period between 7-10 days. Temperatures in tributaries declined following this

warming period (Figure 4), but surveys conducted on spawning rainbow smelt thereafter indicated that spawning had ceased following this time period in all study tributaries.

During 2009, temperature loggers were placed in streams on April 6th, nearly two weeks before spawning was observed. Stream temperatures remained cooler during the 2009 spawning period, and spawning was first observed in the Carp River on April 13th when stream temperatures were approximately 3.5 C. Nunns Creek warmed more quickly than Spring or St. Martin creeks during 2009, but remained cooler (e.g., 6 C cooler on 23-May 2009 compared to the same date in 2008) and few spawning rainbow smelt were observed in Nunns Creek during 2009. Spring Creek and St. Martin Creek remained relatively cold and below 3 C until approximately April 23, and no spawning by rainbow smelt was observed in these smaller tributaries during 2009. Observations of spawning rainbow smelt and recorded water temperatures indicated that most stream spawning in St. Martin Bay during 2009 occurred in the Carp River. Fewer tributaries were utilized by spawning rainbow smelt during 2009 but the estimated spawning period in the Carp River was nearly two weeks longer than 2008 (Figure 4).



Figure 4. Stream temperatures recorded from four St. Martin Bay Spawning tributaries from April-June during 2008 (top panel) and 2009 (lower panel); St. Martin Creek, Spring Creek, Nunns Creek, and the Carp River. Shaded regions indicate the observed duration of spawning by rainbow smelt.

#### Ichthyoplankton surveys

During 2008 and 2009, larval rainbow smelt populations in St. Martin Bay had similar abundance patterns with the highest larval rainbow smelt densities occurring during May. Peak larval density during May 2008 was nearly double that observed during May of 2009 (Figure 5). Irrespective of a shorter spawning period during 2008 (2 weeks shorter than 2009), initial densities of larvae originating from streams were higher than those found in 2009 (Figure 5). Mean larval rainbow smelt density peaked at approximately 60 / 1000 m<sup>3</sup> in 2008, and 30 / 1000 m<sup>3</sup> in 2009 (Figure 5) occurring on May 19 and May 21st, respectively. During 2008, density declined rapidly through June and early July, and then increased during the 2nd week of July concurrent with an increase in smaller, newly hatched larvae entering the population from lake spawning populations. Following this increase, larval abundance declined further during July and August. During 2009, larval density decreased following peak abundance in mid-May, but then increased along with smaller, newly hatched fish during the last week of June (Figure 5). This increase in density during 2009 occurred nearly two weeks earlier than during 2008 due to warmer water temperatures in St. Martin Bay in late June (Figure 6), which resulted in shorter incubation periods for eggs. Abundance trends of larval rainbow smelt in St. Martin Bay indicated that one or more pulses of larvae entered the population during late June and July of 2008 and 2009, after spawning and larval outmigration in tributaries had ceased.



Figure 5. Abundance (Mean No /1000 m<sup>3</sup>) of larval rainbow smelt in St. Martin Bay, Lake Huron from May-August during 2008 (top panel) and 2009 (lower panel). Error bars are 95% confidence intervals.

Spring and summer mean water temperatures and rates of warming in St. Martin Bay differed over the two year period (Figure 6). During both years, water temperatures averaged approximately 13 C over the period from mid May to late August. Mean water temperature increased steadily during 2008 and reached a peak of 19.67 C on August 4th, with an overall warming rate of approximately 0.13 degrees per day. During 2009, water temperature increased rapidly during May and June and reached a peak mean temperature of 20.2 C on June 24, over a month earlier than peak temperatures were reached during 2008. Following this period of rapid warming, mean water temperatures decreased by nearly 10 C during early July and remained notably cooler relative to 2008 (Figure 6). As a result the calculated rate of warming during 2009 was 0.06 degrees per day, approximately half the estimated warming rate during 2008.



Figure 6. Mean water temperature (degrees C) across sampling transects recorded during larval fish surveys, 12 May-5-August, 2008 (closed circle) and 21-May-4-August, 2009 (open circle).

#### Length frequency analysis of larval cohorts

Analysis of length frequency distributions of larval rainbow smelt indicated differences within years relative to the survival of different cohorts. During both years, May larval length frequencies were similar and depicted newly hatched larvae had entered St. Martin Bay (Figures 7, 8). During June 2008, uni-modal length frequency distributions indicated the population was comprised of a single cohort (Figure 7) which was distributed across newly hatched larval lengths. This pattern indicated that larvae hatched during May had experienced high mortality. During June and July 2009, a bi-modal length distribution was evidence that the population consisted of an older (i.e., stream spawned) cohort and a smaller (i.e., lake spawned) cohort (Figure 8).

The occurrence of larval cohorts distinguishable by size facilitated comparison of population growth rates for each larval cohort from late May-July 2009. Only data from 2009 were used to compare growth among cohorts, as this was the only year where early hatched larvae remained in the population throughout the May-July sampling period. Length frequency distributions for 2009 were constructed by individual sampling date to determine the presence of both stream and lake cohorts at a differing temporal scale, and to determine mean length of each cohort. Six out of nine sampling events during 2009 yielded bi-modal length distributions indicative of multiple larval cohorts. Finite mixture models were fit to length frequency distributions observed on 27 May (n = 117), 11 June (n = 69), 18 June (n = 34), 24 June (n = 134), 8 July (n = 47) and 22 July (n = 48), and the mean length of each component distribution was determined (Figure 9). Chi-square tests indicated all model fits were significant and adequately modeled the grouped length frequency data for a given sample period (Table 1).



Figure 7. Length frequency distributions of larval rainbow smelt during 2008 in St. Martin Bay, Lake Huron; May (top panel), June (middle panel), and July (lower panel).



Figure 8. Length frequency distributions of larval rainbow smelt during 2009 in St. Martin Bay, Lake Huron; May (top panel), June (middle panel), and July (lower panel).



Figure 9. Finite mixture models fit to length frequency distributions of larval rainbow smelt observed on 27 May, 11 June, 18 June, 24 June, 8 July and 22 July, 2009. Dashed lines represent component (joint) models and solid lines represent mixed probability density functions. Mean length is indicated by the triangle along the x-axis.

Table 1. Parameter estimates for finite mixture distribution models fit to larval rainbow smelt length frequency distributions during 2009;  $\pi$  = mixing proportions,  $\mu$  = mean cohort length,  $\sigma$  = standard error. Cohort 1 corresponds to the stream spawned larvae, cohort 2 corresponds to lake spawned larvae. Model degrees of freedom (*Df*) and Chi-square goodness-of-fit statistic (*X*^2) are presented for each model. All models were significant at  $\alpha$  = 0.05. Modeled length distributions for 18-June and 8-Jul identified a third mode which was not included in this analysis due to low (i.e., < 10 larvae) sample sizes. Thus, mixing proportions for those sample dates do not add to 1.

