A Dissertation

entitled

Modeling the Effects of Turbidity on Age-0 Yellow Perch (Perca flavescens) in the

Western Basin of Lake Erie

by

Nathan F. Manning

Submitted to the Graduate Faculty as partial fulfillment of the requirements for the

Doctor of Philosophy Degree in Biology

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August, 2013
An Abstract of

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Understanding the effects of turbidity on visually foraging fish species can be difficult due to the dynamic nature of sediment plumes and algal blooms in productive aquatic systems. In this dissertation, I examined the effects of turbidity type, timing and intensity on age-0 yellow perch (Perca flavescens). To accomplish this, I used ArcGIS and generalized additive models (GAMs), individual based models (IBMs) and the Soil and Water Assessment Tool (SWAT). The initial study utilized ArcGIS and GAMs to determine the relationship between turbidity and size and abundance in August of age-0 yellow perch. The GAMs presented in this dissertation show that water clarity (in this case used as a surrogate for turbidity) is an important environmental factor in determining the length and abundances of age-0 yellow perch in western Lake Erie. The results suggest that the influence of water clarity produces a distinct separation of areas of higher growth potential and areas of higher abundances in the western basin. While this division may be attributable to a number of mechanisms, including size dependent predation risk, foraging ability, and density dependent growth, the effects of water clarity, and in particular the negative effects of algal blooms, on foraging ability are of particular
interest in Lake Erie. For the second step in this research I used laboratory derived feeding rates in a range of turbidity types and intensities to inform IBMs that varied the timing, type and intensity of turbidity to determine the effects of changes to a systems turbidity regime on growth and starvation mortality. The results of the model suggest that the timing and persistence of sediment plumes and algal blooms can drastically alter the growth potential and starvation mortality of a yellow perch cohort. The timing of sediment plumes in particular can have significant consequences to the growth, and ultimate success of a yellow perch population. High sediment turbidity early in the season, prior to the ontogenetic shift, can be potentially beneficial to fish growth. However, if high sediment turbidity conditions persist, they can slow growth and increase the starvation mortality of juvenile fish. In contrast, algal blooms, no matter when during the season they occur. In the final study, I used SWAT and IBM models to link watershed level changes in land use and climate to potential changes in age-0 yellow perch growth in the Maumee Bay, Lake Erie. Changes in land-use, either through increased urbanization, or changing agricultural practices, primarily affect fish growth through the alteration in the timing and intensity of sediment plumes. However, it may be that, at least in the Maumee River watershed, the negative effects have reach a plateau of sorts, with significant reductions in fish growth requiring changes to the watershed that are unlikely in the near future due to economic and infrastructure restrictions. Climate change, on the other hand, could potentially compound the effects of current land use practices through the promotion of algal blooms due to increased water temperatures, thus further reducing fish growth. The results of these three studies show that the effects of turbidity on age-0 yellow perch are dynamic, and can vary significantly depending on a
number of different factors. The results of this research help to illuminate these complex interactions, and provide a warning about potential consequences due to anthropogenic alterations of an aquatic system’s turbidity regime.
Acknowledgements

I would like to acknowledge the contributions to this dissertation by my advisors, Drs. Mayer and Bossenbroek, from the Department of Environmental Science at the University of Toledo, my committee members, Dr. Thomas Bridgeman, Dr. David Bunnell, and Dr. Stuart Ludsin, and the many fellow students the University of Toledo who reviewed, edited and commented on the research presented here. I would also like to acknowledge the funding sources that made this research possible, including, the Great Lakes Fishery Commission, the NSF GK-12 fellowship program, and the Lake Erie Protection Fund. Data for this research was provided by Jeff Tyson of the Ohio Department of Natural Resources, Fish and Wildlife Division, and Drs. Jackson and Rudstam from Cornell University.
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GAM ....................... Generalized Additive Models
GCC .......................... Global Climate Change
IBM ........................... Individual Based Model
ODNR ....................... Ohio Department of Natural Resources
SWAT ........................ Soil and Water Assessment Tool
Chapter 1

1.1 Introduction

The visual environment encountered by fish is dynamic, and even seemingly insignificant changes can have wide ranging impacts on fish. Turbidity, the reduction in water clarity due to small, suspended particles in the water column, in particular has been shown to affect the foraging success and predation risk of young fish (Mills et al. 1986; Miner and Stein 1993; Mayer et al. 2000; Harvey and Brown 2004; Reichert et al. 2010; Wellington et al. 2010; Pangle et al. 2012) and, in turn, the growth, recruitment, and subsequent year class strength of a population (Noble 1975; Crecco and Savoy 1985; Tyson and Knight 2001; Reichert et al. 2010). The negative effects of turbidity on foraging tend to increase with fish size because a fish’s field of vision increases as it gets larger, resulting in greater distances between fish and potential prey (DeRobertis et al 2003). This size-dependent effect has the potential to alter how turbidity affects a population as the individuals develop, suggesting that the timing of turbidity events may play a key role in determining how a population would be affected by changes in turbidity. Because of the potentially complex interaction between turbidity and fish, it is important to quantify how the intensity, timing and duration of both sediment plumes and algal blooms may affect fish populations.
Turbidity in aquatic ecosystems is generally of two types; 1) sediment turbidity, which is influenced by runoff from the watershed and resuspension events (Stortz et al. 1976; Uncles et al. 1994; Li and Zhang 1998), and 2) algal turbidity, which is affected by nutrient availability and temperature (Sneller et al. 2003; Paerl and Huisman 2008). Because the sources of turbidity are often influenced by the surrounding watershed, the timing and intensity of sediment plumes and algal blooms can often be altered by human activity. Agriculture, forestry, construction, and channel dredging, can all lead to influxes of sediment and nutrients into aquatic habitats (Baker and Richards 2002; Ouyang et al. 2005). Agriculture, in particular, contributes large amounts of sediment as well as nutrients that fuel phytoplankton blooms, resulting in low water clarity (Nichols and Hopkins 1993; Heisler et al. 2008). The effects of climate change can also alter the turbidity regime of an aquatic system, either through changes in precipitation leading to alteration in runoff cycles from the surrounding watershed, or through increasing temperatures affecting the timing and intensity of algal blooms. Consequently, it is important to understand how human activity in a watershed can affect fish populations by altering the timing, and intensity of sediment plumes and algal blooms in the associated aquatic system.

This dissertation describes the effects of changes in turbidity type and timing on both larval and juvenile yellow perch over the course of the first summer, and quantifies how turbidity effects change as these individuals develop. Previous research has often focused on a single developmental stage, and so this dissertation helps to connect changing turbidity regimes to the development of these fish. Additionally, this research addresses the effects of human impacts in associated terrestrial environments, and how
man made impacts can affect yellow perch through alterations in the sediment and nutrient inputs to an aquatic system. Prior studies have attempted to link changes in the aquatic community to changes in the surrounding watershed, but few have been able to describe the mechanisms involved. This research is able to describe these mechanistic links by modeling not only how changes in the surrounding watershed alter the visual environment of the aquatic system, but how those changes affect the bioenergetics, and this growth and survival of age-0 yellow perch in these systems.

The overall goal of this dissertation is to determine how alterations to turbidity type, intensity, and timing affect age-0 yellow perch in productive aquatic systems. I will examine how lengths and abundances of age-0 yellow perch are related to water clarity, how the timing and intensity of sediment plumes and algal blooms affect growth and starvation mortality, and link changes in the land use and climate of the surrounding watershed to potential impacts on fish production. To accomplish this goal, I apply an array of modeling techniques, including Generalized Additive Models (GAM), Individual Based Models (IBM), and the Soil and Water Assessment Tool (SWAT), to long term data sets for the western and central basins of Lake Erie, and Oneida Lake, NY.

In the course of this research I address six specific objectives: 1) Quantify the shape and fit of the relationships of age-0 yellow perch abundance and size-at-age with water clarity, 2) determine if turbidity explains more variability in age-0 yellow perch size and abundance than other environmental factors by comparing a suite of candidate GAMs to find the best-fit model. 3) Determine if an IBM that uses laboratory derived feeding rates to estimate daily consumption can adequately describe the growth and starvation mortality of age-0 yellow perch in productive aquatic systems, 4) Quantify the
potential impacts on yellow perch growth and starvation mortality due to changes in plume and bloom dynamics. 5) Identify the potential effects on the growth of yellow perch in the Maumee Bay due to current and possible land use practices in the Maumee River watershed, and 6) Predict potential impacts on yellow perch growth due to changes in the watershed based on predicted climate alterations.
Chapter 2

Effects of Water clarity on the Length and Abundance in August of Age-0 Yellow Perch in the Western Basin of Lake Erie

2.1 Introduction

Water clarity is a defining feature of aquatic habitats and shapes the physical environment fish encounter through changes to primary productivity, habitat availability, and light limitation. Such environmental changes subsequently affect fish behaviors including predator avoidance, habitat selection, and foraging time and ability. Experimental and field-based studies have shown that water clarity affects foraging by young fish (Mills et al., 1986; Miner and Stein, 1993; Mayer et al., 2000; Harvey and Brown, 2004; Wellington et al., 2010) and, in turn, the growth, recruitment, and subsequent year class strength of a population (Noble, 1975; Crecco and Savoy, 1985; Tyson and Knight, 2001; Reichert et al., 2010).

Multiple factors mediate the effect of water clarity on fish foraging, including fish species (Rowe and Dean, 1998; DeRobertis et al., 2003), developmental stage (Bohlert and Morgan, 1985; Crowl, 1989; Utne-Palm, 2002), and turbidity type and intensity (Carton, 2005; Radke and Gaupisch, 2005). For example, in a series of laboratory
experiments with larval and juvenile yellow perch \((\text{Perca flavescens})\), Wellington et al. (2010) found that sediment and algal turbidity differentially affected foraging in larval and juvenile yellow perch. Specifically, high sediment turbidity did not reduce the foraging rate of larval yellow perch, but did reduce the foraging of juveniles (Wellington et al. 2010). Alternatively, algal driven turbidity (at all intensity levels) reduced the foraging ability of both larvae and juveniles (Wellington et al., 2010). While turbidity, in general, lowers food consumption, the negative effects on visual foraging become more pronounced as fish size increases (Diehl, 1988; Hartman and Margraf, 1993; Wahl et al., 1993; DeRobertis et al., 2003; Chiu and Abrams, 2010) and so, age-0 survival may increase as clarity decreases, due to a reduction in predation pressure from larger, visually foraging species. Consequently, age-0 fish may experience a tradeoff with greater food consumption and higher growth in clear water but greater survival and hence higher abundance in turbid water.

Water clarity offers an important management lever for fish populations. Unlike many of the factors that influence the survival of age-0 fish, such as temperature, water movement and zooplankton abundance (Hoffman et al., 2001; Olson et al., 2001; Paukert and Willis, 2001; Clapp and Detmers, 2004; Hargeby et al., 2007) water clarity can be changed by altering land use practices. Agriculture, forestry, construction, and channel dredging, lead to influxes of sediment and nutrients into aquatic habitats (Baker and Richards, 2002; Ouyang et al., 2005) that promote sediment plumes and phytoplankton blooms, resulting in low water clarity (Nichols and Hopkins, 1993; Heisler et al., 2008). These anthropogenically driven sediment plumes and algal blooms have become widespread in coastal systems that are often important nursery areas for age-0 fish (Nack et
al., 1993; Jones et al., 2003). The Mississippi Delta (Green et al., 2006), Chesapeake Bay (Gitelson et al., 2007), and the western basin of Lake Erie (Ludsin et al., 2001) have all experienced problems with sedimentation and harmful algal blooms. Such coastal systems are economically and ecologically valuable and so it is important to understand how sediment and algal turbidity affects the fish populations that utilize these areas.

The western basin of Lake Erie presents a valuable system for the study of water clarity effects on fish because the two major tributaries entering the lake, the Maumee and Detroit Rivers, differ widely in flow volume, total suspended solids and phosphorus concentrations (Reichert et al., 2010). The Maumee River contributes less than 15% of the total water that flows into the western basin of Lake Erie, but it contributes more than half of the suspended sediments input, and more than 2,240 tons of phosphorus annually (Moorhead et al., 2003) influencing sediment plumes (Paul et al., 1982) and algal blooms in the western basin (Smith, 1982; Correll, 1998). The Detroit River discharge averages 5,324 m$^3$/s, much higher than the Maumee’s average discharge of 150 m$^3$/s, and has much lower concentrations of both sediment and phosphorus (OEPA, 2010). The contrast between these tributaries produces a split in western Lake Erie, with the southern shore dominated by the warm, turbid water of the Maumee, and the northern shore reflecting the cold, clearer water of the Detroit River (Reichert et al., 2010). In this study I take advantage of long-term, basin-wide surveys of an abundant and ecologically important visually feeding fish (yellow perch) in the western basin of Lake Erie to build predictive models of the response of age-0 fish to varying water clarity.

I suggest that yellow perch caught from clearer water will be larger than those in turbid areas, perhaps due to an increased ability to forage, and greater size selective
predation by visually foraging predators. Alternatively, fish may be more abundant in turbid water that affords some refuge from predation, but will be smaller due to reduced foraging ability. Also, given the high contrast in water clarity in the western basin of Lake Erie, I hypothesize that water clarity will be more important than other physical factors in explaining variability in age-0 yellow perch size and abundance. I quantified the relationships between turbidity and abundance and length of age-0 yellow perch using Generalized Additive Models (GAMs). This approach allowed us to: 1) quantify the shape and fit of the relationships of age-0 yellow perch abundance and size-at-age with water clarity and, 2) determine if turbidity explains more variability in age-0 yellow perch size and abundance than other environmental factors by comparing a suite of candidate GAMs to find the best-fit model.