Date	Cohort	π	μ	σ	Df	$X^2$	p-value
27-May	1	0.068	5.070	0.066	5	4.624	0.463
	2	0.932	6.865	0.772			
11-June	1	0.184	6.949	0.292	15	20.752	0.145
	2	0.816	10.664	2.078			
18-June	1	0.434	7.498	1.160	5	10.531	0.062
	2	0.448	11.310	0.906			
24-June	1	0.467	7.057	1.248	11	15.242	0.172
	2	0.532	12.469	2.223			
8-July	1	0.306	9.832	1.181	6	3.588	0.732
	2	0.629	14.068	1.287			
22-July	1	0.196	9.734	1.356	20	21.599	0.3627
	2	0.610	16.277	1.707			

### Larval Growth

Growth and mortality rates were calculated for larvae ranging from 5 to 19 mm in length, corresponding approximately to the first 50 days of growth. Growth rates varied between years and exponential growth models indicated that larval growth was higher during 2009; the average growth rate was 0.16 mm d<sup>-1</sup> during 2008 and 0.23 mm d<sup>-1</sup> during 2009 (Figure 10). Daily growth rates ranged between 0.11 - 0.19 mm d<sup>-1</sup> during 2008 and between 0.15 – 0.30 mm d<sup>-1</sup> during 2009. General linear models confirmed that the average growth rate was significantly higher during 2009 ( $F_{3, 25} = 5.72$ , P = 0.02, Figure 11). During 2009, mean growth rates were higher for the early hatching stream cohorts, but this difference was not significant between stream (G=0.014) and lake cohorts (G=0.012) ( $F_{3, 8} = 1.35$ , P = 0.28, Figure 12). However, length intercepts were significantly different indicating cohorts had distinct growth trajectories ( $F_{2, 9} = 41.23$ , P = 0.0001).

#### **Larval Mortality**

Exponential models indicated instantaneous mortality rates during 2009 were higher (z = 0.050) than those found for 2008 cohorts (z = 0.045). However, general linear models confirmed that mortality was not significantly different between years ( $F_{3, 24} = 0.27$ , P = 0.61). Log density at peak abundance was significantly different ( $F_{2, 25} = 16.65$ , P = 0.0004) and higher during 2008, indicating significantly more larvae were present during May in 2008 (Figure 13).



Figure 10. Modeled exponential growth curves for larval rainbow smelt during 2008 (top panel) and 2009 (bottom panel) showing the relationship between estimated age and length of size classes.


Figure 11. General linear model regressions (log (e) length (mm) v. estimated age) comparing growth of larval rainbow smelt during 2008 (top panel) and 2009 (lower panel) in St. Martin Bay, Lake Huron.



Figure 12. General linear model regressions (log (e) length (mm) v. estimated age) comparing growth of early stream spawned (circle) and late lake spawned (triangle) larval rainbow smelt cohorts during 2009 in St. Martin Bay, Lake Huron.



Figure 13. Larval rainbow smelt catch curves (log (e) density v. estimated age) comparing instantaneous mortality rate of larval rainbow smelt during 2008 (triangle) and 2009 (circle), in St. Martin Bay, Lake Huron.

# Discussion

Rainbow smelt were the most abundant ichthyoplankter in St. Martin Bay, Lake Huron from May-July during 2008 and 2009. These populations were characterized by contrasting patterns in abundance, growth, and survival during both years of this study, with growth rates differing significantly between years. During 2009, growth rates were significantly higher for larval rainbow smelt, indicating that water temperatures and zooplankton dynamics were more favorable for growth and survival of larvae than during 2008. Despite a relatively short (7-10 day) spawning period in 2008 and a more protracted spawning period in 2009 (15-20 days), initial densities of larval rainbow smelt were higher during May of 2008, with peak density nearly double that estimated during 2009. The original hypothesis that a longer spawning period would result in higher densities of larval rainbow smelt was thus unsubstantiated, and it appears that the number of streams utilized for spawning is more important than length of the spawning period. This would suggest that given optimal water temperatures and flow rates in streams, spawning can successfully occur over a shorter time period (7-10 days) than has previously been observed in the Great Lakes region (Owens 1982; Brown 1994).

Within years, changes in size distributions of larval rainbow smelt indicated that populations consisted of at least two cohorts; early hatching larvae entering the bay during May and early June and late hatching larvae entering the bay during late June and early July, a pattern also seen by Brown (1994) in this same system. These late hatching larval cohorts were likely from lake spawned origins, as larval outmigration from tributaries typically ends by the first week in June (Brown 1994). During 2009, these cohorts of late hatching larvae began approximately two weeks earlier than in 2008, likely due to warmer water temperatures in St. Martin Bay which accelerated incubation during June of 2009. Although distinct stream and lake cohorts developed during both sampling seasons, stream hatched larvae apparently experienced large-scale mortality between May and early June of 2008, as indicated by a paucity of larger (15-20 mm) larvae and a population consisting primarily of smaller (6-7 mm) larvae during June.

The present study was in part a reassessment of the work of Brown (1994) who conducted research on rainbow smelt populations in St. Martin Bay, Lake Huron during 1991-93. That study determined that strong year classes developed when tributary production of larvae

was strong and spatial overlap with their zooplankton food resources was high. More importantly, estimates of growth and mortality appeared highly correlated with zooplankton populations. For instance, high growth rates and relatively low mortality during 1991 (G=0.031, Z=0.098) resulted in the highest year class recorded and an estimated 46 million larvae produced from tributaries within St. Martin Bay (Brown 1994). During 1992, low tributary production estimated at 13 million larvae was associated with low zooplankton densities, low spatial overlap with prey, and subsequent low growth and high mortality of larvae within the bay (G=0.018, Z=0.184; Brown 1994).

Significant inter-annual differences in growth of larval rainbow smelt populations were observed in St. Martin Bay during 2008-2009, similar to variability in growth rates observed by Brown (1994) in this same embayment. This finding, that large variation in growth rates occurs during rainbow smelt early life history, has important implications for recruitment of this species in the Great Lakes, as growth and mortality are linked processes during fish early life history that are often highly correlated (Cushing 1975; Houde 1997). Thus, growth and mortality can act to control year-class strength. For instance, reduced growth rates can result in protracted developmental stage durations, effectively prolonging vulnerability of larvae to size dependent mortality sources such as starvation or predation (Pepin 1991; Rice et al. 1993). Thus, in years where larval growth is higher, probability of survival would accordingly be higher for developing larval cohorts. High recruitment from larval to juvenile stages in fish populations is associated with fast growth, which allows for individual larvae to better exploit optimal temperature and food gradients (Cowan and Shaw 2002), and to evade predation, one of the primary sources of early life stage mortality in fishes (Houde 2008). As an example, reduced risk of size-dependant predation and an increase in recruitment potential resulting from increased

and variable growth rates were described through model simulations for bloater (*Coregonus hoyi*), a common pelagic species in the Great Lakes (Rice et al. 1993).

Many environmental factors can influence fish growth (e.g., zooplankton, salinity, oxygen, solar intensity; Brett 1979), but temperature can impart profound changes on both the development of eggs and growth of larvae (Blaxter 1969; Fry 1971). Because temperature can influence the availability of zooplankton and the amount of food required by larval fish, temperature directly influences fish growth rates (Jones 2002). While water temperature was not directly correlated to fish growth rates for the present study, contrasting patterns in St. Martin Bay water temperatures that were observed over the course of this study could have resulted in the observed disparity in population growth rates between years. For instance, water temperatures in St. Martin Bay during June 2008 slowly increased (i.e., from 10-13 C over a 14 day period) but during June 2009 bay temperatures increased dramatically (i.e., from 12-20 C over a similar 14 day period). During July of 2008, water temperatures increased gradually and averaged 17 C, while notably cooler temperatures persisted during July 2009 when the average surface temperature was 13 C. Young of the year rainbow smelt prefer water temperatures in the range of 13-14 C (Brandt et al. 1980), and temperatures during July 2009, when most larval cohorts had entered the population, appear to have created optimal conditions for rainbow smelt growth within St. Martin Bay. Conversely, during July 2008 average water temperatures in St. Martin Bay exceeded the preferred range for rainbow smelt and likely contributed to the lower growth rates observed.

The earlier emergence of lake spawned larval cohorts during 2009 may also have been a result of temperature patterns in St. Martin Bay. Elevated temperatures increase development rates and accelerate hatching in fish eggs (Braum 1978). In rainbow smelt, the relationship

between temperature and time to hatch appears to be nonlinear, with cold temperatures (i.e., 2 and 4 C) resulting in hatch times of approximately 78 and 55 days, respectively, and warmer temperatures (i.e., 8 and 10 C) resulting in hatch times of 24 and 17 days, respectively (Owen 1982). In the Miramachi River, McKenzie (1964) reported hatching of rainbow smelt eggs in 29 days at 6-7 C, but temperatures near 12 C resulted in hatching occurring after only 11 days. Average water temperatures of 16.5 C resulted in Lake Erie rainbow smelt hatching between 7-8 days (Cooper 1978). These empirical studies indicate that rainbow smelt hatch over a wide range of temperatures, and warmer temperatures (i.e., > 8 C) appear to substantially accelerate egg development, likely as a result of cumulative degree days, which is the product of time to development and temperature (Braum 1978). Although temperatures were not recorded at deeper depths where lake spawned cohorts were likely hatching, St. Martin Bay is fairly shallow (average depth 8 meters) and rarely stratifies during summer (Brown 1995), which would suggest that warmer surface water temperatures during June 2009 would have in turn warmed the deeper waters of the bay, thus causing the earlier emergence of lake spawning cohorts that was observed during this year.

Mortality during the early life history of fishes can occur for a variety of reasons including starvation, advection to suboptimal habitats, and predation (Houde 2002). During 2008, causes for the failure of early hatching stream cohorts were not apparent but were likely related to lower growth rates and increased susceptibility of larvae to size specific mortality sources, namely predation. Because growth is highly correlated to mortality in larval fish (Houde 2002), it is reasoned that lower growth rates would complement higher mortality during 2008. Poor growth can function as a source of indirect mortality by increasing vulnerability to predation mortality, which is considered to be the largest single cause of mortality during fish

early life history (Paling 1971; Houde 2002). Size-dependent predation is closely associated with growth and survival in larval fish populations because fish larvae are exposed to predators longer and have a higher capture probability due to small size (Luecke 1990; Houde 2002). For example, bloater larvae held in laboratory experiments under varied growth conditions showed a 50 fold increase in survival rate when rate of growth per day was increased from 0.3 to 0.5 mm  $d^{-1}$ , with predation being the only form of mortality induced (Luecke et al. 1990). Rainbow smelt are a key prey in the Great Lakes for lake trout *Salvelinus namaykush* (Diana 1990; Madenjian et al. 2006) and introduced salmonines *Oncorhynchus spp*. (Kocik and Taylor 1987; Diana 1990). In addition, rainbow smelt predation can also occur through cannibalism, which has been shown to be an important source of mortality on young of the year rainbow smelt populations (Henderson and Nepszy 1989; Lantry and Stewart 2000; Parker Stetter et al. 2007).

This researched has described the relationship between growth and survival dynamics in larval rainbow smelt populations, and provides an understanding of the influence of these processes on recruitment variation of rainbow smelt in Lake Huron. To fully understand and appreciate the complexities of relating larval growth and mortality rates to recruitment, one must acknowledge first that many processes act in concert to influence these fundamental rates throughout fish early life history (Cowan and Shaw 2002; Houde 2008). Secondly, poor growth and survival rates can function as a "single process", which effectively introduces sources of size specific mortality, such as predation (Cushing 1975). Finally, while the exact mechanisms through which larval growth and mortality are influenced may not be evident, it has been shown that small changes in these rates, especially growth rates, can strongly influence recruitment by modifying survival to the end of the first year of life (Houde 1987; 1989). Processes reducing survival during early life stages may be episodic or subtle in nature, and thus are typically

difficult to detect, and the result of both biotic and abiotic factors affecting growth and mortality rates through modification of larval dispersal, nutrition, and predation (Houde 2002).

Higher growth and survival rates during 2009 would suggest the formation of a stronger year class relative to 2008, and this was substantiated through fishery independent mid-water trawl surveys conducted by the USGS Great Lakes Science Center in the main basin of Lake Huron. Hydroacoustic mid-water trawl surveys of Lake Huron's main basin determined a sharp increase in YOY rainbow smelt abundance during 2009, but during 2008 YOY rainbow smelt abundance was low, reflecting poorer conditions for growth and survival during that year (Schaeffer et al. 2009). Relative to 2008, this survey detected a 13-fold increase in YOY rainbow smelt during the survey occurring in US waters (Schaeffer et al. 2009). These high estimates of age-0 density were comparable in magnitude to densities observed during 1997, when rainbow smelt populations were relatively abundant in Lake Huron (Warner et al. 2005).

Relating the 2009 rainbow smelt year class to predator response was accomplished through a piscivore diet study that documented high predation on YOY rainbow smelt in the main basin of Lake Huron. Species such as chinook salmon *Oncorhynchus tshawytscha*, coho salmon *Oncorhynchus kisutch*, and lake trout contained high numbers of YOY rainbow smelt, occurring in 25-35% of stomachs examined for these species (*Edward Roseman, USGS Great Lakes Science Center, personal communication*).

This research has increased our understanding of growth and survival during rainbow smelt early life history, and provides insight into factors that influence recruitment, including variable survival of stream hatching cohorts and significant variation in growth rates during May-July. Rainbow smelt year class formation in St. Martin Bay is in part controlled by survival

of stream cohorts, which establishes the initial age-0 population during May and early June. However, once these populations are established, high growth must be maintained by larvae throughout the summer months for age-0 recruits to reach the end of their first year of life. Both Brown (1994) and the present study have documented this important variation in survival and growth during rainbow smelt early life history, and its relationship to year class strength. This variation in growth and survival appears to be mediated by water temperatures which can drive early emergence of lake spawning cohorts and sustain high growth rates throughout the larval period. After the first year of life, subsequent recruitment of rainbow smelt to older age classes is likely a function of predation, suggesting that recruitment of rainbow smelt in Lake Huron may be controlled at the juvenile stage.

## **CHAPTER TWO**

# EFFECTS OF STOCK SIZE, CLIMATE, AND PREDATION ON RAINBOW SMELT RECRUITMENT IN WESTERN LAKE HURON, 1976-2009

# Introduction

Recruitment and its relationship to adult spawning stock is central to the study and management of fish populations (Myers 1996), but is generally the most challenging aspect in the biological assessment of fish populations (Hilborn and Walters 1992). In studying fish population dynamics the goal is often to determine if spawning stock, environmental factors, biological processes, or some combination of these is responsible for observed patterns in the relationship between the stock and its recruitment. Environmental factors such as temperature and precipitation have been studied in relation to fishery recruitment for at least the last century (Cushing 1982), but many apparent environment-recruitment correlations do not appear to persist over long periods of time (Myers 1998). Furthermore, the number of apparent correlations between environmental variables and recruitment can increase as the number of predictor variables increases (Ricker 1975) and thus, the legitimacy of specific environmental predictors can be difficult to ascertain (Francis 2006). Regardless, processes responsible for recruitment in fish populations often relate to multiple biotic and abiotic factors working in concert to modify growth and survival during their larval and juvenile stages.