2.2 Methods

Environmental and fisheries data were provided by the Ohio Department of Natural Resources (ODNR) and the Ontario Ministry of Natural Resources (OMNR). Inter-agency trawl data were collected during June, July and August, 1986 – 2006, using techniques described in Tyson et al. (2006). Environmental data used in this research include: bottom oxygen levels (mg/L), bottom water temperature (°C), water depth (m), Secchi depth (m) (used as a surrogate for transparency), and geographic location (decimal degrees). Fisheries data recorded included fish species caught, individual fish age as determined by ODNR personnel, individual fish lengths (mm), trawling speed, time and gear used, and total catch numbers. For this study, environmental data for all months were included in my analyses, while only the August fish data were considered because this is when age-0 yellow perch have become demersal and are regularly captured by the
trawls. Catch numbers for the age-0 yellow perch were converted into catch per unit effort (CPUE) by standardizing total catch by swept area and time for each trawl (Tyson et al., 2006), and used to assess total abundance of age-0 yellow perch during August. The individual fish lengths and CPUE were also relativized across all years, to remove the effect of year-to-year variation while still maintaining any long-term trends in the data. Using these data, I did three general analyses: 1) visualized the data using GIS to aid in candidate model selection, 2) tested for differences in the distribution of lengths in August of yellow perch between the fish caught in areas influenced by the Detroit River compared to the Maumee River, and 3) used Generalized Additive Models to analyze the relationships between environmental variables and abundance and size of yellow perch.

Data Visualization & Trend Analysis

The data points for environmental and fish variables were visualized in ArcGIS 9.3 (Johnston et al., 1995) and tested for spatial autocorrelation using the geoR package in R (Ribeiro and Diggle, 2001). Given the obvious trends in water clarity in Lake Erie, I tested my length, CPUE and Secchi depth locations for spatial autocorrelation using the method described in Kaluzny et al. (1998). First I used General Linear Models to remove the trends in the data using the general equation: \( f(x) = \text{Latitude} + \text{Longitude} \). Semivariograms of the residuals of these models were assessed for spatial autocorrelation. No autocorrelation was detected for length, CPUE or Secchi depth after accounting for the general trends. The water clarity data points from the inter-agency trawls were then used to create predictive surfaces, i.e. maps, of the western basin using universal kriging. Universal kriging accounts for both trends and auto-correlation between known points to
predict values of a specified parameter in areas not directly measured (Johnston et al., 2003).

Kolmogorov-Smirnov test

One obvious pattern observed in my GIS analysis is the difference in water clarity between the clearer output of the Detroit River and the more turbid output of the Maumee River. To quantify differences between these areas, I defined four regions of the western basin of Lake Erie, the northern and southern halves separated to distinguish the Detroit River inputs from the Maumee River, and the eastern and western halves separating the basin via the portion of the basin influenced by a series of islands (Fig. 2-1A).

Figure 2-1 A and B. Maps of the western basin of Lake Erie showing: (A) Approximate distribution of sample locations. The dotted lines indicate the approximate divisions used to separate the four sections of the basin. (B) Kriging map of average August transparency levels in the Western basin of Lake Erie, 1986 - 2006.

All four regions included at least 45 unique sample locations and more than 300 observations across all included years. A Kolmogorov-Smirnov (KS) test was performed using R (v. 11.1) to determine whether size distributions of age-0 yellow perch from different regions of the basin were statistically different. For this test I focused on the two
regions identified in the data visualization with the greatest difference in mean age-0 yellow perch length in August which were the NW and SE quadrants.

Model Construction

Generalized Additive Models were used to analyze the relationships between environmental variables and abundance and size of yellow perch because of their flexibility when handling non-normal data (Yee and Mitchell, 1991). They allow the inclusion of both parametric and non-parametric data, which allows for a potentially better fit to non-normal data sets (Faraway, 2006). The non-parametric nature of GAMs allows for the determination of the shape of the response curves from the data as opposed to a priori, parametric linear models. The GAM fits a number of linear regressions to the data and then uses a series of smoothing splines to fit a regression line that best describes non-normal data (Faraway, 2006). In this application, GAMs were used to model the effect of a suite of environmental variables on yellow perch abundance and length in August. I used the gam function of the mgcv package in R (v. 11.1), specifying a Gaussian family with an identity link function. The gam function fit a cubic smoothing spline to the dynamic factors included in each of the candidate models if doing so lowered the generalized cross validation (GCV) score of the model. The models were then compared using Akaike’s Information Criterion (AIC) to identify the one model with the most reduction in deviance, and thus the best “fit” to the data. AIC is a goodness of fit index that penalizes a model based on the number of parameters included to reduce the probability of over-fitting (Akaike, 1987). The Δ AIC values (the difference between the best-fit model and any other model) were used to compare the relative fit of the
compared models, where a difference > 2 is considered a meaningful difference in the “fit” of the models (Hilborn and Mangel, 1997).

I developed a suite of a priori candidate models to examine the importance of transparency in explaining patterns of relative abundance and size of age-0 yellow perch. The factors included in the candidate models were based on relationships found in the literature, and preliminary visualization of the maps in Figure 2-1. For example, feeding rates of yellow perch larvae and juveniles are affected by both the intensity and type of turbidity that they encounter (Wellington et al., 2010). Temperature (Enders et al., 2006), dissolved oxygen levels (Kramer, 1987), and spawning depth (Williamson et al., 1997) have also been shown to affect the growth of yellow perch.

I constructed ten candidate models to predict relative CPUE, and length of the age-0 yellow perch in August (Table 2.1). The parameters that were considered for inclusion were the June, July and August values for Secchi depth, bottom temperature and bottom oxygen. Data from previous months (June and July) were included as I assume that growth and abundance are a result of both past and current additions. I make the assumption that the conditions in past months at a specific site are the best available measure of the environmental conditions experienced by fish captured at that site. Larval fish are planktonic and subject to dispersal by hydrodynamic movement, but once they become demersal they search out near-shore habitats and are much less prone to involuntary dispersal (Post and McQueen, 1988). The Secchi depth, bottom temperature and bottom oxygen are listed as my “dynamic” factors, as their values can change from sample to sample. I also considered the values for depth at each sampling site and the latitude and longitude for each sample. These values are termed “static” factors, as these
values remain the same for a given site across years. The final combination of factors included in each of the candidate models was determined by creating combinations of factors that may have an ecological impact on the growth and abundance of the yellow perch. A base model, which only included August Secchi depth, was included, as was a “full” model, which included all of the factors used in one or more of the candidate models.

Table 2.1. Model Structure for the candidate models and the respective AIC and ΔAIC values. Model number is indicated on the left. Highlighted cells indicate that a factor was included in that candidate model. Factors listed under “Dynamic Factors” were smoothed when included in a model, while “Static Factors” were not smoothed.

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<th>Model</th>
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The candidate models were designed to examine the effects of conditions at the time of capture as well as prior conditions encountered by the yellow perch.

Combinations of the June, July, and August values for the three dynamic factors were used to create the ten candidate models with values for the static factors (depth, latitude and longitude) included in model numbers 2 through 10 and the full model (Table 2.1). Temperature data from all months were included, as others have shown that juvenile
yellow perch grow at temperatures greater than 13.5°C and lake temperatures generally exceeded this threshold in all three months (Power and Van Den Heuvel, 1999). July and August bottom oxygen levels were included, as bottom oxygen levels in these months can decrease to levels considered stressful to yellow perch as compared to the June values where the basin is still fairly well mixed.

Additionally, I ran a set of time-of-capture models on a sub-set of the larger data suite to assess the relative importance of individual conditions at the time of capture, to determine if previous conditions significantly improved the fit of the models, and to examine the effect of the static variables on the population structure at the time of capture. These models included all combinations of the August dynamic variables, with and without the static variables and are designated as models 1-14 (Table 2.2). Two of the models (7 and 14) included in this set of supplemental models were also included in the a priori model suite.

Table 2.2. Model structure for the supplemental models, and their respective AIC and ΔAIC values. Model number is indicated on the left. Highlighted cells indicate that a factor was included in that candidate model. Factors listed under “Dynamic Factors” were smoothed when included in a model, while “Static Factors” were not smoothed.
2.3 Results

Data Visualization and Basin Comparison

Preliminary exploration of my data indicated Secchi depth was consistently lower (indicating low transparency) along the south and southeastern shore of the western basin (Fig. 2-1 B). During 1986 – 2008, the mean CPUE (± 1 s.d.) of age-0 yellow perch basin-wide was 40.6 ± 217.4 individuals per trawl. The CPUE in the southeast portion of the basin was nearly twice the overall mean with 79.5 ± 115.3 individuals, whereas the northwestern quadrant of the basin was about 1/4th of the overall mean, at 11.6 ± 24.8 individuals. Age-0 yellow perch CPUE values for the northeast and southwest portion of the basin fell between these two extremes, at 14.6 ± 37.2 and 56.4 ± 77.1 individuals, respectively. Mean length (± 1 s.d.) of age-0 yellow perch basin-wide in August was 66.4 mm ± 4.8 mm, and averaged 67.8 mm ± 2.2 mm in the northwest and 64.9 mm ± 1.9 mm in the southeast. Again, the values for the northeast and southwest regions fell between the values of the northwest and southeast, with age-0 yellow perch averaging 66.8 mm ± 2.3 mm in the northeast and 65.8 mm ± 3.6 mm in the southwest.

A Kolmogorov-Smirnov test of the August length distributions between the northwestern and southeastern populations indicated that the length distributions between the two populations were statistically significantly different (K-S test, p< 0.001; Fig. 2-2). For both distributions, the most frequently occurring size class was the 60-65 mm, but there were just as many occurrences of fish in the 65-70 mm size class in the northwestern end of the basin. Further, the samples from the northwestern end of the basin contained several individuals larger than 80 mm, while the southeast samples contained no individuals larger than 80 mm. More small individuals were found in the
Figure 2-2. Length-frequency distributions of age-0 yellow perch for the northwestern and southeastern portions of the western basin of Lake Erie. Distributions are significantly different (K-S test, p<0.001) between the two areas, with larger fish occurring in the northwestern portion of the basin.

southeast than in the northwest, with several occurrences of individuals smaller than 30 mm. In contrast, no individuals smaller than 30 mm were found in the northwest portion of the basin (Fig. 2-2).

Abundance in August Model

My results indicate that the highest abundances of age-0 yellow perch occurred in areas of low clarity, such as north of Sandusky Bay, and along the south shore of the western basin of Lake Erie (Fig. 2-1 B). Among the candidate models used to explain variation in age-0 yellow perch abundance, model 10 had the lowest AIC value, while the next best-fit model had a ΔAIC value of 24.79 (Table 2.1). This best-fit model explained
73.6% of the deviance observed in the data (Table 2.1). Model 10 indicated that abundance of August age-0 yellow perch varied based on June, July, and August transparency, August bottom oxygen concentration, August bottom temperature, depth, and spatial location (Table 2.1). The smoothing function for August transparency levels indicated peak yellow perch abundances corresponding to the lowest Secchi depths (i.e., lowest transparency), with a sharp decline in abundance as water clarity increased (Fig. 2-3 A).

![Figure 2-3 A-C.](image)

The relationship between yellow perch and August bottom temperature was positive, with increasing abundance in warmer water. August bottom oxygen levels had a humped
response, with the highest yellow perch abundances occurring at approximately 4 mg/l, which, while relatively low, is still above hypoxic levels. The relationships for the static factors (i.e. depth, latitude and longitude) were negative, indicating that highest abundances were found in the shallower areas of the southeastern portion of the basin.

*Length in August Model*

In contrast to the abundance results, the largest individuals during August were found along the northwestern and northern shores of western Lake Erie, areas with the highest levels of clarity throughout the season. The model of age-0 yellow perch length that had the lowest AIC value included all factors except bottom dissolved oxygen (Model 7; Table 2.1) with the next best-fit model having an ΔAIC of 3.76. Model 7 explained 59.7% of the deviance observed in the data. The smoothing function of transparency for length in August increased as Secchi depth increased (Fig 2-4 A). This relationship is seen in all three months included in the model. Bottom temperature displays a general positive trend, with larger individuals predicted in warmer water. This relationship is not as smooth as that of transparency, and displays peaks and valleys across the entire range of temperatures. The June and July data are less noisy, and display a possibly bi-modal distribution, with the largest fish occurring at either end of the temperature spectrum (Fig. 2-4 B). For the static factors, depth was negative, while latitude and longitude were positive, indicating that the largest individuals were found in shallower water in the northwest portion of the basin.

*Time of capture Models*

The time of capture models (Table 2.2) show that the inclusion of prior conditions significantly increased the deviance explained by the models for both length and
Figure 2-4 A and B. — Relationship between August length and the smoothing functions for (A) Secchi depth, and (B) bottom temperature. The solid line is the predicted value of the dependent variable as a function of the x-axis. The small lines along the x-axis are the "rug", showing the value of individual observations. The y-axis is a logit function with values centered on 0 (50/50 odds), and extends to both positive and negative values. The dotted lines are the 95% confidence interval.

abundance (Tables 2.1 and 2.2). For abundance, the best-fit time-of-capture models, model 7 and model 14, had a $\Delta$ AIC value of 0 indicating no significant difference in fit between models. While both models included all three dynamic variables, only model 14 included the static variables, indicating that while the static variables may be important in the determination of August abundance, they do not add enough explanatory power to overcome the bias against model complexity inherent in AIC. The time-of-capture models for August length exhibited a similar pattern, with models 7 and 14 again being selected as the best-fit. The largest change in AIC values was seen when removing Secchi (and thus, transparency) from the models.
2.4 Discussion

Water clarity is an important factor in explaining the variance in length and abundance of age-0 yellow perch in the western basin of Lake Erie. While all of the factors included in my model may play some role in determining the length and abundance of yellow perch, water clarity explained a large portion of the observed deviance of the best-fit models for both abundance and length. The shapes of the observed relationships show that transparency was negatively related to fish length but positively related to abundance, suggesting a trade-off between areas where growth is optimal and where high abundance occurs.

The environmental conditions, including water clarity, from previous months influence both length and abundance of age-0 yellow perch, which was demonstrated by my time-of-capture models. These models also show that static factors, i.e. depth and location, have little effect on length or abundance once the yellow perch have reached the juvenile stage and become demersal. The static factors were included in the best-fit full models, suggesting that location within the basin may be more important early in the growing season when the fish are still in a planktonic-larval state. Further, these results support the notion that habitat is heterogeneous across the basin, and this heterogeneity is driving differences in growth and survival early in the development of these fish.

Several mechanisms, including the effects of water clarity on fish growth and susceptibility to predation, may underlie the observed differences in abundance and length of yellow perch in the western basin of Lake Erie. Further, these mechanisms may interact, such as water clarity interacting with predation by affecting the total number of fish that are consumed, as well as the size distribution of prey. It has been shown that
much of the mortality observed in age-0 fish is due to predation (Forney, 1971; Lyons and Magnusson, 1987), and age-0 fish will often congregate in the littoral zone to avoid pelagic predators (Dorner et al., 1999). Further, low water clarity reduces the rate at which fish can consume prey, especially for large visual predators (Diehl, 1988; DeRobertis et al., 2003). Therefore, turbid areas of the Western Basin may provide lowered predation risk. For example, the Maumee River plume may provide some survival advantage to pelagic larval yellow perch by reducing predation mortality (Reichert et al., 2010). My results show higher abundances in the shallower, more turbid waters of the southeast portion of the western basin, and support the idea that the highly turbid, coastal areas of the western basin of Lake Erie may provide age-0 yellow perch with refugia from pelagic, visual predators.

Water clarity may also affect the size of yellow perch in different areas via size selective predation, which has been shown to be a driver of yellow perch population structure (Nielsen, 1980; Post and Evans, 1989). The primary predators of age-0 yellow perch in the western basin, such as walleye (Sander vitreus) and white perch (Morone americana), are visual foragers, and exert size-selective pressure on age-0 yellow perch (Brandt et al., 1987; Post and Prankevicius, 1987; Parrish and Margraff, 1990; Fulford et al., 2006). The higher water clarity in the northwestern portion of the basin may allow predators to more easily see and consume small yellow perch, contributing to the larger size distribution found in these areas. However, the occurrence of individuals larger than 80 mm in the northwest portion of the basin, with none in the southeast, suggests that size selective predation may not be the only mechanism, and that there may also be a growth advantage to individuals in the clearer water.
Higher growth due to visual conditions and density dependent growth could both potentially explain larger individuals in clear water. Areas with clearer water had lower abundances of yellow perch, which exhibit density dependent growth (Bystrom and Garcia-Berthou, 1999; Irwin et al., 2009). However, in Oneida Lake when the effect of density dependent growth was accounted for, age-0 yellow perch still had significantly increased growth that was attributed to water clarity (Mayer et al., 2000), indicating that changes in water clarity have effects on foraging and growth that are distinct from density dependence. Additionally, laboratory studies show that increasing turbidity, particularly phytoplankton, reduces the consumption of prey items (Wellington et al., 2010) as well increasing behavioral costs due to a higher number of failed attacks (Granqvist and Mattila, 2004; Ljunggren and Sandström, 2007). Both density dependence and increased foraging ability likely contribute to the differences seen in yellow perch length, with fish in clearer water experiencing both a reduced competition for prey items, and an increased ability to consume them.

Gear-bias can sometimes explain differences in sampled size and abundance distributions (Hayward et al., 1989; Breen and Ruetz, 2006); though, gear-avoidance is not consistent with finding larger fish in clearer water. Larger fish theoretically should be more able to avoid the trawl and therefore should be less vulnerable in clearer water, a pattern opposite to my observation. Increased catchability in the more turbid waters of the south and southeast may play some role in the larger CPUE observed, but the combination of trawling speed, gear size, and limited mobility of the age-0 yellow perch would decrease the impact of catchability in these observations. Consequently, my results show that while several mechanisms may be affecting the observed patterns of yellow
perch length and abundance, they are all shaped by alterations of the visual environment for both the age-0 fish and their predators.

My results suggest a tradeoff between habitat types for the first season of development for some fish populations such as yellow perch, with clear water favoring faster growth, and turbid water allowing for higher abundance. The effects of water clarity on fish populations are likely not limited to the western basin of Lake Erie, as other large coastal systems, such as Green Bay on Lake Michigan (Brazner, 1997), Saginaw Bay on Lake Huron (Vanderploeg et al., 2001), the Chesapeake Bay (Fisher et al. 1988, Gitelson et al., 2007) and the Mississippi Delta (Green et al., 2006), support populations of visual predators, and experience intense sediment and algal turbidity events. Increasingly frequent and intense harmful algal blooms (HABs) in the western basin of Lake Erie (Rinato-Kanto et al., 2005; Chaffin et al., 2011) and other coastal areas (Hallegraeff, 1993; Anderson et al., 2002; Backer et al., 2006) will likely lead to reduced food consumption (Wellington et al., 2010) and growth (Metcalf, 1986) of the yellow perch. Anthropogenic activity has made many outwelling zones more turbid and larger (Johnson et al., 1995; Wood and Armitage, 1997), potentially reducing fish growth, but additional stresses on fish populations from introduced predators and competitors may mean that such turbid refugia remain important in maintaining the abundance of river-associated stocks.
Chapter 3

Modeling plumes and blooms: turbidity type and intensity effects on the growth and starvation mortality of age-0 yellow perch

3.1 Introduction

Water clarity is an important component of aquatic environments and often serves as an indicator of overall aquatic ecosystem health (Borja et al. 2004; Young and Collier 2009). Reductions in water clarity, which are linked to changes in land use and climate patterns (Allan 2004), are increasing across a range of ecosystem types, from the Great Barrier Reef (Orpin et al. 1999; Neil et al. 2002; Hoegh-Guldberg et al. 2007) to small freshwater marshes (Crosbie and Chow-Fraser 1999; Scavia et al. 2002; Johnson and Rejmánková 2005). Water clarity affects the biota of a system in many ways, from altering primary productivity (Goldman 1988) to modifying the foraging activity of visual feeders (McMahon and Holanov 2005; Turesson and Brönmark 2007). Many fish are visual foragers, and so their recruitment can hinge on their visual environment and the resultant growth and survival of the age-0 year class (Ware 1975; Crowder et al. 1987; Post and Evans 1989; Rice et al. 1993a; Cowan et al. 1996; Sogard 1997; Bergenius et al. 2002). Therefore, quantifying the relationship between water clarity and age-0 fish
growth and survival may help predict year-class strength, especially under changing environmental conditions.

High levels of suspended particles limit the feeding ability of visual predators through light attenuation and degradation in the apparent contrast between a prey item and its background (De Robertis et al. 2003). The negative effects of turbidity on foraging tend to increase with fish size because a fish’s field of vision increases as it gets larger resulting in greater reaction distances between predator and potential prey (De Robertis et al. 2003). Thus, the effects of a given level of turbidity can change with fish ontogeny and vary across the range of fish sizes present in a population at a given time.

The source of turbidity (sediment vs. phytoplankton) also affects fish foraging. In larval fish, high sediment turbidity can increase feeding ability relative to the juvenile or adult stages, possibly due to increased visual contrast of prey items at the small perceptive scale utilized by larval fish (Boehlert and Morgan 1985; Wellington et al. 2010). High sediment turbidity may also confer a larval survival advantage, either through reduced predation pressure (Reichert et al. 2010), or through reduced starvation mortality during the critical period post yolk-sac absorption (Houde 1975; Munk and Kiørboe 1985). The ability of larvae to feed in high sediment turbidity conditions may indicate an adaptation to near-shore nursery areas that are often productive and influenced by sediment-laden river plumes. However, increasing flashiness of tributaries due to climatic and land-use changes may lead to an alteration of the timing of sediment plumes (Cooper 1995; Friedl and Wüest 2002; Pfister et al. 2004), producing turbid conditions during periods that have historically been clear-water phases (Sutherland et al. 2002) potentially reducing the feeding ability of larger individuals.
Algae are an additional source of turbidity, and are primarily affected by nutrient availability and temperature (Anderson et al. 2002; Paerl and Huisman 2008). Unlike sediment turbidity, which may provide some feeding advantage to larval fish, in productive aquatic systems, algal blooms have been shown to significantly reduce the foraging rate of both larvae and juveniles, even at low intensities (Diehl 1988; Radke and Gaupisch 2005; Wellington et al. 2010). Globally, algal blooms are increasing in intensity and duration (Hallegraeff 1993; Landsberg 2002), and have become problematic in a number of aquatic systems, particularly in Green Bay, Lake Michigan, and the western basin of Lake Erie (Dyble et al. 2003; Bridgeman and Penamon 2010; Bridgeman et al. 2012). The global trend of escalating algal blooms makes it increasingly important to quantify how the intensity, timing and duration of these blooms may affect fish populations.

For this research, I sought to quantify the possible population-level influence of sediment plumes and algal blooms on yellow perch (Perca flavescens), a visual predator often found in systems with dynamic water clarity regimes. Temporal variability in water clarity conditions and the potentially size dependent nature of its effects compel the use a model type that can include both extrinsic and intrinsic variability to describe the possible effects of water clarity on fish growth. Therefore, I chose to use an Individual Based Model (IBM), which allowed us to include both variance in water clarity conditions over time and variance in a population’s response due to the distribution of individual sizes. In doing so, I developed an IBM to track the growth and starvation mortality of larval and juvenile yellow perch under different turbidity scenarios. The IBM integrated the results of a laboratory study that described larval and juvenile yellow perch feeding rates for
different levels of sediment and algal driven turbidity and zooplankton densities. I validated my model using observed environmental data from three different systems and created an array of scenarios that predict how age-0 yellow perch are likely to respond to potential alterations to sediment plume and algal bloom dynamics. In doing so I address two questions: 1) Can an IBM that uses laboratory derived feeding rates to estimate daily consumption adequately describe the growth and starvation mortality of age-0 yellow perch in different systems, and 2) What are the potential impacts on yellow perch growth and starvation mortality due to changes in plume and bloom dynamics?

3.2 Methods

I modified existing IBMs describing generalized larval fish (Letcher et al. 1996b) and larval yellow perch (Fulford et al. 2006a, 2006b) growth and survival by explicitly including the effects of turbidity based on laboratory-derived ingestion rates (Wellington et al. 2010). These measured feeding rates replaced encounter and consumption rates that are traditionally indirectly calculated using swimming speed, light levels and prey densities. My model simulated the daily ingestion, growth, and starvation mortality of larval and juvenile yellow perch through the first 124 days post-hatch. This period covered the majority of the first growing season, and corresponded to when juvenile yellow perch were regularly captured by the Ohio Department of Natural Resources’ (ODNR) trawls, which is one of the data sets used for model validation.

Model Description

General

My base model was constructed using the simcol package in R v.2.15.1 and consisted of an initial cohort of individuals that passed through a series of sub-models
over a course of daily time steps. The sub-models included: 1) daily ingestion, 2) daily bioenergetic growth, and 3) starvation mortality (Fig. 3-1). Each model trial was initiated with a cohort of 10,000 individuals and run for 124 time steps (i.e. days). The initial length of each individual was drawn from a normal distribution (Table 1) and weight was then calculated using a length-weight regression (Table 3.1). For the first four days individuals were considered yolk-sac larvae and did not feed; they grew at a standardized rate of 0.02 g/g⁻¹/day⁻¹ (Gordon 1982) and did not experience starvation mortality. After

Figure 3-1. Flow diagram of the Individual Based Model.
the yolk-sac period, individuals were passed through the three sub-models (ingestion, growth, starvation) each day and size and survival status were updated for all individuals.

Table 3.1. Variable and parameter names, values and sources.

<table>
<thead>
<tr>
<th>Variable or Parameter Name</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial Number of Individuals</td>
<td>10,000 (per cohort)</td>
<td></td>
</tr>
<tr>
<td>Initial length distribution</td>
<td>( \mu = 5.3\text{mm}, \text{s.d.} = 0.3\text{mm} )</td>
<td>Fulford et al. 2006a</td>
</tr>
<tr>
<td>Length to weight equation</td>
<td>( W_k = 0.519^*(\text{length})^{3.293} )</td>
<td>Fulford et al. 2006a</td>
</tr>
<tr>
<td>Ingestion rate, larval in sediment (#/hr)</td>
<td>( i_{LS} = 0.120^*(\text{NTU})+29.248 )</td>
<td>Wellington et al. 2010</td>
</tr>
<tr>
<td>Ingestion rate, larval in algae (#/hr)</td>
<td>( i_{LA} = -0.265^*(\text{NTU})+31.104 )</td>
<td>Wellington et al. 2010</td>
</tr>
<tr>
<td>Ingestion rate, juvenile in sediment (#/hr)</td>
<td>( i_{JS} = -0.359^*(\text{NTU})+86.975 )</td>
<td>Wellington et al. 2010</td>
</tr>
<tr>
<td>Ingestion rate, juvenile in algae (#/hr)</td>
<td>( i_{JA} = -0.449^*(\text{NTU})+35.919 )</td>
<td>Wellington et al. 2010</td>
</tr>
<tr>
<td>Secchi to NTU equation</td>
<td>( \text{NTU} = 5847.4(\text{Secchi})^{-1.371} )</td>
<td>Bridgeman (unpublished)</td>
</tr>
<tr>
<td>Average prey mass (planktonic)</td>
<td>( 8.70 \times 10^{-5} \text{g} )</td>
<td>Rose et al. 1999</td>
</tr>
<tr>
<td>Average prey mass (small benthic)</td>
<td>( 3.81 \times 10^{-3} \text{g} )</td>
<td>Rose et al. 1999</td>
</tr>
<tr>
<td>Average prey mass (large benthic)</td>
<td>( 8.52 \times 10^{-3} \text{g} )</td>
<td>Schlosser and Nalepa 2001</td>
</tr>
<tr>
<td>Starvation threshold</td>
<td>0.53</td>
<td>Fulford et al. 2006a</td>
</tr>
<tr>
<td>CMax Intercept</td>
<td>2.8275</td>
<td>Letcher et al. 1996a</td>
</tr>
<tr>
<td>CMax Exponent</td>
<td>0.8496</td>
<td>Letcher et al. 1996a</td>
</tr>
</tbody>
</table>

Each trial continued for 124 days or until all individuals were dead. Using my base model, I altered parameters within the daily ingestion sub-model to create hypothetical scenarios or historical scenarios that mimic real-world conditions (see below).