Environmental variability during spring and summer has been linked to rainbow smelt (*Osmerus mordax*) recruitment dynamics in the Great Lakes region. Sluka (1991) reported that rainbow smelt abundance in Green Bay, Lake Michigan during 1966-89 was related to spawner abundance, mean solar intensity in the previous spring, and air temperature in the previous spring (Sluka 1991). Additionally he found that during the time period 1975-86, young-of-the-year

(YOY) rainbow smelt abundance at stations off Alpena, Michigan (Lake Huron) was related to spawner abundance and spring temperature, with the effect of cannibalism also presumed to be an important source of YOY predation. Brown (1994), however, found that year class strength and recruitment of these fish in St. Martin Bay, Lake Huron during 1991-1993 was influenced by differences in growth rates mediated by water temperatures and zooplankton dynamics. Furthermore, he reported that depressed stream water temperatures during spring spawning resulted in low survival of eggs and larvae from tributaries (Brown 1991), further influencing year class strength and recruitment to the population in Lake Huron in the fall.

Recruitment trends of rainbow smelt in Lake Huron have been monitored since the early 1970s through annual bottom trawl surveys conducted by the US Geological Survey Great Lakes Science Center (GLSC). Between 1973 and 1991, yearling-and-older (YOA) rainbow smelt were abundant (i.e., mean density > 700 fish/ha., Figure 2). However, from 1994 to the present, YAO rainbow smelt abundance has been declining (i.e., mean density < 475 fish/ha., Figure 2) and currently the population is approximately 40% reduced from the 1976-1991 time period (Riley et al. 2008). Abundance of YOY rainbow smelt was typically low during 1976-1991 (i.e., mean density < 600 fish/ha., Figure 2), but during 1994-2009 YOY abundance was relatively high (i.e., mean density > 1900 fish/ha., Figure 2), primarily as a result of several large year classes that occurred during this period (e.g., 2005, YOY density > 5500 fish/ha.). However, underscoring the complexity of the recruitment process, substantial recruitment to older age groups did not occur following the formation of these large year classes in this lake.

Traditional stock-recruit methods typically involve analysis of empirical estimates of spawning stock size and subsequent progeny produced in a given year (Hilborn and Walters 1992). One of the inherent difficulties in assessing the influence of stock size on subsequent

production of recruits is that variation in annual production can also arise from changes in environmental conditions, which often match or exceed the influence of changing stock size (Ricker 1975). As such, environmental variation is often suspected to influence survival during early life stages, and these specific variables can be integrated into traditional stock-recruit models (Quinn and Deriso 1999). Additionally, species interactions such as predation or competition can also be integrated into traditional stock-recruit models much in the same way that environmental variation is incorporated (Hilborn and Walters 1992; Quinn and Deriso 1999).

The goal of this research was to examine stock-recruit relationships for Lake Huron rainbow smelt in the context of potentially important environmental and biological variables. Two factors that have been shown to significantly affect egg survival in streams and larval growth rates during summer include spring precipitation (Hoff 2004) and water temperature (Sluka 1991), and both were selected for integration into stock-recruit models. Additionally, water levels have been linked to production and recruitment in fish populations (Jude and Pappas 1992; Rowe et al. 2002; Clark et al. 2008) and because rainbow smelt spawn and spend part of their early life history in streams and nearshore areas, Lake Huron water levels were selected as a third variable for stock recruit models. I hypothesized that higher water levels and warmer water temperatures would influence recruitment positively, and that above average precipitation would negatively influence recruitment. Finally, since lake trout predation is important in Great Lakes rainbow smelt populations (Diana 1990; Madenjian et al. 1998; Madenjian et al. 2006; Gorman 2007), lake trout abundance (catch-per-unit-effort) was included as a species interaction in stockrecruit models that was hypothesized to negatively influence recruitment.

This chapter has two primary objectives; 1) Develop stock-recruit models for rainbow smelt populations in Lake Huron during 1976-2009 based on fishery independent bottom trawl collections, and 2) Integrate water temperature, water level, precipitation, and lake trout abundance time series data into stock-recruit models as explanatory variables. Specifically, I wanted to test the hypothesis that the abundance of young-of-the-year rainbow smelt in Lake Huron was influenced by water temperature, water levels, precipitation, rainbow smelt stock size, and lake trout CPE, or some combination of the these variables.

### Methods

## **Bottom trawl collections**

Rainbow smelt populations were sampled in Lake Huron from 1976-2009 during bottom trawl surveys conducted by the USGS GLSC. From 1976-1991, a 12 m headrope bottom trawl with 4.76 mm square cod end mesh was used. From 1992-2009, a 21 m headrope bottom trawl was used with 4.76 mm cod end mesh (Riley et al. 2009). Bottom trawls were towed on contour at fixed transects for 10 minutes at approximately 2.2-2.4 m/h during daylight hours. These surveys sample the same transects annually at depths from 9-110 m spaced at 9 m intervals throughout the western main basin of Lake Huron (Figure 13). Surveys were typically carried out between early October and mid November; however surveys during 1992-93 were conducted during September and thus were excluded from analysis due to potential seasonal differences in fish distributions (Riley et al. 2009). Additionally, no data were available from 2000 and 2008 as surveys were not completed during these years due to inclement weather. To account for a change in trawling gear that occurred during the 1992 field season, fishing power corrections

(FPC) were developed to standardize estimates of CPE among gears (Adams et al. 2009). FPC were developed for yearling-and-older (YAO) rainbow smelt, but high variability in catches of young-of-the-year (YOY) rainbow smelt resulted in no estimable FPC for this life stage (Adams et al. 2009). To adequately evaluate rainbow smelt densities given the change in sampling gear, stock recruit models were constructed for 1976-2009 with corrected YAO catch data (1976-1991 data corrected to reflect 21 m trawl), and for the 1976-1991 and 1994-2009 time periods separately with no corrected data.



Figure 14. Bottom trawl sampling locations in the main basin of Lake Huron, 1976-2009.

## **Stock-recruit models**

Analysis of stock-recruit models used length to partition bottom trawl catch data into YOY (recruits) and YAO (stock) components for the time series. While age-length keys have not been developed for Lake Huron rainbow smelt, previous work has indicated spawners are typically 100 mm in length or greater (Brown 1994). This was further substantiated from a survey of spawning rainbow smelt in St. Martin Bay, Lake Huron during 2008-09 (see Chapter 1) where length data indicated that spawners averaged between 135-140 mm, and no spawners were less than 108 mm. For the 1976-2009 time series, catches of rainbow smelt were partitioned into YOY and YAO components based on length frequency analysis, which was year specific and resulted in YOY length cutoffs ranging from 75-105 mm (Riley and Adams 2010, Table 2). Based on this information, the spawner component of stock-recruit models was determined as numeric density (No./ha.) of rainbow smelt  $\geq$  the estimated YOY length cutoff for a given year, while recruits were considered to be the numerical density of fish  $\leq$  year specific cutoffs.

Stock-recruit models were initially constructed for all time periods (1976-2009, 1976-1991, and 1994-2009) using the models of Ricker (1975) and Beverton and Holt (1957). In the general form the Ricker model is represented by the equation:

$$R = \alpha S e^{-\beta S} \varepsilon$$

Where R = number of recruits, S = stock size,  $\alpha$  is a model parameter describing productivity,  $\beta$  is a parameter describing density dependence in the population, and  $\varepsilon$  is a lognormal error. This relationship assumes that increasing spawning stock will hinder recruitment at some stock size through density dependent processes such as cannibalism (Ricker 1975; Quinn and Deriso 1999).