**Daily Ingestion**

The daily ingestion sub-model estimated the total mass of prey ingested \( I \) by each individual fish each day as:

\[
equ. 1 \quad I = \sum (i_{th} \ast c_{mass}),
\]
where $i_{ih}$ is the total number of prey items consumed by an individual in a given hour, and $c_{mass}$ is the mass of those prey items consumed. I assumed a twelve hour period of active feeding (daylight hours) as a simplification for modeling purposes (Fulford 2006b). The 12 values for $i_{ih}$ were converted to hourly consumed mass by multiplying $i_{ih}$ by the mass of the average prey type consumed ($c_{mass}$, Table 3.1) and then summing across the 12 hours to determine $I$. $I$ varied as a function of three factors: turbidity type and intensity, life stage of the individual, and prey types consumed (Fig. 3-1). Turbidity type and intensity were assigned based on values derived from my hypothetical and historical scenarios described below. The life stages of yellow perch include an ontogenetic shift from pelagic larvae and post-larvae to more benthic juveniles at $> 30$ mm total length (TL) (Wu and Culver 1992). The 12 hourly ingestion rate values, $i_{ih}$ (Table 3.1) were drawn from a normal distribution based on the results of Wellington et al. (2010), in which ingestion rates varied hourly depending on turbidity type and intensity, zooplankton density and life stage. The range used to calculate the distribution was the values of prey consumed for larvae and juveniles in low (10 zp/l) medium (100 zp/l) and high (300 zp/l) zooplankton densities at a given turbidity type/ intensity combination. If an NTU value used in the model was equal to an NTU value used in the experimental data, then the observed standard deviation was used in the normal distribution, otherwise, the standard deviation of the distribution was the average of the two nearest observed NTU levels. Converting the laboratory data into a normal distribution in this way allowed for stochasticity in feeding rates based on turbidity intensity and type, fish developmental stage, and zooplankton density within day, between day, and between individuals.
The shift from pelagic larvae to benthic juveniles in yellow perch typically results in a switch from an entirely zooplankton diet to one composed of both zooplankton and benthic macroinvertebrates (Wu and Culver 1992). Thus, in my model $c_{mass}$ for individuals smaller than 30 mm TL consisted entirely of planktonic prey, while for individuals larger than 30 mm TL, the change in individual diet composition was achieved by partitioning the calculated values of $c_{mass}$ into 70% zooplankton ($Daphnia$ sp.), 20% small benthic invertebrates (chironomids), and 10% large benthic invertebrate (mayfly larvae), and multiplying those percentages by the respective prey masses (Table 2.1). The partitions were set to be representative of typical diet composition of yellow perch juveniles in Lake Erie (Parrish and Margraff 1994; Tyson and Knight 2001).

Because my ingestion sub-model had the potential to allow an individual fish to feed at or near its maximum feeding rate for multiple hours, it was necessary to limit daily ingestion to a size specific daily maximum ($C_{max}$). If an individual's projected consumption exceeded maximum consumption, the mass of food eaten was set to $C_{max}$ defined as:

$$equ. 2 \ C_{max} = C_{MaxInt} \ast Weight^{C_{MaxExp}}$$

where $C_{MaxInt}$ and $C_{MaxExp}$ were derived from Letcher et al. (1996a) (Table 3.1). This function decreased $C_{max}$ as a percentage of an individual's body weight as fish size increased from a maximum of 200% body weight/day for small larvae to approximately 60% of body weight/day for larger juveniles.

*Bioenergetic Growth*

The bioenergetic sub-model determined individual gains or losses ($\Delta M$) in a day, and was defined as:
\[ \text{equ. 3 } \Delta M = I \cdot AE - TC, \]

where \( I \) (\( \mu g \) ingested/day) is the ingestion rate from above, \( AE \) is the assimilation efficiency set at 0.8, which is the asymptotic maximum identified in Letcher et al. (1996a). Total Costs \( (TC) \) equaled the sum of routine metabolism \( (RM, \mu g/day) \), activity metabolism \( (AM, \mu g/day) \), and specific dynamic action and egestion \( (SDA+E) \):

\[ \text{equ. 4 } TC = RM + AM \cdot 0.5 + I \cdot SDA + E, \]

\( RM \) was a function of fish mass and temperature and was calculated as in Kitchell et al. (1977) and Post (1990). \( AM \) equaled 4.4 times \( RM \) during active feeding hours and 0 during non-feeding times (Post 1990). \( SDA+E \) were defined as a constant proportion of \( I \) (0.30; Letcher et al. 1996a). The value of \( \Delta M \) was then applied to the individual, and the individual’s weight was increased or decreased for the next day cycle. Length could increase due to mass gain; however, it could not decrease due to mass loss. If the individual attained a new maximum weight \( (W_{\text{max}}) \), it was recorded for comparison to subsequent weights in the starvation sub-model.

**Starvation**

Individuals in the model were subject to starvation mortality if they lost a predetermined proportion of their previous maximum body mass. In the model,

\[ \text{equ. 5 } W_s = \text{Thresh} \cdot W_{\text{max}}, \]

where \( W_s \) is the mass at which death is caused by starvation, \( \text{Thresh} \) was the proportion of \( W_{\text{max}} \) at which an individual starved. Individuals that attained \( W_s \) for any value of \( W_{\text{max}} \) died of starvation (Letcher et al. 1996a). The starvation threshold for this model was set to 0.53, a value that has been used for yellow perch (Fulford 2006a), but is conservative.
in that it allows for a greater percentage of mass loss before mortality relative to values (0.58 to 0.87) used for other fish species (Letcher et al. 1996a).

Model Testing and Application

Model Evaluation

To evaluate the performance of my IBM, I compared model output, (mean length at 124 days post hatch) to data collected in the field for three different systems: the western and central basins of Lake Erie, and Oneida Lake, New York. For each comparison, I used field observations of turbidity type and clarity to set the parameters in the daily ingestion sub-model and temperature values to set the bioenergetics sub-model. Using these parameters, I generated results that could be compared to corresponding observed data on fish length.

Data from Lake Erie were collected by the ODNR inter-agency trawl surveys. For the western basin of Lake Erie I considered the years 1987 – 2007, and for the central basin, the years 1990 -2011. For both basins of Lake Erie, individual years of data were included if they had at least two observations for temperature (surface and bottom) and water clarity (Secchi depth) in all months between May and September, and included fish length data from the last week of August and/or the first two weeks of September. Monthly mean field observations of temperature, turbidity and/or water clarity for each system were used to inform the model parameters for each year included in the comparison. For the pelagic larval stage I used surface water temperatures in my model, and bottom temperatures after the ontogenetic shift to more demersal juveniles. The turbidity type was not specified in the water quality data, and so to differentiate between sediment and algal turbidity I used records of phytoplankton density and total suspended
solids by date in the western basin of Lake Erie (Chaffin et al. 2011) for the years 2002 through 2009. In years that phytoplankton density data was unavailable I needed to estimate the start date of an algal bloom. To estimate these bloom dates I used the data from Chaffin et al. (2011) to identify environmental thresholds that best described the onset of algal blooms. For the years 2002-2009, no blooms occurred when surface water temperatures were below 21°C. When this temperature threshold was exceeded, observed Secchi depth was negatively correlated with phytoplankton density, but not to sediment, suggesting that any reduction in water clarity observed in the ODNR data when surface water temperatures exceeded 21°C was likely due to algal turbidity. This corresponds to the general pattern of turbidity observed in the western basin of Lake Erie, with sediment turbidity peaking in the spring and early summer months, and algal blooms being more prominent later in the season (fig. 3-2 A-C). For use in my IBM, an algal bloom was considered to have started if there was an observed decrease in water clarity from the ODNR data and surface water temperature exceeded 21°C, and would end if water temperatures dropped below the threshold value. For both basins of Lake Erie, a May 1st hatch-out date was assumed, as that date is generally the first week in which temperature days have exceeded the 90% hatch-out threshold (Guma’a 1978).

The Oneida Lake data was collected by the Cornell University Biological Field Station, and I included the years 1981-2011. For Oneida Lake, sampling was conducted more frequently, which allowed us to use weekly field observations to set model parameters for each year included. Data for particular years were included if they contained at least one field record per week for temperature, turbidity level, and turbidity type in all months between May and September, and mean fish weights for the 17th and
18\textsuperscript{th} weeks post-hatch. These weights were then converted to length using regression (Schael et al. 1991) for comparison to model results. For Oneida Lake, hatch-out was assumed to be 1 week prior to the first records of 8mm fish, which made hatch-out the last week of April or the first week of May, depending on the year.

Figure 3-2 A-C. Average monthly values for (A) sediment turbidity, B) algal turbidity, and C) surface water temperatures for the western and central basins of Lake Erie and Oneida Lake for years included in the IBM.
The field-measured values for water clarity were converted into nephelometric turbidity units (NTU) using a Secchi depth to NTU conversion equation (Table 3.1) in order to compare with the laboratory-derived feeding rates (Table 3.1). Model output was obtained by running each year in each lake/basin five times, for a total of 50,000 individuals. The daily ingestion sub-model was modified by using the weekly or bi-monthly average NTU values and turbidity types collected in the field. The daily records of individual length, weight, and survival status were averaged within each model run and then across the model runs to produce daily average cohort length and survival values to allow for comparison to field based data from Lake Erie and Oneida Lake.

Average length of age-0 yellow perch at ~124 days post-hatch from the observation data were compared to the length of individuals from the model using linear regression to determine the precision with which the model predicted growth of yellow perch in conditions that mimic natural temporal variations in turbidity type and intensity. ANCOVA for parallel slopes was used to determine if the predicted regression lines were parallel to a 1:1 relationship, indicating no bias for over or under prediction in the model.

Sensitivity Analysis

I used the individual parameter perturbation and sensitivity calculations described in Letcher et al. (1996a) to test the sensitivity of my model outputs of growth and starvation mortality to changes in key parameters. I adjusted the following parameters by ±10% independently: larval and juvenile feeding rates in both sediment and algal turbidity, and temperature. The sensitivities were calculated as

\[ \text{equ 6} \quad \frac{y_+ - y_-}{(y_0 \times 0.2)} \]
where $y_+$ and $y_-$ were the output with the individual parameters adjusted ±10% (five replicates), and $y_0$ was the mean output value (10 replicates) using the unadjusted parameter values. A sensitivity value >1 indicates that the selected parameter had a disproportionately large effect while a value <1 indicates that the change in the individual parameter value had a less than proportional effect on the output.

**Model Scenarios**

I designed twelve scenarios to predict age-0 yellow perch growth across a range of possible future turbidity conditions. First, I conducted “static” runs whereby four possible turbidity type-intensity combinations were held constant for the entire 124-day period: low (~5 NTU) sediment turbidity, high (~100 NTU) sediment turbidity, low algal turbidity, and high algal turbidity. These scenarios span the range observed in the systems and were designed to bracket the responses of both larval and juvenile fish. Growth and survivorship curves were generated for each scenario and examined to determine the relative effects of turbidity type and intensity on growth and starvation rates during the larval and juvenile stages. I also noted the number of days it took for the average individual to reach ≥ 30mm total length (TL) and make the switch to the juvenile feeding regime. Temperature regimes for all twelve scenarios were set to the long-term average in the western basin of Lake Erie for each week included.

Second, I developed eight dynamic scenarios that exposed yellow perch cohorts to hypothetical changes in the intensity and timing of sediment plumes and algal blooms. For these simulations, turbidity conditions were altered based on a series of environmental scenarios that were informed by locally downscaled climate change models for the Great Lakes Basin (e.g. Mortsch and Quinn 1996; Goyette et al. 2000).
These climate change models were used to broadly define generic scenarios that would correspond to potential changes in turbidity regime, such as an especially wet spring prolonging the sediment plumes from surface run-off, or extended periods of high temperatures and low precipitation allowing algal blooms to start earlier in the season. These dynamic scenarios included:

1. A hypothetical “best-case” in which the results of the static, single condition model scenarios were used to determine a sequence of turbidity conditions that would result in maximal growth and survival at the end of the 124 day period. (Scenario 1)

2. Two-, four-, and eight-week high intensity algal blooms (~100 NTU) during the juvenile phase (i.e. late summer) (Scenarios 2-4)

3. A one week high intensity algal bloom during the larval phase (i.e. late spring) (Scenario 5)

4. High sediment conditions (~100 NTU) two, four and eight weeks past the ontogenetic shift (Scenario 6-8)

For scenarios 2-4, time periods that were not specifically manipulated were set to the turbidity regime in scenario 1, i.e. the best-case scenario. Growth and survivor curves were generated for each experimental perturbation and compared to the ideal growth curve to determine the reduction in growth, potential delay in timing of the ontogenetic shift, and changes in the starvation mortality potential.

3.3 Results

Model Evaluation
My IBM explained a majority of the variance in yellow perch length for the data sets from the western and central basins of Lake Erie and Oneida Lake, with $R^2$ values ranging from 0.611 to 0.742 (Fig.3-3 A-C). The regression for the western basin was not significantly different from a 1:1 ratio (ANCOVA test for parallel slopes, d.f. = 15, $P > 0.05$), indicating that model results for this system are balanced between over- and under-prediction of observed fish lengths. The regressions for the central basin of Lake Erie and for Oneida Lake, however were significantly different from 1:1 (ANCOVA test for parallel slopes, d.f. =10, $P < 0.05$, and d.f. =31, $P < 0.05$, respectively). For the central basin, the model over-predicted mean length by 12% when observed individuals were, on average, smaller than 73 mm, and under-predicted by 8% for years in which average length exceeded 73 mm. For Oneida Lake, the model over-predicts length by 11% on average. The three under-predictions for Oneida Lake were for the years with the greatest observed lengths. It should be noted that, while the long-term model fit for these systems is good, the within-year differences between predicted and observed lengths could represent a biologically significant amount of variation.

The patterns of starvation mortality of yellow perch predicted by the model in all years, and in all systems were similar. Starvation mortality was highly size dependent, with the greatest daily mortality rates occurring within days of each other, regardless of year or system. Daily mortality rates peaked between seven and twelve days post-hatch, and rapidly declined until starvation mortality rates neared zero for individuals larger than 50 mm in length. The only significant starvation events for larger individuals occurred in years with prolonged, high intensity algal blooms; however, these rates never
exceeded 5%/ day, far less than the peak mortality rates of nearly 20%/ day for smaller size classes.

Figure 3-3 A-C. Linear regressions of model predictions vs. observed lengths (mm) 124 days post-hatch for A) the western basin of Lake Erie, B) the central basin of Lake Erie, and C) Oneida Lake, New York. The dashed line = 1:1.
Sensitivity Analysis

The sensitivity analysis indicated that both growth and starvation mortality were strongly influenced by algal turbidity during the larval phase (Table 3.2). Juvenile feeding rates in algal turbidity were of secondary importance in the determination of growth, but had less effect on the starvation mortality, indicating that while algal turbidity impaired their ability to grow, the larger size of juveniles in the model made them less susceptible to starvation mortality. Sediment turbidity during the larval phase was important for both growth and starvation, but not for juveniles. Temperature had the lowest proportional effect on starvation, and surprisingly, had a proportional sensitivity <1 for growth as well. This relatively low proportional effect of temperature, particularly on growth, may be because a 10% change in temperature would be within the normal daily range of conditions encountered. In order to produce proportional effects similar to algal turbidity, it would require a change of >±25% in temperature, or about 6°C.

Table 3.2. Proportional sensitivities (number after parameter name) of the five parameters tested for both growth and starvation mortality. A value >1 indicates a disproportionately large effect on the response variable (growth or starvation), and <1 indicates a less than proportional effect.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Growth</th>
<th>Sensitivity</th>
<th>Starvation</th>
<th>Sensitivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Larval Algal Turbidity</td>
<td>2.89</td>
<td>Larval Algal Turbidity</td>
<td>1.59</td>
</tr>
<tr>
<td>2</td>
<td>Juvenile Algal Turbidity</td>
<td>2.09</td>
<td>Larval Sediment Turbidity</td>
<td>1.41</td>
</tr>
<tr>
<td>3</td>
<td>Larval Sediment Turbidity</td>
<td>1.52</td>
<td>Juvenile Algal Turbidity</td>
<td>1.39</td>
</tr>
<tr>
<td>4</td>
<td>Temperature</td>
<td>0.87</td>
<td>Juvenile Sediment Turbidity</td>
<td>0.56</td>
</tr>
<tr>
<td>5</td>
<td>Juvenile Sediment Turbidity</td>
<td>0.71</td>
<td>Temperature</td>
<td>0.30</td>
</tr>
</tbody>
</table>

Model Scenarios

Growth, timing of ontogenetic shifts, and starvation mortality differed substantially among the hypothetical IBM scenarios that simulated a static turbidity type and intensity. Cohorts modeled with high sediment turbidity had the highest larval
growth rate and on average underwent the ontogenetic shift five days earlier than cohorts modeled with low sediment turbidity (Fig.3-4A). However, the larval growth advantage did not continue into the juvenile phase when sediment turbidity remained high; the low sediment fish quickly exceed the high sediment fish in length. Low sediment conditions produced fish that were 25% larger than high sediment fish (82 mm to 63 mm, Fig. 3-4A) at 124 days. Higher total growth, however, did not confer higher survival, as high sediment conditions produced the lowest starvation mortality rate (Fig.3-4B).

Fish grew more slowly in algal turbidity compared to those in sediment turbidity (Fig 3-4A). Constant low algal conditions produced fish that averaged 38 mm in length, and did not make the ontogenetic shift until approximately 100 days post-hatch (Fig.3-4A). Cohorts modeled with continuous high algal conditions averaged only 24 mm in length, and these individuals generally never achieved the size associated with the ontogenetic shift (Fig. 3-4A). The algal cohorts also had significantly increased starvation mortality when compared to the sediment cohorts. Individuals in low algal conditions experienced nearly 80% mortality, and high algal conditions experiencing over 99% mortality due to starvation (Fig. 3-4B). Because survival was very poor in the high algal conditions, additional runs were completed to improve the sample size of survivors in order to estimate growth.
Figure 3-4A & B. Predicted (A) growth (measured as length) and (B) survivorship curves for yellow perch cohorts modeled with four static turbidity conditions for 124 days post-hatch. The four scenarios were: low sediment, high sediment, low algae & high algae. The grey box denotes fish that have not yet made the ontogenetic shift.

Using the relationships observed in the static condition scenarios, I developed a “best growth” model, which would represent growth of yellow perch under ideal turbidity conditions. The best growth model applied high sediment turbidity until the average cohort length exceeded the threshold to switch to the juvenile feeding regime. Turbidity was then switched to a low sediment regime to best maximize juvenile stage growth through the remaining days. No algal turbidity was applied to this group, as even low
levels of algal turbidity reduced growth rates in both developmental stages. The cohorts in these model conditions averaged 96 mm in length at 124 days post-hatch, approximately 4% larger than the largest observed length (Western Basin 1987, 92.4 mm, Fig. 3-3 A).

My algal turbidity scenarios, which simulated algal blooms lasting for two, four and eight weeks at the end of the season, produced reductions in growth of 11%, 23%, and 45.5% respectively from the best-case scenario (Fig. 3-5A). Additionally, starvation mortality increased from < 10% in the best growth model to > 60% mortality in the eight-week algal bloom treatment (Fig. 3-5B). A one week algal bloom during the second week of the larval stage produced results similar to a two week bloom during the juvenile phase, with a 10% reduction in average cohort length (Fig. 3-5A), and starvation mortality of 19% (Fig. 3-5B). An algal bloom during the larval phase also delayed the ontogenetic shift in these cohorts by approximately 12 days (Fig. 3-5A).

My IBM predicts that the effects of prolonged sediment turbidity after the ontogenetic shift are less severe than the effects of algal turbidity, but still produce reductions in growth and increases in starvation mortality when compared to the best growth model. The two week extension of high sediment conditions only produced a 3% reduction in average cohort length at 124 days post-hatch (Fig. 3-6A), and a 2% increase in starvation mortality (Fig. 3-6B). The four week extension of high sediment produced a 12.5% reduction in growth (Fig. 3-6A) and a 22% increase in starvation mortality (Fig. 3-6B); results that are similar to a two week algal bloom late in the season (Fig. 3-5A and B). The eight week sediment turbidity treatment resulted in a 26% reduction in average cohort length (Fig. 3-6A) and an increase of 28% in starvation mortality (Fig. 3-6B).
Figure 3-5 A&B. Predicted A) growth (measured as length) and B) survivorship curves for the best growth model and models of high algal conditions for final 2 weeks, 4 weeks, and 8 weeks of 124 days and high algal conditions for 1 week during the larval phase. The grey box denotes fish that have not yet made the ontogenetic shift.
Figure 3-6A&B. A) Growth and B) mortality curves for best growth and individuals exposed to high sediment conditions after the ontogenetic shift for 2 weeks 4 weeks and 8 weeks. The grey box denotes fish that have not yet made the ontogenetic shift.

3.4 Discussion

My bioenergetics IBM showed that turbidity-dependent consumption rates and temperature are key components in determining growth and starvation mortality of age-0 yellow perch, thereby linking fish production to land-based processes that influence water clarity. My model validation showed that in Lakes Erie and Oneida the visual environment encountered by age-0 yellow perch, and its effects on prey consumption, explained substantial variability in growth. Further, the results of my water clarity
scenarios suggested that the timing and duration of sediment turbidity may have a strong influence on larval fish growth; with early, but not late season sediment turbidity increasing larval growth and reducing starvation mortality. In contrast, algal-based turbidity always reduced age-0 fish growth, and increased starvation mortality. Recruitment of a cohort is strongly influenced by growth and survival of age-0 individuals (Miller et al. 1988; Madenjian et al. 1996; Schlosser 1998; MacKenzie 2000). Therefore, my results help connect the timing and intensity of sediment plumes and algal blooms, which are often due to anthropogenic actions (Nichols and Hopkins 1993; Anderson et al. 2002; Otero and Seigel 2004), to the potential year class success of an economically important fish species.

While my model was successful at explaining average fish length at the end of the growing season, other factors likely contribute variability to fish growth. For example, density dependent growth may explain some of the deviation of my model results from observed growth (Sable and Rose 2010), particularly for Oneida Lake, a system that has been shown to exhibit strong density dependent growth (Mayer et al. 2000; Irwin et al. 2009). My model consistently over-predicts size at date for this system, which is consistent with a system in which there are high levels of intraspecific competition for prey items. Size-dependent predation is another factor not considered in my model that can shape size distributions of yellow perch, favoring the survival of the fastest growing individuals (Brandt et al. 1987; Post and Evans 1989; Rice et al. 1993). However, the effect of size dependent predation mortality may be reduced in my models. Size dependent predation and starvation mortality interact through compensatory processes (Letcher et al. 1996a) such that many of the individuals in my models that succumbed to
starvation would likely be in poor condition and have been consumed by predators prior to reaching their starvation threshold. It is often difficult to identify the cause of mortality in a natural system, and so determining an actual starvation mortality rate for comparison is not feasible. However, the estimates produced with this model are relatively similar to starvation mortality rates and timing of starvation events published in other modeling efforts (Letcher et al. 1996a, Letcher et al. 1996b). While there are multiple sources of variability not included in my model that may influence my results, I believe the inclusion of natural variability in fish size distributions and zooplankton densities, in conjunction with the laboratory derived feeding rates, makes this a robust model when predicting the growth and starvation mortality potential of age-0 yellow perch.

The effects of sediment turbidity on yellow perch growth in my models depended primarily on the developmental stage of the individuals. While increased fish growth has been linked to increasing water clarity (Mayer et al 2000; Idrisi et al. 2001; Lathrop et al 2002), these studies often focus on a specific life stage and so do not distinguish how turbidity may affect a succession of developmental stages of fish. High sediment turbidity increased the growth rate of larval fish, and these fish underwent their ontogenetic shift four days earlier than their low sediment counterparts. The rapid early growth experienced by larvae in high sediment conditions does result in lower starvation mortality, and thus may result in higher survival and numerically larger cohorts. The increased survival in high sediment conditions supports previous studies that have shown both higher survival (Reichert et al. 2010), and higher abundances (Manning et al. 2013) of age-0 yellow perch are associated with the sediment rich out-flow of the Maumee River into the western basin of Lake Erie. Therefore, larval yellow perch that experience
an early season sediment plume are likely to grow faster than fish in clear water and they will also be less vulnerable to predation because predators, with relatively large reactive distances, forage less efficiently in turbid water.

While my model predicts that sediment plumes are beneficial to the growth and survival of larval yellow perch, late season plumes may reduce growth and increase starvation during the juvenile phase. Yellow perch are often associated with river mouths, which are historically turbid systems (Mulder et al. 1998; Moorhead et al. 2008), particularly during spring runoff. The higher larval growth rate in high sediment conditions may be indicative of natural adaptation to historic turbidity regimes in these systems that produce higher sediment turbidity conditions during the spring. However, anthropogenic activity has increased sediment transportation in many systems (McDonnell and Pickett 1990; Waters 1995; Li and Zhang 1998), and has likely extended the duration and altered the timing of high sediment conditions (Uncles et al. 1994; Prosser et al. 2001; Sutherland et al. 2002; Paul et al. 2008). This anthropogenic alteration of sediment plume dynamics has the potential to change the role of river associated sediment plumes, with the implication that longer duration sediment turbidity may reduce growth rates in juvenile fish and ultimately reduce survival.

In contrast to the developmental-stage dependent effects of sediment turbidity, algal turbidity was always detrimental to growth and increased starvation. For larval fish, algal turbidity has the potential to reduce growth and delay the ontogenetic shift (Wu and Culver 1992; Graeb et al 2006) to benthic prey, which can have serious repercussions on the growth and survival of age-0 fish, as well as reducing the long-term success of a population (Forseth et al 1994; Olsen 1996; Post 2003). Algal blooms during the juvenile
phase also reduced growth, but perhaps more importantly, increased the susceptibility to starvation in these larger fish. However, age-0 fish may experience lower predation mortality when algal turbidity is high. For example in western Lake Erie, at the end of August age-0 yellow perch were more abundant but smaller in highly turbid areas, suggesting a turbidity-mediated tradeoff between growth and survival (Manning et al. 2013). Therefore, the effect of algal blooms on recruitment are likely complex. Blooms should increase rates of starvation, and lower the condition of surviving juveniles thereby increasing overwinter mortality (Post and Evans 1989) and size-based vulnerability to predation (Rice et al. 1993; Lundvall et al. 1999). In contrast predators should also forage inefficiently during algal blooms, possibly contributing to a pattern of small but abundant fish in turbid water (Irwin et al. 2009; Reichert et al. 2010; Manning et al. 2013). High mortality and reduced condition of fish are associated with large algal blooms (Burkholder 1998; Malakoff 1998; Kempton et al. 2002), and it is likely that the balance of effects of algal blooms on yellow perch and other fish populations is highly negative.