This model was linearized and parameters were estimated through linear regression using the equation:

$$\log_{e} \frac{R}{S} = \log_{e}(\alpha) - \beta S + \log_{e}(\varepsilon)$$

The Beverton-Holt model in the general form is represented by the equation:

$$R = \frac{aS}{b+S}e^{\frac{\sigma^2}{2}}$$

Where R = number of recruits, S = stock size, a is the productivity parameter, b is a parameter controlling the level of density dependence, and e<sup>( $\sigma^2/2$ )</sup> is the bias adjustment factor. This relationship increases with increasing spawner abundance and approaches an asymptote at some level of stock size (Quinn and Deriso 1999). This model was transformed and parameters estimated through non-linear regression using the form:

$$\log_{e} \frac{R}{S} = \log_{e} \left( \frac{aS}{b+S} \right) + \log_{e}(\varepsilon)$$

After fitting stock recruit models, second order Akaike's Information Criterion (AICc, Burnham and Anderson 2002) was used to compare models and determine which stock recruit relationship was the most accurate reflection of rainbow smelt dynamics in Lake Huron. Results indicated that both models were similar based on reduced SSE, however, the Ricker model was selected because it accounts for compensation at high stock sizes from sources such as cannibalism (Ricker 1954; 1975), and because initial stock recruit models appeared to show densitydependence at higher stock sizes; a phenomenon noted by earlier investigators for Lake Huron rainbow smelt (Sluka 1992). Additionally, this aspect of the model is particularly relevant to rainbow smelt, which are known to exhibit cannibalism (Henderson and Nepszy 1989, Parker Stetter et al. 2007). Final model fitting for basic Ricker stock-recruit functions was accomplished through non-linear regression (PROC NLIN, SAS Institute), and model parameter estimates were then corroborated with initial estimates determined through linear regression.

Measures of uncertainty for Ricker stock-recruit parameters were estimated through a bootstrap procedure (Hillborn and Walters 1992; Efron 1993), which removes the assumption of normality and allows the computation of parameter confidence intervals. For all three stock-recruit models (1976-2009, 1976-1991, and 1994-2009), linear regression residuals were resampled with replacement and added to predicted values to estimate new parameters. This procedure was repeated 1000 times for each model and bootstrapped parameters were saved after each step (Neter et al. 1996; Hilborn and Walters 1992). Saved parameter estimates from the bootstrap procedures were then used to construct frequency distributions, estimate the variance, and determine 95% confidence intervals of simulated parameters. All bootstrap procedures were programmed using Visual Basic for Applications (VBA), implemented through Microsoft Excel.

Table 2. Year specific YOY length cutoffs (mm) for rainbow smelt in Lake Huron, 1976-2009. Cutoffs were determined from length frequency analysis and applied to fishing power corrections as determined by Adams et al. (2009).

YOY length	75	85	90	95	100	105
cutoff						
Years	85, 89, 92,	81, 83, 86-	05-06	73-76, 78-	07-09	77
applied	93	87, 90-91,		80, 82, 84,		
		95-96, 99,		88, 94, 97,		
		01-02, 04		03		

#### **Integrated stock-recruit models**

In order to evaluate predator impact on rainbow smelt population dynamics, lake trout CPE (No./1000 ft of gill net) for the Michigan waters of Lake Huron's main basin was determined from spring gill net surveys conducted by the Michigan Dept. of Natural Resources and Environment and the Chippewa Ottawa Resource Authority. Lake trout captured in this survey were larger than 250 mm (*Ji He, Michigan Department of Natural Resources and Environment, personal communication*), which is consistent with lake trout sizes known to prey on rainbow smelt in the Great lakes (Madenjian et al. 1998). For inclusion in stock recruit models, lake trout CPE was expressed as the deviation from the mean CPE for the whole time period.

Lakes Huron-Michigan water levels (meters) were included as an additional variable in stock recruit models that could potentially influence survival of rainbow smelt during early life stages. Water level data (meters) for Lakes Michigan-Huron were obtained from the United States Army Corps of Engineers, Detroit District (USACE). Water level parameters in stock recruit models were calculated as the deviation of March-May mean values from annual mean values, as suggested by Hilborn and Walters (1992).

Precipitation data included in stock-recruit models were obtained from NOAA's Great Lakes Environmental Research Laboratory's hydrologic database (Croley and Hunter 1994) of monthly records of overbasin precipitation in m^3/sec. (not including Georgian Bay) during 1976-2007. Precipitation data for 2009 were estimated by using the mean precipitation (m^3/sec.) for the whole time period. Precipitation parameters in stock recruit models were calculated as the deviation of March-May mean values from annual mean values (Hilborn and Walters 1992).

Water temperatures (degrees C, 0-20 meter average) were determined from ice thermodynamic models developed by researchers at the Great Lakes Environmental Research Laboratory (Croley and Assesl 1994). This model generates daily water temperature values throughout the water column by incorporating air temperature, wind speed, cloud cover, and humidity recorded at several locations across the lake (Croley and Assel 1994). Mean water temperatures from the top 20 meters were used, as this corresponds to epilimnetic waters where age-0 rainbow smelt are typically found (Parker Stetter et al. 2008). Similar to lake trout CPE, water temperatures were expressed as the deviation from the grand mean for the time series.

Water temperatures, water levels, over basin precipitation, and lake trout CPE were first incorporated into Ricker stock-recruit models using the form:

$$R = S e^{\alpha - \beta S + c_1 X_1 + \dots + c_n X_n}$$

Where  $x_1$  to  $x_n$  are *n* explanatory variables and  $c_1$  to  $c_n$  are the estimated coefficients (Maceina and Pereira 2007). For each time series, 16 model combinations were considered and parameters were estimated through linear regression (Proc REG, SAS Institute) with the model form:

$$log_e R/S = a - bS + cX + \varepsilon$$

### **Model selection**

For each model considered, AICc was calculated (sum of squared error) using the equation:

$$AICc = -2\log(\mathcal{L}(\theta)) + 2K + \frac{2K(K+1)}{n-K-1}$$

Where  $\theta$  is the SSE objective function, *K* is the number of parameters, and *n* is the number of observations in the data set. AICc differences were then calculated using the equation:

$$\Delta_i = AIC_i - AIC_{min}$$

Where  $\Delta_i$  is the AICc deviation of each model from the best model (Burhnam and Anderson 2002). The relative likelihood of each model (expressed as e^-1/2  $\Delta_i$ ) was then used to compute Akaike weights  $w_i$ , which are expressed as:

$$w_{i} = \frac{\exp\left(-\frac{1}{2} \Delta i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2} \Delta r\right)}$$

Where *r* is the number of candidate models (Burhnam and Anderson 2002). These normalized relative likelihoods provide a weight of evidence for model plausibility and were used in selecting the best model(s) for the 1976-2009, 1976-1991, and 1994-2009 time series. Evidence ratios ( $w_I/w_j$ ) were then computed as a further quantitative measure of distance between two models (Burhnam and Anderson 2002).

## Results

Rainbow smelt recruitment in Lake Huron during 1976-2009 varied considerably and was characterized by a period of high stock and low numbers of recruits (1976-1991) and a period of low stock and higher production of age-0 fish (1994-2009). Mean density of YAO rainbow smelt was approximately 1,975 fish/ha during 1976-1991, but decreased to 474 fish/ha. during 1994-2009. The mean density of YOY rainbow smelt was highly variable between time periods, ranging from 598 fish/ha. during 1976-1994 to over 1,950 fish/ha. during 1994-2009. There tended to be distinct time periods (almost decadal) where successive years would cluster along the stock-recruitment curve. For instance, most observations for 1980-89 occur over the period of time where Lake Huron populations had the highest recorded stock sizes and during a period of low recruitment (Figure 14). During 1999-2009, however, the highest indices of recruitment were recorded, and observations occurred over the ascending portion of the Ricker curve where stock size is lowest. The recruitment model for 1976-1991 is nearly asymptotic in appearance with little variation in recruitment occurring over a broad range of stock sizes (Figure 14). Furthermore, during 1976-1991, the production of age-0 fish was limited despite relatively abundant spawning stocks. This relatively flat stock-recruitment curve for 1976-1991 was contrasted by a more classical Ricker curve for 1994-2009, when compensatory affects were more evident at higher stock sizes (Figure 14). During 1994-2009, density of age-0 recruits in the fall was high relative to 1976-1991 when abundances were lower (< 400 fish/ha.); however, overcompensation due to cannibalism or predation (Ricker 1954) is evident at higher stock sizes (> 500 fish/ha).



Figure 15. Stock-recruit relationships for Lake Huron rainbow smelt modeled by the Ricker function for the years 1976-2009 (top panel), 1976-1991 (middle panel), and 1994-2009 (lower panel).

# **Stock-recruit models**

Stock recruit models converged quickly with one or two iterations, and multiple starting values produced repeatability in parameter estimates (Table 3). For the three time series analyzed, stock-recruit relationships were modeled best by the following equations;

1976 – 2009	$R = 5.42  S  e^{-0.0013  S}$
1976 — 1991	$R = 1.54  S  e^{-0.0009  S}$
1994 – 2009	$R = 13.79  S  e^{-0.0024  S}$

Table 3. Original parameter estimates, approximate standard error, and 95% confidence intervals for stock-recruit models of rainbow smelt recruitment (1976-2009, 1976-1991, and 1994-2009).

Model	Parameters	Estimate	Std. Error	95% CI
1976-2009	$Ln(\alpha)$	1.690	0.294	[1.086, 2.2938]
	β	-0.0013	0.00018	[-0.0016, -0.0009]
1976-1991	$Ln(\alpha)$	0.0431	0.326	[-0.269, 1.131]
	β	-0.0009	0.00043	[-0.0018, -3.29E-6]
1994-2009	$Ln(\alpha)$	2.624	0.3942	[1.756, 3.4912]
	β	-0.0024	0.00069	[-0.0039, -0.0009]

Precision estimates of the  $\alpha$  and  $\beta$  parameters were evaluated through a bootstrap procedure and these results indicate that parameters were well estimated and approximated results attained analytically. Frequency distributions for bootstrap parameter estimates were normally distributed with means close to original estimates (Figures 16-18). Variance ranged from 0.076 - 0.129 for the alpha parameter and 2.95E-08-3.86E-07 for beta, and the 1994-2009 time series had the largest amount of variability around bootstrap parameter estimates (Table 4).
Confidence intervals around bootstrap parameter estimates were quite similar to those determined through analytical procedures (Table 3, 4). Bootstrap re-sampling indicated parameters were reasonably well estimated, with the 1994-2009 time series having the most uncertainty regarding accuracy in parameter estimates.

Table 4. Mean, variance, and 95% confidence intervals of bootstrap parameter estimates for stock-recruit models of rainbow smelt recruitment (1976-2009, 1976-1991, and 1994-2009). Statistics are based on 1000 bootstrap samples.

Model	Parameters	Mean	Variance	95% CI
1976-2009	$Ln(\alpha)$	1.681	0.076	[1.127, 2.220]
	β	-0.0013	2.95E-08	[-0.0016, -0.0009]
1976-1991	$Ln(\alpha)$	0.438	0.086	[-0.129, 1.014]
	β	-0.0009	1.50E-07	[-0.0017, -0.0001]
1994-2009	$Ln(\alpha)$	2.609	0.129	[1.880, 3.283]
	β	-0.0024	3.86E-07	[-0.0036, -0.0012]



Figure 16. Frequency distributions of bootstrapped parameter estimates (log  $\alpha$ ,  $\beta$ ) for the Ricker stock-recruit model for the 1976-2009 time series. Approximate location of "true" parameter estimates are indicated by arrows.



Figure 17. Frequency distributions of bootstrapped parameter estimates (log  $\alpha$ ,  $\beta$ ) for the Ricker stock-recruit model for the 1976-1991 time series. Approximate location of "true" parameter estimates are indicated by arrows.



Figure 18. Frequency distributions of bootstrapped parameter estimates (log  $\alpha$ ,  $\beta$ ) for the Ricker stock-recruit model for the 1994-2009 time series. Approximate location of "true" parameter estimates are indicated by arrows.

#### Effects of stock size, climate, and predation

Rainbow smelt recruitment in Lake Huron during 1976-2009 was influenced by stock size, lake trout abundance, Lake Huron water levels, and over basin precipitation. Moreover, based on Akaike weights (AIC weights) and interpretation of evidence ratios, recruitment models considered most plausible for each time period had a strong predatory component as a unifying factor. For the three time periods modeled, a total of 48 models were compared, 16 for each time period. For the 1976-2009 stock-recruit analysis, the most plausible model ( $\approx$  31% of the weight of evidence) included rainbow smelt stock size, lake trout abundance, water levels, and over basin precipitation as factors influencing recruitment (Table 5). AIC weight for the model incorporating stock size, lake trout abundance, and precipitation accounted for 13% of the evidence and was ranked as the next most plausible model (Table 5). All subsequent models weighted between 3-10% included stock size, lake trout abundance, precipitation, and water levels, with temperature not factoring in as an important environmental variable (Table 5).

For the time period from 1976-1991, the best model included only lake trout abundance, and accounted for 24% of the weight of evidence among models (Table 6). The second best model included only stock size and accounted for 20% of the evidence among models. The model combining water levels and lake trout abundance was weighted  $\approx$  13% and AIC weights were distributed among subsequent models containing lake trout abundance, precipitation, or temperature (Table 6). The most important factors influencing recruitment during 1976-1991 were stock size, lake trout abundance, and water levels, with much of the evidence suggesting that the combined influence of lake trout abundance and stock size have the strongest influence on age-0 recruitment to the population.

During 1994-2009, the model containing rainbow smelt stock size and lake trout abundance accounted for  $\approx 62\%$  of the weight of evidence among models (Table 7). The next most plausible model, accounting for only 12% of the weight included precipitation in addition to the previous model variables. The evidence ratio between these two models indicates that the best model is five times more likely and better supported by the data than the second best model.

Table 5. Model selection results for rainbow smelt recruitment in Lake Huron, 1976-2009, based on Akaike weights *wi* and ranked top (best model) to bottom (least plausible model). Also shown are sums of squared errorr, AICc,  $\Delta i$  (AICc differences),  $e^{(-1/2*\Delta i)}$  (model likelihoods), and evidence ratios. All model combinations are shown with Ricker parameters ( $\alpha$ ,  $\beta$ ) and explanatory variables; LT = lake trout CPE, P = overbasin precipitation, W = Lake Huron-Michigan water levels, and T = mean lake temperature 0-20 meters.