My model suggests that the timing and persistence of sediment plumes and algal blooms can drastically alter the growth potential and starvation mortality of a yellow perch cohort. The timing and duration of algal blooms in particular can substantially reduce growth and survival of a cohort, and ultimately their recruitment success. Even short duration algal blooms during the larval phase can significantly reduce the growth of a cohort, and long duration blooms during the juvenile phase (mid to late summer), as have become increasingly frequent in many systems, can have dire consequences on a population. While short duration sediment plumes early in the season may not have a
large effect on a cohort, plumes that occur later in the season, due to resuspension events or dredging and dumping, could have a much larger negative effect. Sediment plumes and algal blooms are tied to land-use and can be altered through directed management actions in the watershed. Therefore, the potentially negative effects of increased turbidity on fish should be considered when management actions are planned that may alter the turbidity regime of a system.
Chapter 4

Connecting fish to the landscape: Land use and climate change effects on yellow perch growth in Maumee Bay.

4.1 Introduction

The rapid pace of land use and land cover (LULC) alteration and global climate change have the potential to alter both the form and function of a wide range of ecosystems. Coastal areas are particularly vulnerable because more than half of the world’s population lives and works within a coastal watershed. In many places the population and their impacts on the landscape is expected to increase rapidly in the decades to come (McGranahan et al. 2002; Faulkner 2004). Human alterations in coastal areas can lead to declining water quality, including reduced water clarity (Howrath et al. 1991). Low water clarity affects multiple aspects of aquatic ecosystem function and can degrade ecosystem services (Booth and Jackson 1997). Therefore, my goal was to connect potential changes in land use and climate to fish production (an important ecosystem service) via changes in water clarity in a large coastal ecosystem, the Maumee Bay of Lake Erie.

Human-driven watershed disturbance and anticipated climate change can reduce water clarity in downstream water bodies via two pathways: increased sediment turbidity
and the promotion of phytoplankton blooms. Agriculture, construction, and deforestation lead to the reduction and elimination of wetlands and riparian zones (Horn et al. 2001; Pauchard et al. 2006), which act as a buffer between terrestrial and aquatic systems (May et al. 1997; Kundzewicz and Menzel 2003). The loss of buffer systems can increase particulate loads that contribute to sediment plumes in coastal areas (Castelle et al 1994; Falcini et al. 2012). Additionally, increasing flashiness of tributaries due to climatic and land-use changes may lead to an alteration of the timing of sediment plumes (Pfister et al 2004), producing turbid conditions during times of the year that have, historically, been periods of high water clarity (Sutherland et al. 2002). Secondly, agricultural runoff and municipal waste can increase transport of nutrients that promote increased algal turbidity (Anderson et al. 2002), and increased temperatures due to climate change are also likely to foster phytoplankton blooms (Paerl and Huisman 2008). In many places algal blooms are increasing in intensity and duration (Hallegraeff 1993; Sneller et al. 2003), and have become the focus of considerable concern (Gilbert et al. 2001, Dyble et al. 2003; Bridgeman and Penamon 2010; Bridgeman et al. 2012). The continuing alteration of coastal systems makes it increasingly important to quantify how watershed influenced water clarity reductions can affect aquatic populations.

Water clarity affects the feeding of visual predators, such as fish, through light attenuation and degradation in the apparent contrast between a prey item and its background (De Robertis et al 2003). Reduced foraging rates associated with low water clarity can affect the growth of visually foraging species (Manning, Chapter 3), which may then affect recruitment success of a population (Manning et al. 2013). Even small variations in age-0 fish growth can result in large differences in the subsequent
recruitment of a population (Miller et al. 1988; Houde 1989; Leggett and DeBlois 1994; Ludsin and Devries 1997; Bergenius et al. 2002) as recruitment often hinges on growth and survival of the age-0 year class (Ware 1975; Crowder et al 1987; Post and Evans 1989; Rice et al. 1993; Cowan et al. 1996; Sogard 1997). Age-0 yellow perch (*Perca flavescens*) are visually feeding fish that are found across a range of turbidity levels and/or ecosystem types. The effects of turbidity on feeding and growth of age-0 yellow perch have been shown to vary based on the type and intensity of turbidity (sediment v. algal), and the life stage of the fish (larval v. juvenile) (Mayer et al. 2000; Radke 2005; Wellington et al. 2010, Manning et al. Chapter 3). Because numerous fish species utilize near-shore habitats that are influenced by nutrient and sediment rich rivers, quantifying how watershed level changes can affect fish production is important to the continued management of this important ecosystem service.

The goal of this research is to link anthropogenic alterations in the agriculturally dominated Maumee River watershed to potential changes in the growth of age-0 yellow perch in the Maumee Bay, Lake Erie. To accomplish this goal I used the Soil and Water Assessment Tools 2005 (SWAT) to model the potential changes in the sediment and phosphorus inputs from the Maumee River watershed due to both increasing urbanization and GCC scenarios. I then link those terrestrial impacts to alterations in sediment plume and algal bloom cycles, and ultimately, yellow perch growth in the Maumee Bay using an Individual Based Model (IBM; Manning, Chapter 3). I address two specific questions: 1) What are the potential effects on the growth of yellow perch in the Maumee Bay due to current and possible land use practices in the Maumee River watershed, and 2) What are the potential impacts on yellow perch growth due to changes in the watershed based on
predicted climate alterations? Connecting terrestrial and aquatic ecosystems in a modeling framework allows for a better understanding of how human actions can indirectly impact organisms in a wide range of near shore systems that are influenced by terrestrial inputs.

4.2 Methods

Study Area

The Maumee River forms at the confluence of the St. Mary and St. Joseph Rivers, near Ft. Wayne, Indiana. The River flows northeast for approximately 120 miles to Toledo, Ohio, where it empties into the western basin of Lake Erie through Maumee Bay (Fig. 4-1).

Figure 4-1. Map of the Maumee River watershed, including the main branch, as well as the major tributaries. The Maumee River flows Northeast from the confluence of the St. Mary’s and St. Joseph’s rivers near Ft. Wayne, Indiana. The River empties into the Maumee Bay, Lake Erie at Toledo, Ohio.
The Maumee River drains the largest watershed in the Great Lakes Basin (ca. 17,000 Km²) including portions of Northwestern Ohio, Southern Michigan and Northeastern Indiana. Land use in the watershed is dominated by traditional row crop agriculture, which covers > 75% of its area, with a further 15% urban/suburban. This intensive agricultural use has contributed to the Maumee River having the highest suspended sediment discharge rate of any Great Lakes tributary. While the Maumee River contributes < 25% of the total water that flows into the western basin of Lake Erie, it contributes more than half of the suspended sediments input, and a significant portion of the total phosphorus (Moorhead et al 2008). This disproportionately large contribution to sediment and phosphorus along with contamination from a long history of industrial usage, particularly in the Toledo area, have led to portions of the river and bay being listed as an Area of Concern (AOC) under the US-Canada Great Lakes Water Quality Agreement (US Army Corps of Engineers, 2009).

The Maumee Bay is a semicircular bay at the southwestern end of Lake Erie between 41°41’N and 41°45’N latitude, and 83°20’W and 83°29’W Longitude. The bay is defined from the main body of Lake Erie by two spits, Woodtick Peninsula to the north, and Little Cedar Point to the East. Maumee Bay has a surface area of approximately 48 km², which comprises approximately 5% of the surface area of the western basin of Lake Erie, and is uniformly shallow, with an average depth of only 1.7m. The bay is bisected by a 60 m wide, 10 m deep shipping channel that runs from the mouth of the Maumee River, 20 miles northeast into the western basin of Lake Erie. The Maumee River is Maumee Bay’s largest source of water, sediment and nutrients. Because of the Bay’s shallow depth it has a relatively short water retention time, of only 5 days, as
compared to 53 for the entire western basin, and 1,007 for Lake Erie as a whole, and so water clarity conditions in the bay are often reflective of the outflow of the Maumee River.

Model implementation

The goal of this research was to connect anthropogenic alterations of anticipated climate and land use changes in a large, agriculturally dominated watershed to the growth of an important fish species in an associated aquatic system. To accomplish this, it was necessary to link three distinct models of hydrologic and biological processes (Fig. 4-2).

![Diagram of model implementation](image)

Figure 4-2. Conceptual model of the linkages between the SWAT, volumetric model and IBM. Spatial data that informs the SWAT model include land usage, soil type and slope. Weather Data for the SWAT include daily min and max values for temperature, precipitation and humidity from selected weather stations, or from the climate change models. Weather data used in the prediction of algal blooms was daily temperature, used to calculate water temperature for the years 2015 to 2025.
A SWAT model was used to predict changes in daily values for flow (m$^3$/s), total sediment transport, and phosphorus concentrations in the Maumee River due to changes in land use and climate. Results of the SWAT model were then used to inform a volumetric concentration equation of the Maumee Bay, in order to predict daily sediment and phosphorus concentrations input to the Maumee River. The sediment and phosphorous loadings of the Maumee Bay volumetric model were then incorporated into an IBM of yellow perch growth (Manning, Chapter 3). By linking these three models I attempt to show how changes in the physical and hydrologic structure of a watershed can alter the foraging and bioenergetics processes of an organism in a connected aquatic environment.

**SWAT model**

The Soil and Water Assessment Tools 2005 (SWAT) is a physically based, daily time step model developed to predict the impacts of management actions on water, sediment and agricultural chemical yields in large basins or watersheds (Santhi et al. 2001). The model divides a watershed into hydrologic response units (HRUs) that are spatially heterogeneous descriptors of land cover and soil types. For each HRU, the model estimates changes to the relevant hydrologic components, including surface runoff, baseflow, and evapotranspiration (Wu and Johnston 2007). The specific model algorithms, parameters, and execution procedures for the implementation of SWAT models are provided in Arnold et al. (1998) and Santhi et al. (2001), and will not be repeated here.
Data for SWAT Implementation

I created a SWAT model of the Maumee River watershed using spatial data including: digital elevation maps (DEM), land use and land cover (LULC), soil type and climatological data. A DEM with a scale of 1:24000 (30 m DEM), and LULC data were retrieved from the Seamless Data Distribution System, National Center for Earth Resources Observation and Science (EROS), USGS (http://seamless.usgs.gov/, accessed on 6/13/2012) and processed using ArcGIS 9.3 (ESRI 2003). The LULC were from the 2001 National Land Cover Data (NLCD). Soil data were from the State Soil Geographic (STASGO) database (UDSA ARS, 1991). Three weather stations within the Maumee River basin were selected based on completeness of data for the time periods modeled, and coverage of the Maumee Basin with minimal spatial overlap. Daily values for minimum and maximum air temperature (°C), and precipitation (mm/d) for each were obtained from the NOAA National Climatic Data Center (NCDC, http://ncdc.noaa.gov/, accessed on 6/14/2012).

Initial SWAT implementation

The Maumee River basin was divided into 19 sub-watersheds, and initial model calibration and sensitivity analyses were performed on the sub-watershed that included the gauging station located at Waterville, Ohio (USGS Stn #04193500), as this monitoring station has the most extensive daily data set available in the Maumee River basin. Daily stream flow (ft^3/s) and sediment concentration (mg/l) records for the Waterville station were retrieved from the USGS NWISWeb (http://http://nwis.waterdata.usgs.gov/, accessed 6/13/2012). Phosphorus concentrations (mg/l) were retrieved from the Heidelberg University National Center for Water Quality
Research (http://www.heidelberg.edu/academiclife/distinctive/ncwqr/data/data accessed 6/19/2012). Model calibrations were performed on the hydrologic and phosphorus parameters for the years 1980 to 2010 and for the sediment parameters for the years 1980 to 2003. Simulations were initiated from 1980, but that year was not included for comparison, as that year is used as a stabilization, or burn-in, period.

After calibration, the model was extended to the entire Maumee River watershed, with the assumption that the adjoining sub-watersheds were similar enough in hydrologic response that the optimum parameter values identified in the initial calibration would be valid for these other sub-watersheds. This initial model implementation created a flow, sediment, and nutrient regime for the Maumee River that represented historical conditions, and was used to verify the ability of the volumetric model and IBM to predict water clarity conditions, and ultimately yellow perch growth in the Maumee Bay. These models were run five times, and the average daily value for each factor was used to assess overall model fit. The fit between the average predicted and observed values for streamflow, phosphorus and sediment concentrations were assessed using the Nash-Sutcliffe efficiency (Nash and Sutcliffe, 1970). Values for the Nash-Sutcliffe efficiency vary from 1 for a perfect model fit, to 0 when the model prediction is no better than the average of observed values, as well as negative values when the model performs worse than the average of observed values.