Model	SSE	AICc	Δi	e(-1/2*Δi)	Akaike weight	Evidence ratio
$\alpha$ - $\beta$ S-LT-W+P	18.65	-0.193	0.000	1.000	0.309	1.00
$\alpha$ - $\beta$ S-LT+P	21.87	1.483	1.676	0.433	0.134	2.31
$\alpha$ - $\beta$ S-LT	24.71	2.322	2.516	0.284	0.088	3.52
$\alpha$ - $\beta$ S+P	24.74	2.356	2.549	0.280	0.086	3.58
α-βS-LT-W+P- T	18.37	2.576	2.769	0.250	0.077	3.99
$\alpha$ - $\beta$ S-W+P	22.98	2.924	3.117	0.210	0.065	4.75
α-βS	27.82	3.257	3.450	0.178	0.055	5.61
$\alpha$ - $\beta$ S-LT-W	23.83	3.969	4.162	0.125	0.039	8.01
$\alpha$ - $\beta$ S-LT+P-T	21.87	4.425	4.618	0.099	0.031	10.06
$\alpha$ - $\beta$ S+P+T	24.42	4.684	4.877	0.087	0.027	11.46
$\alpha$ - $\beta$ S-LT-T	24.71	5.028	5.221	0.073	0.023	13.61
$\alpha$ - $\beta$ S+T	27.50	5.424	5.618	0.060	0.019	16.59
$\alpha$ - $\beta$ S-W	27.58	5.499	5.692	0.058	0.018	17.22
$\alpha$ - $\beta$ S -W+P+T	22.87	5.718	5.911	0.052	0.016	19.21
$\alpha$ - $\beta$ S-LT-W-T	23.74	6.807	7.000	0.030	0.009	33.12
$\alpha$ - $\beta$ S-W+T	27.34	7.953	8.146	0.017	0.005	58.74

Table 6. Model selection results for rainbow smelt recruitment in Lake Huron, 1976-1991, based on Akaike weights *wi* and ranked top (best model) to bottom (least plausible model). Also shown are sum of squared errorr, AICc,  $\Delta i$  (AICc differences), e<sup>(-1/2\*\Delta i)</sup> (model likelihoods), and evidence ratios. All model combinations are shown with Ricker parameters ( $\alpha$ ,  $\beta$ ) and explanatory variables; LT = lake trout CPE, P = overbasin precipitation, W = Lake Huron-Michigan water levels, and T = mean lake temperature 0-20 meters.

Model	SSE	AICc	Δi	e(-1/2*Δi)	Akaike weight	Evidence ratio
α-βS-LT	1.95	-25.689	0.000	1.000	0.242	1.00
α-βS	2.42	-25.316	0.374	0.830	0.200	1.21
α-βS-LT-W	1.67	-24.509	1.180	0.554	0.134	1.80
α-βS-W	2.19	-23.849	1.840	0.399	0.096	2.51
α-βS-Ρ	2.21	-23.703	1.986	0.370	0.089	2.70
α-βS-LT-P	1.90	-22.489	3.200	0.202	0.049	4.95
α-βS-Τ	2.39	-22.393	3.297	0.192	0.046	5.20
α-βS-LT-Τ	1.93	-22.211	3.479	0.176	0.042	5.69
α-βS-W-P	2.07	-21.090	4.599	0.100	0.024	9.97
$\alpha$ - $\beta$ S-LT-W-T	1.64	-20.425	5.265	0.072	0.017	13.91
$\alpha$ - $\beta$ S-P+T	2.16	-20.382	5.308	0.070	0.017	14.21
$\alpha$ - $\beta$ S-W+T	2.17	-20.354	5.335	0.069	0.017	14.40
α-βS-LT-W-P	1.67	-20.186	5.504	0.064	0.015	15.67
α-βS-LT-P-T	1.89	-18.168	7.521	0.023	0.006	42.97
$\alpha$ - $\beta$ S-W-P+T	2.04	-16.992	8.697	0.013	0.003	77.38
$\alpha$ - $\beta$ S-LT-W-P-T	1.64	-15.092	10.598	0.005	0.001	200.10

Table 7. Model selection results for rainbow smelt recruitment in Lake Huron, 1994-2009, based on Akaike weights *wi* and ranked top (best model) to bottom (least plausible model). Also shown are sum of squared errorr, AICc,  $\Delta i$  (AICc differences), e<sup>(-1/2\*\Delta i)</sup> (model likelihoods), and evidence ratios. All model combinations are shown with Ricker parameters ( $\alpha$ ,  $\beta$ ) and explanatory variables; LT = lake trout CPE, P = overbasin precipitation, W = Lake Huron-Michigan water levels, and T = mean lake temperature 0-20 meters.

Model	SSE	AICc	Δi	e(-1/2*Δi)	Akaike weight	Evidence ratio
α-βS-LT	5.18	-3.299	0.000	1.000	0.619	1.0
α-βS-LT-P	4.76	-0.071	3.228	0.199	0.123	5.0
$\alpha$ - $\beta$ S-LT-W	4.94	0.414	3.713	0.156	0.097	6.4
$\alpha$ - $\beta$ S-LT+T	5.17	1.025	4.324	0.115	0.071	8.7
α-βS	10.35	2.237	5.536	0.063	0.039	15.9
$\alpha$ - $\beta$ S+T	9.79	4.979	8.277	0.016	0.010	62.7
α-βS-LT-W-P	4.72	5.403	8.702	0.013	0.008	77.5
α-βS-LT-P-T	4.75	5.488	8.787	0.012	0.008	80.9
$\alpha$ - $\beta$ S+P	10.21	5.528	8.827	0.012	0.008	82.6
$\alpha$ - $\beta$ S+W	10.23	5.549	8.848	0.012	0.007	83.4
$\alpha$ - $\beta$ S-LT-W-T	4.91	5.927	9.225	0.010	0.006	100.8
$\alpha$ - $\beta$ S+W+T	9.48	8.896	12.195	0.002	0.001	444.7
$\alpha$ - $\beta$ S+P+T	9.63	9.093	12.392	0.002	0.001	490.8
$\alpha$ - $\beta$ S+W+P	10.18	9.827	13.126	0.001	0.001	708.3
α-βS-LT-W-P-T	4.70	12.773	16.072	0.000	0.000	3089.6
$\alpha$ - $\beta$ S+W+P+T	9.47	14.455	17.754	0.000	0.000	7163.8

## Discussion

Variation in density of age-0 rainbow smelt recruits in the fall over the entire time series (1976-2009) was best described by a Ricker stock recruit model that incorporated values of the stock abundances of rainbow smelt and lake trout CPE as biological variables, and water levels and over basin precipitation as physical factors contributing to recruitment variability during the first year of life. These results were taken to indicate precipitation had a strong positive influence on stream conditions for egg and larval survival through modification of stream environments, while water levels change had a negative effect on recruitment. Substantial empirical support (i.e., AIC  $\Delta i < 2$ , Burnham and Anderson 2002) was also found for the Ricker model with lake trout CPE and over basin precipitation for the entire time series, with Lake Huron water levels not factoring in as an important influence on recruitment. Additionally, water temperature was not an important environmental variable that influenced age-0 recruitment to the population during these years. When this time series was split into two periods (1976-1991 and 1994-2009) to eliminate any possible sampling biases based on the change in trawling gears that were used, similar results were obtained. During 1976-1991, the Ricker stock recruit model including stock size and lake trout CPE best explained the variation in recruitment. Substantial support (i.e., AIC  $\Delta i < 2$ ) also existed for one model including lake trout CPE and Lake Huron water levels, and for models including only stock size, Lake Huron water levels, or precipitation alone. The Ricker model that best described variation in recruitment from 1994-2009 included only lake trout CPE as an explanatory variable. Evidence in support of this model was confirmed by a relatively large AIC weight (AIC w = 0.62) and no other model with substantial empirical support (i.e., no model with AIC  $\Delta i < 2$ ). These results suggest that rainbow smelt stock size and lake trout CPE are key factors regulating recruitment of rainbow

smelt in Lake Huron, as these factors were common to the most plausible models identified for the three time periods. These results were interpreted to mean lake trout predation had a strong influence on the abundance of rainbow smelt spawning stock, thereby limiting reproductive capacity of the population through removal of these spawning stocks. Lake trout predation was also considered to be an important regulator of age-0 or juvenile abundance during this time period. Rainbow smelt stock size was probably important for two reasons. First, increased density of reproductive age fish increases the egg and larval densities produced by the population (Ricker 1975). Secondly, at higher stock sizes, cannibalism became an important regulator of age-0 density. This phenomenon can be seen for most observation during the 1980s in the 1976-2009 model.