*Volumetric concentration equation*

In order to parameterize my IBM, I needed to estimate daily sediment and phosphorus concentrations ($C$) in the Maumee Bay. Therefore, I used the daily output for
flow volume ($Q$) and sediment and phosphorus concentrations ($C_{in}$) from the SWAT models to inform a steady-state volumetric concentration equation of the Maumee Bay:

$$\Delta C \Delta t = Q \cdot V \cdot (C_{in} - C)$$

The volumetric conversion equation used a fixed volume ($V$) of $83 \times 10^6$ m$^3$ (i.e. the volume of Maumee Bay), and daily outflow was equal to $Q$. I assumed that the primary input for water, and the only source of sediment and phosphorus in the model was the Maumee River, with daily values for these parameters coming from the SWAT model. A secondary input for water was included, which was a fixed value of $14,342$ m$^3$/d, an average of daily discharge values found in the literature for the Ottawa River, the second largest input of the Maumee Bay. Sediment and phosphorus concentrations varied daily, and for model simplification, it was assumed that daily concentrations represented the entirety of the Maumee Bay (i.e. no diffusion time). These daily sediment and phosphorus concentration values were calibrated and corroborated using data collected in the field between 2002 and 2011 (Chaffin et al. 2012). Estimates from the volumetric conversion equations were compared to the corresponding dates from the field data, and it was found that the best fit for both sediment and phosphorus concentrations was achieved by taking the average of the estimated day and the periods directly preceding and following the estimate (Fig. 4-3 A-B). The daily sediment and phosphorus concentrations calculated using the volumetric equation were then used to parameterize an IBM previously developed for larval and juvenile yellow perch (Manning, Chapter 3).

*Individual Based Model*

My IBM was designed to assess the impact of sediment and algal turbidity on the growth and survival of age-0 yellow perch (Manning, Chapter 3). To examine
differences in yellow perch response to different turbidity conditions, my IBM (Fig. 4-4) explicitly includes the effects of turbidity type and intensity based on laboratory-derived ingestion rates from Wellington et al. 2010 as opposed to encounter and consumption rates, which

Figure 4-3 A and B. Linear regressions of observed and predicted A) Sediment concentrations and B) Phosphorus concentrations from the volumetric model of Maumee Bay
are traditionally calculated using swimming speed, light levels and prey densities (e.g. Letcher et al. 1996; Fulford et al. 2006). The input requirements for my IBM include sediment concentrations and timing and intensity of algal blooms. Values for sediment concentration from the SWAT model were incorporated directly in the IBM; however, phosphorus concentration and water temperature were used to calculate the timing and intensity of algal blooms. The timing of algal blooms in my model signals a switch in the feeding behavior of age-0 yellow perch, which is different from feeding behavior in sediment turbidity (Wellington et al. 2010). For years where bloom start dates are known

![Flow diagram of the Individual Based Model showing primary submodels and parameters that inform each.](image)

Figure 4-4. Flow diagram of the Individual Based Model showing primary submodels and parameters that inform each.
(2002-2010), the observed data were used to set the timing of the switch to the algal feeding regime. For other years where data do not exist, such as for my future predictions, I needed to estimate the start date of an algal bloom. To estimate bloom dates I used observed values of phosphorus concentrations, water temperatures and phytoplankton biovolume to identify environmental thresholds that best describe the onset of algal blooms. No blooms occurred when surface water temperatures were below 21°C or when phosphorus concentrations were below 0.05 mg/l. When both of these conditions were exceeded, mean algal biovolume was 153 ml/m². For use in my IBM, an algal bloom was considered to have started when both temperature and phosphorus concentrations exceeded these thresholds, and would end when either one or both dropped below the threshold values. Validation of my IBM model was conducted using turbidity data from 1981 to 2010 and then comparing model results to the interagency trawl data provided by the Ohio DNR.

**Land Use and Land Cover Change SWAT models**

I used my SWAT model to determine the impact of land use change, specifically increasing urbanization in a predominately agricultural watershed, on the growth and survival of yellow perch. I ran my SWAT model in three ways that simulated an increase in the percentage of land use classified as urban (open/brownfield, low, medium, and high density), by 10, 25, and 50% over the NLCD 2001 classifications. Land use within the basin was divided into three groups: agricultural, urban, and other. To simulate increasing urbanization in the basin, the percentage of the basin classified as other (wetlands, non-agricultural grassland/herbaceous, shrub/scrub, and forested) was reclassified as one of the four urban types. When possible, the reclassification of cover
type was done evenly within each group to preserve the relative percentage of each type. These models were run for the same time period as the initial model implementation, and used the optimum parameter estimates identified previously. Urbanization could not be increased by more than 50% as that forced land uses classified as other to be reduced to 0% of the watershed. Additionally, I created a model which reduced agricultural and urban usage to 0%, and set the remaining land cover classification percentages to reflect pre-settlement conditions (Richards et al. 2008). This model was created to quantify the impacts of current land usage, and in particular, the effects of agriculture, which account for nearly 80% of current land-use in the Maumee Basin. By simulating elimination of agricultural and urban influences on the Maumee River, and restoring historical wetlands and riparian zones, I hoped to be able to determine the impact of current land use practices on both water clarity and age-0 yellow perch growth.

The output from the increasing urbanization SWAT models were then converted to concentrations within Maumee Bay and used as inputs for the IBM in the same manner as described above. Average length of age-0 yellow perch at ~124 days post-hatch from each of the increasing urbanization and pre-settlement scenarios were compared to the estimate from the initial model implementation (0% change scenario) and each other using ANOVA and Tukey’s Honest Significant Difference (HSD) test.

Climate Change Model

Future climate change scenarios for the Maumee River basin were created using predictions from the NOAA Geophysical Fluid Dynamics Laboratory’s CM2Q-h1_SresA1B_x2 experiment. These data were accessed from the NOAA portal (http://nomads.gfdl.noaa.gov/dods-data/gfdl_cm2_1/CM2.1U-
The NOAA experiment is on a global scale, and so only data from the grid that covers the Maumee River basin were used. Daily predictions for minimum and maximum air temperature, precipitation and atmospheric humidity for the years 2015 to 2025 were used to create three weather stations that took the place of the three original weather stations in my SWAT model. Because no flow or sediment values are available for these future time frames, the previously identified optimal flow and sediment parameters were used in this SWAT model.

The average mean length of age-0 yellow perch for each of the years included were then compared to the long term average of age-0 yellow perch length in the Maumee Bay from the initial model implementation, and to each other using ANOVA and Tukey’s HSD to determine if there were any significant changes between the treatment groups as well as within the group.

**Determination of significant environmental factors**

I used Generalized Linear Models (GLM) and Akaike’s Information Criterion (AIC) to describe the linear relationships between environmental factors and fish growth, and to determine which combination of environmental factors best describe the variation seen in the length of fish from my urbanization and climate change models. For each model scenario, I created a GLM (glm function of the mgcv package in R; v. 11.1), specifying a Gaussian family with an identity link. Environmental factors considered for inclusion in the GLMs were: average daily stream flow, average daily sediment load, and average daily phosphorus load from the SWAT models, average daily sediment concentration and average daily phosphorus concentration from the volumetric model, and average daily surface water temperature from the IBM. For all considered factors,
values were divided into early season (Apr – Jun), late season (Jul-Sept), and yearly average (Jan-Sept). Factors were added or removed from the models in a stepwise manner using the `step` function in R. The resulting models were then compared using AIC to identify the model with the most reduction in deviance, and thus the best “fit” to the data. AIC is a goodness of fit index that penalizes a model based on the number of parameters included to reduce the probability of over-fitting (Akaike, 1987). The Δ AIC values (the difference between the best-fit model and any other model) were used to compare the relative fit of the compared models, where a difference > 2 is considered a meaningful difference in the “fit” of the models (Hilborn and Mangel, 1997).

4.3 Results

My initial SWAT model implementation was able to accurately predict average daily stream flow, as well as phosphorus and sediment concentrations over an extended time period. The Nash-Sutcliffe efficiency results were 0.845 for stream flow, 0.771 for sediment concentration, and 0.622 for phosphorus concentration. Additionally, my IBM of age-0 yellow perch growth in Maumee Bay using input from my SWAT model was able to describe over 70% of the observed variation in the inter-agency trawl data (Fig 4-5).

Land Use and Land Cover Change

Increasing urbanization in the Maumee River watershed resulted in a significant reduction in average fish length in the Maumee Bay, but only when urbanization was increased by 50% (Fig. 4-6). The Tukey HSD test indicated that the 50% increase treatment was significantly different from the 0% and 10% increase treatments, but not the 25% increase, and the 25% increase was not significantly different from any of the
Figure 4-5. Linear regression of the observed age-0 yellow perch lengths from the multi-agency trawl data and predicted lengths 124 days post-hatch from the Individual Based Model.

other treatments (Table 1). The best-fit GLM for the increasing urbanization scenarios had an AIC score of 145.128, and included both early and late season values for Maumee River flow volume, total sediment loading and Maumee Bay sediment concentration. The next best fit model had a ΔAIC score of 3.342, indicating a significant reduction in goodness-of-fit. The best fit model indicates that the reduction in growth seen in my scenarios is best described by changes in flow, sediment loading, and sediment concentration. My model predicted a 10% increase in early season (Apr-Jun) flow volume from the Maumee River as urbanization in the watershed increased, but only a 1.7% increase in late season (Jul-Sept, Fig.4-7A). Additionally, the model predicted early season sediment loading in Maumee Bay to increase by 5%, and late season loading
Figure 4-6. Average fish length 124 days post hatch for four urbanization treatments, the pre-settlement scenario (PS), and the observed fish lengths from the multi-agency trawl data (obs). Error bars are 1 s.e. Letters denote significant differences between treatments.

Table 4.1. Tukey’s HSD comparison table for the treatments used in the urbanization models. An adjusted p value < 0.05 indicates a significant difference between treatments.

<table>
<thead>
<tr>
<th>Treatment Comparisons</th>
<th>diff</th>
<th>lwr</th>
<th>upr</th>
<th>p adj</th>
</tr>
</thead>
<tbody>
<tr>
<td>0% - 10%</td>
<td>0.625</td>
<td>-5.11613</td>
<td>6.366135</td>
<td>0.998165</td>
</tr>
<tr>
<td>0% - 25%</td>
<td>-2.125</td>
<td>-7.86613</td>
<td>3.616135</td>
<td>0.842571</td>
</tr>
<tr>
<td>0% - 50%</td>
<td>7.291667</td>
<td>1.550532</td>
<td>13.0328</td>
<td>0.005528</td>
</tr>
<tr>
<td>0% - PS</td>
<td>3.212</td>
<td>1.1126</td>
<td>5.6921</td>
<td>0.001341</td>
</tr>
<tr>
<td>10% - 25%</td>
<td>-2.75</td>
<td>-8.49113</td>
<td>2.991135</td>
<td>0.674106</td>
</tr>
<tr>
<td>10% - 50%</td>
<td>7.916667</td>
<td>2.175532</td>
<td>13.6578</td>
<td>0.001997</td>
</tr>
<tr>
<td>10% - PS</td>
<td>5.5673</td>
<td>1.8675</td>
<td>9.7753</td>
<td>0.000112</td>
</tr>
<tr>
<td>25% - 50%</td>
<td>5.166667</td>
<td>-0.57447</td>
<td>10.9078</td>
<td>0.098972</td>
</tr>
<tr>
<td>25% - PS</td>
<td>-6.943</td>
<td>-10.774</td>
<td>-2.3356</td>
<td>0.000064</td>
</tr>
<tr>
<td>50% - PS</td>
<td>-7.712</td>
<td>-12.153</td>
<td>-3.663</td>
<td>0.000021</td>
</tr>
</tbody>
</table>

to increase by nearly 25% (Fig. 4-7B). This large increase in late season loading, with little change in overall flow volume leads to an 18% increase in average late season sediment concentrations in Maumee Bay (Fig.4-7C). The late-season increase in sediment
Figure 4-7 A-C. Change in A) Maumee River streamflow, B) total sediment transport and C) average daily sediment concentration in the Maumee Bay for both early (Apr-Jun, dotted line) and late (Jul-Sept, solid line) seasons as predicted by the percentage change in urbanization.
concentrations in the 50% increase model reduced juvenile yellow perch prey consumption in the IBM by an average of 11%/fish/day, and resulted in a significant reduction in fish length at the end of the season.

The pre-settlement scenario resulted in a significant increase in average fish length in the Maumee Bay when compared to current land-use conditions in the Maumee River watershed, as well as my increased urbanization scenarios (Fig 4-6, Table 4.1). Fish in the pre-settlement scenario averaged 81.3 mm, a 6.5% increase over the current land use conditions model. My stepwise GLM analysis resulted in a best-fit GLM for the pre-settlement scenario with an AIC score of 173.231, and included both early and late season values for Maumee River flow volume, sediment loading, sediment concentration, and phosphorus concentration in the Maumee Bay. The next best fit model had a ΔAIC value of 4.021. Flow volume from the Maumee River in the pre-settlement scenario was reduced by 5% in both early and late seasons and total sediment loading was reduced by as much as 75% in the early season and 40% in the late season. Large reductions in total sediment loading exiting the Maumee River resulted in similar reductions in sediment concentrations for the Maumee Bay in both time periods. Perhaps most important to the difference seen in predicted fish length, was the reduction in phosphorus concentrations, which were reduced by nearly 90%, and resulted in concentrations never exceeding the algal bloom threshold. The clear water conditions in the late season, coupled with the lack of any algal turbidity resulted in an increase of 8%/fish/day in late season prey consumption over the current conditions model.
Global Climate Change

Changes in temperature and precipitation due to climate change resulted in a predicted reduction of 10% in average fish length by the end of the eleven years analyzed (Fig. 4-8).

![Graph showing predicted average length of age-0 yellow perch 124 days post hatch for the years included in the GCC model.](image)

The best-fit GLM for my climate change scenario included early and late season river flow volumes, early and late season Maumee Bay sediment concentrations, late season phosphorus concentration for Maumee Bay, and late season surface water temperature for Maumee Bay. My model predicted that flow volume and sediment concentrations would display some year-to-year variation, but that there would be no significant trend through time for these water quality parameters (Fig. 4-9 A and B). Late season phosphorus concentrations did rise over the years included in this model and these concentrations exceeded my bloom threshold in all years included (Fig. 4-10A). Average late season
Figure 4-9 A and B. Line graphs showing the change in A) average daily Maumee River streamflow and B) the average daily sediment concentrations in the Maumee Bay in early (dotted lines) and late (solid lines) season for the years included in the GCC model.