No similar stock-recruit analysis has been published for Lake Huron rainbow smelt populations, but previous studies focusing on rainbow smelt populations in Lakes Superior and Erie have considered abiotic and biotic influences on its recruitment dynamics. For instance, lake trout populations during 1974-2005 were closely associated with population dynamics of rainbow smelt in Lake Superior (Gorman 2007). Successful plantings built up the lake trout population during the 1970s and large predatory demand by these populations resulted in large declines in rainbow smelt abundance during the early 1980s (Gorman 2007). Gorman (2007) further suggested that cisco populations served as a predatory buffer between lake trout and rainbow smelt, and that poor cisco production was linked with further declines in rainbow smelt.

Further support for the recruitment model developed for rainbow smelt in Lake Huron comes from Hoff (2004) who found May rainfall, rainbow smelt stock size, and bloater (*Coregonus hoyi*) biomass to be the most important factors influencing rainbow smelt recruitment in Lake Superior. The interaction between bloater biomass and lake trout was found

to positively influence rainbow smelt recruitment in Lake Superior, with bloater presumably serving as a buffer to lake trout predation on rainbow smelt (Hoff 2004). While this relationship to lake trout was indirect, this represents the important predatory influence lake trout may have on rainbow smelt populations in other Great Lakes. In Lake Erie, recruitment of YOY rainbow smelt was not related to water temperature or rainbow smelt stock size but appeared inversely related to age-1+ rainbow smelt abundance, indicating cannibalism was a significant controlling factor at times in these populations (Henderson and Nepszy 1989). While salmonid predation was not found to be correlated with recruitment, the authors posit that rainbow smelt year classes were largest in Lake Erie during years when lake trout and pacific salmon plantings were low (Henderson and Nepszy 1989).

The approach of modeling rainbow smelt recruitment for three separate time blocks was to account for a change in bottom trawling gear that occurred in the USGS GLSC bottom trawl survey after 1991. Because fishing power corrections developed by Adams et al. (2009) could not resolve differences in trawling gear catchability for age-0 rainbow smelt (i.e., no correction factor to recast age-0 catches during 1976-1991), splitting the 1976-2009 time series into two periods (1976-1991 and 1994-2009) allowed for the separate analysis of stock recruit relationships for each trawl and served as an alternative approach that would acknowledge potential differences in age-0 catchability between trawling gears. This approach resulted in the model for 1976-1991 having a limited number of observations at low stock sizes, often where the stock-recruit relationship is best defined (Hilborn and Walters 1992). In contrast, models for 1976-2009 have a broad range of stocks sizes which help define depensatory and compensatory processes important to understanding stock-recruit relationships (Hilborn and Walters 1992). Thus, the attempt to deal with variable catchability by treating these data as two
time series yielded two models that described the stock-recruit relationship well and one model that had low power to detect the stock recruit relationship at low stock sizes (i.e., 1976-1991).

These recruitment models are useful for understanding factors associated with rainbow smelt recruitment in Lake Huron, the Great Lakes, and large systems where this species occurs. Based on the history of lake trout stocking in Lake Huron, recent evidence of natural reproduction of this species in Lake Huron (Riley et al. 2007), and models presented here, results indicate that predation by lake trout was a strong regulator of recruitment during 1994-2009. During 1994-2002, lake trout stocked in US waters of Lake Huron averaged 4 million fish, and during subsequent years an average 1.5 million lake trout have been stocked annually (FWS/GLFC). Evidence of natural reproduction by lake trout was first detected in 2004, indicating that wild lake trout were in the population (Riley et al. 2007). Furthermore, lake trout predation on rainbow smelt has been well documented in Lake Huron (Diana et al. 1991, Madenjian et al. 2006) and Lake Michigan (Madenjian et al. 1998).

The best model selected for recruitment during 1994-2009, which included only lake trout abundance, is also supported based on the recent changes in size structure of the rainbow smelt population in Lake Huron. During 1997, hydroacoustic surveys of Lake Huron's main basin identified a population comprised of multiple age classes, with approximately 40% of the population age-0 fish (Warner et al. 2004). However, in 2004 this survey found age-0 fish to make up approximately 60% of the total rainbow smelt density, indicating substantial declines had occurred in the abundance of adults. Bottom trawl surveys during 2004-2009 corroborated this general trend of the rainbow smelt population dominated by small (<90mm) rainbow smelt with greatly reduced numbers of older age classes (Roseman et al 2008; Riley et al. 2009). Low stock sizes during 2005 produced the largest index of age-0 abundance during the entire 1976-

65

2009 time period, but subsequent years failed to indicate substantial recruitment to older age classes. In fact, the 1994-2009 time series had the five highest recruitment events for the entire 29 year period, all of which failed to result in increased abundance of adults in subsequent years. The paucity of older age classes in recent years suggests that predation occurring on age-1+ rainbow smelt was substantial in Lake Huron, similar to predator induced changes that occurred in Lake Superior rainbow smelt populations during 1974-2005 (Gorman 2007).

This research has identified a strong trophic link between lake trout and rainbow smelt that has implications for future rehabilitation efforts of lake trout in Lake Huron and the Great Lakes. First, rainbow smelt are the dominant prey species in Lake Huron following the collapse of alewife (*Alosa psuedoharengus*) populations after 2003 (Riley et al. 2010). Secondly, rainbow smelt are important in the diet of lake trout during young-of-the-year (Swedberg and Peck 1984), juvenile (Eck and Wells 1983), and adult (Madenjian 2006) stages, thereby indicating their importance to lake trout populations over a wide range of age classes. Finally, lake trout will need to compete with stocked salmonines, percids and other predators for low prey resources in Lake Huron. Managers should be concerned that consumption by predators in Lake Huron could approach the level of production by prey species (Bence 2005), and result in poor growth or condition of economically valuable sport fishes.

Because the prey fish community available to salmonine predators in Lake Huron is currently dominated by one species, the rainbow smelt, and because Lake Huron is a multijurisdictional resource with competing socioeconomic and ecological needs (i.e., sustenance of hatchery dependant sport fisheries, lake trout restoration, and commercial fisheries), allocation of this important prey resource among fishery components will remain a challenge for fishery managers. As such, the primary tools for allocating prey resources are either to control the

66

number of predators via stocking or limit the harvest of prey or predator species (Brown et al. 1999). Furthermore, while state or provincial boundaries exist for management of Lake Huron's fisheries, the fish communities, particularly the predator-prey assemblages, are part of larger ecosystems, and thus must be managed through cooperative means across jurisdictions (Brown et al. 2009). This research further supports the assertion that continued rehabilitation efforts of lake trout and maintenance of current stocks of introduced salmonines in Lake Huron will be dependent on the availability of rainbow smelt populations as a principal forage base, with other species such as bloater (*Coregonus hoyi*) or cisco (*Coregonus artedii*) further diversifying the prey assemblage.

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