Water temperatures, while displaying some year-to-year variation, increased by 4 to 5 degrees by the end of the model (Fig. 4-10B). The predicted increase in water temperatures, in conjunction with the small increase in phosphorus concentrations, lead to algal blooms starting between 1 and 4 weeks earlier by the fourth year of the model.
Each additional week of algal bloom included in my model reduced fish growth by an average of 3% per week, and was the primary driver in the predicted reduction in fish length over the eleven years included.

Figure 4-10 A and B. Change in A) late season phosphorus concentrations in the Maumee Bay, and B) average late season surface water temperatures in Maumee Bay for the years included in the GCC model.
Figure 4-11. Change in number of weeks post-hatch in which a bloom was predicted to have started for the years included in the GCC model.

4.4 Discussion

The results of my study show that alterations in land-use and climate in a watershed can be linked to reductions in the growth of age-0 fish. There are significant correlations between alterations to a watershed and fish growth (Schindler et al., 2000), community structure (Meador and Goldstein, 2003), and the availability and quality of suitable habitat (Evans et al. 1996). However, it has often proven difficult to quantify the mechanisms that drive the observed changes. My model results suggest that in a heavily modified watershed, the effects of further urbanization on the growth of age-0 yellow perch will be incremental. In contrast, anticipated climate change scenarios that may lead to increased algal blooms are predicted to substantially lower the growth of age-0 yellow
perch. The results of this study describe a mechanistic link between actions in a watershed and potential changes to the fish production in the associated aquatic system.

The implications of my increasing urbanization scenarios are two-fold. First, these models show that increasing urbanization has the potential to reduce age-0 yellow perch growth primarily through the alteration of the timing and intensity of sediment plumes. Increasing urbanization in the Maumee River watershed has the potential to reduce early season sediment concentrations in the Maumee Bay, which could negatively impact larval yellow perch growth, as well as increase the threat of predation on these fish. Previous studies have highlighted the importance of turbid river plumes for the growth and survival of larval fish (Grimes and Kingsford 1996, Reichert et al. 2010; Manning et al. 2013). A number of mechanisms have been shown to contribute to increased growth and survival in larval fish, including increased productivity and prey availability (Giovanni and Chester 1990), as well as reduced threat from larger, visual predators (Reichert et al., 2010). Thus, the predicted reduction in sediment concentrations during the larval phase of development may have the potential to both reduce growth and increase predation mortality of age-0 yellow perch in the Maumee Bay.

Conversely, increasing urbanization in the Maumee River basin could potentially increase the intensity and duration of sediment plumes later in the season, after age-0 yellow perch have made the ontogenetic shift. Shifting sediment plumes to later in the season has the potential to significantly reduce juvenile growth, as the negative effects of decreasing water clarity become more pronounced as fish size increases, primarily due to the increased focal length of larger fish (DeRobertis et al. 2003). It has been shown that increasing turbidity can reduce the juvenile foraging ability of a number of fish species
(DeRobertis et al. 2003), including yellow perch (Wellington et al. 2010). This reduction in feeding rate is evidenced in my results, which show a reduction of 11% in prey consumed by juveniles in the 50% increase model. Therefore, increasing urbanization in the Maumee River watershed has the potential to reduce fish growth during both the larval and juvenile phases of development by shifting sediment plumes to later in the season.

The second major implication of this research is that in an agriculturally dominated watershed, such as the Maumee River basin, the hydrologic and sediment inputs from agricultural runoff are already so influential that it may require the complete elimination of wetlands, forested areas and other buffers zones to influence water clarity conditions in the connected aquatic systems. The effects of land-use changes on water clarity and fish growth described in this study required a substantial increase in the amount of urbanization within the Maumee River watershed. Virtually all non-agricultural land-use had to be reclassified as urban in order to see a significant change in the growth of age-0 yellow perch. The large increase in urban land use required to affect changes in fish growth point to the overwhelming influence of agricultural sources of sediments and nutrients in the Maumee River watershed. The influence of agriculture on the water clarity conditions of the Maumee Bay is borne out by my pre-settlement scenario, which showed that when agricultural uses are removed from the watershed water clarity conditions improved significantly. Most importantly, however, may be the reduction in phosphorus inputs to the Maumee Bay, and the subsequent elimination of harmful algal blooms.
The global climate change scenario shows that predicted changes in temperature and precipitation in the Maumee River watershed could lead to significant reductions in the growth of age-0 yellow perch in Maumee Bay in as little as 10 years. The predicted reduction in growth is primarily driven by an increase in summer water temperatures, which promote an earlier onset, and increased duration of algal blooms. Increasingly frequent and intense algal blooms have become more common in a number of coastal regions (Hallegraff, 1993; Anderson et al., 2002; Rinato-Kanto et al., 2005; Chaffin et al., 2011), and the results of this study suggest that these blooms could become more severe in the future. An increased frequency of blooms is particularly concerning as algal turbidity has been linked to increased fish mortality and reduced condition of fish (Burkholder 1998; Malakoff 1998; Kempton et al. 2002). In juvenile yellow perch, Wellington et al. (2010) showed that prey consumption was significantly lower in algal than in sediment turbidity across all turbidity levels, while the negative effects for larvae were only apparent at high turbidity levels. The distinctions between age groups are important as the seasonal timing of sediment plumes and algal blooms exposes juveniles more predominately to algal driven turbidity.

The Maumee River watershed, and in particular the area surrounding the Maumee Bay has been subjected to significant human modification over the past two centuries, from draining of wetlands for agriculture to the development of large urban areas. These historical changes have possibly resulted in reduced fish biomass production, as indicated by the significant difference in fish length between the pre-settlement and current land use scenarios. However, my land use scenarios suggest that the effects of changing land use in the Maumee River watershed are approaching a kind of asymptote, now requiring
an increase in urbanization that is likely economically unfeasible to further negatively impact fish growth. Thus, for the Maumee River watershed, and possibly other large agriculturally dominated watersheds, further changes in fish production are likely to be due to changes in climate. My climate change results show reduced fish growth, with land use being held at current conditions. Even small changes in land use, in conjunction with projected climate alterations would then have the potential to accelerate any negative impacts on the fish of the Maumee Bay.

This study highlights the interactions between terrestrial and aquatic systems. In particular, my results show how changes in land use and climate in a watershed can significantly reduce the growth of an important visually foraging fish species in an associated water body through alteration of the visual environment. The changes associated with these two anthropogenic factors, on the surface, appear to be distinct from one another. Changes in land-use, either through increased urbanization, or changing agricultural practices, primarily affect fish growth through the alteration in the timing and intensity of sediment plumes. Climate change, on the other hand, could potentially reduce fish growth through the promotion of algal blooms due to increased water temperatures. As human populations continue to grow in coastal watersheds, the rate at which these systems are modified will increase rapidly. Whether it is through changes in land use, or changes in climate, the effects of human impacts will continue to alter how terrestrial and aquatic systems interact. However, it may be possible to mitigate the effects of climate change through directed management actions within the watershed. Reducing the agricultural contributions to sediment and phosphorus loading in an aquatic system could potentially improve water clarity, and thus fish growth, by both reducing
late season sediment plumes, and reducing the availability of terrestrially sourced phosphorus, thus mitigating the effects of increased water temperatures on algal blooms.
Chapter 5

5.1 Conclusion

Turbidity is a principal component of the visual environment fish encounter, and, can be a significant factor in determining the potential success of a population. Humans have, through changes to the land and climate, altered the historical patterns of turbidity in many aquatic systems, and the rate of change is likely to increase in the foreseeable future. Therefore, the results of this research can help understand how not only current conditions affect age-0 yellow perch populations, but how future actions may further impact these fish.

The GAMs presented in this dissertation show that water clarity (in this case used as a surrogate for turbidity) may be an important environmental factor in determining the length and abundances of age-0 yellow perch in western Lake Erie. The results suggest that the influence of water clarity produces a distinct separation of areas of higher growth potential and areas of higher abundances in the western basin. While this division may be attributable to a number of mechanisms, including size dependent predation risk, foraging ability, and density dependent growth, the effects of water clarity, and in particular the negative effects of algal blooms, on foraging ability are of particular interest in Lake Erie.
Increasingly frequent and intense harmful algal blooms in the western basin of Lake Erie (Rinato-Kanto et al., 2005; Chaffin et al., 2011) will likely lead to reduced food consumption (Wellington et al., 2010) and growth (Metcalf, 1986) of age-0 yellow perch. The potential for significant impacts due to algal blooms, in conjunction with alterations to sediment inputs due to human activity, make it increasingly important to understand how changes in the turbidity cycle of a system can alter age-0 yellow perch growth and survival.

The bioenergetics IBM focused on the potential effects of changing turbidity regimes, and showed that turbidity-dependent consumption rates are a key component in determining age-0 yellow perch growth and starvation mortality. The results of the model suggest that the timing and persistence of sediment plumes and algal blooms can drastically alter the growth potential and starvation mortality of a yellow perch cohort. The timing of sediment plumes in particular can have significant consequences to the growth, and ultimate success of a yellow perch population. High sediment turbidity early in the season, prior to the ontogenetic shift, can be potentially beneficial to fish growth by increasing feeding ability of larval fish, while simultaneously reducing the foraging ability of their predators. However, if high sediment turbidity conditions persist, they can slow growth and increase the starvation mortality of juvenile fish. This suggests that these fish have become adapted to a historical turbidity cycle which produced large sediment plumes early in the season due to spring runoff, and periods of relatively clear water during the drier summer months. In contrast, algal blooms, no matter when during the season they occur, have a negative impact on the growth and mortality of yellow perch, with even short duration algal blooms during the larval phase significantly
reducing the growth of a cohort, and long duration blooms having the potential to reduce the survival of age-0 individuals to nearly zero. The sediment plumes and algal blooms modeled in this study are often directly influenced by terrestrial processes in the surrounding watershed. Therefore, it is necessary to examine how changes in the watershed can drive the potentially negative effects of turbidity on fish.

The land use and climate study focused on the interactions between terrestrial and aquatic systems, and described a mechanistic link between changes in a watershed to potential changes in fish production. Changes in land-use, either through increased urbanization, or changing agricultural practices, primarily affect fish growth through the alteration in the timing and intensity of sediment plumes. However, it may be that, at least in the Maumee River watershed, the negative effects have reach a plateau of sorts, with significant reductions in fish growth requiring changes to the watershed that are unlikely in the near future due to economic and infrastructure restrictions. Climate change, on the other hand, could potentially compound the effects of current land use practices through the promotion of algal blooms due to increased water temperatures, thus further reducing fish growth. The potential compounding effects of land use and climate change on the growth of age-0 yellow perch highlights the need for further investigations into the effects of climate and how it could interact with land use management strategies.

In conclusion, the effects of turbidity on age-0 yellow perch are dynamic, and can vary significantly depending on a number of different factors. The results of this research help to illuminate these complex interactions, and provide a warning about potential consequences due to anthropogenic alterations of an aquatic system’s turbidity regime.
This research shows that not all turbidity is equal, and that in the right circumstances, high levels of turbidity may be beneficial to fish production. However, the results also show that any positive effects can be quickly nullified by prolonged periods of high turbidity. This research helps to link terrestrial and aquatic systems, and provides insight into how alteration of turbidity regimes can potentially impact an economically and ecologically important fish species.
References


OEPA (Ohio Environmental Protection Agency). 2010. Ohio Lake Erie phosphorus task force Final Report Executive Summary. Columbus, OH.


Appendix A

Generic R code for the Individual Based Model used in chapters 2 and 3.

Lines preceded by “##” are not read by the simulation and are included for annotation purposes. Lines preceded by “#” are functions that are turned off in this build of the model, but can be applied by deleting the “#”.

###define starting cohort number, mean length and mean weight

length<-rnorm(10000,5.3,0.3)

weight<-0.519*(length)^3.293

#source(""

###read in simecol package

library("simecol")

###define class of model

setClass("indbasedModel",
    representation (parms = "list",
                 init = "data.frame"
    ),
)
contains = "simObj"
)

## setup new model run

newrun<- new("indbasedModel",
#defines main structure of model
main = function(time, init, parms) {
  init <- grow(init, parms)

#init <- die(init, parms)

init
},
# define the equations for the objects
equations = list(
  grow = function(init,parms){
    with(parms,
    
    ##Define temp and turbidity values: replace "x" with user defined values

    NTU1 = x
    NTU2 = x
    NTU3 = x
    NTU4 = x
    NTU5 = x
    NTU6 = x
    NTU7 = x
    NTU8 = x
NTU9 = x
NTU10 = x
NTU11 = x
NTU12 = x
NTU13 = x
NTU14 = x
NTU15 = x
NTU16 = x
temp1 = x
temp2 = x
temp3 = x
temp4 = x
temp5 = x
temp6 = x
temp7 = x
temp8 = x
temp9 = x
temp10 = x
temp11 = x
temp12 = x
temp13 = x
temp14 = x
temp15 = x
temp16 = x

###determine mean for distribution based on turbidity and day or size

T1 = ifelse(init$day<8,(1.12*NTU1+29.247),
      ifelse(init$day<15,(1.12*NTU2+29.247),
      ifelse(init$day<22,(1.12*NTU3+29.247),
      (1.12*NTU4+29.247)))))

T2 = ifelse(init$day<29,(0.3594*NTU5+86.975),
      ifelse(init$day<36,(0.3594*NTU6+86.975),
      ifelse(init$day<43,(0.3594*NTU7+86.975),
      (-0.3594*NTU8+86.975)))))

T3 = ifelse(init$day<50,(0.3594*NTU9+86.975),
      ifelse(init$day<57,(0.3594*NTU10+86.975),
      ifelse(init$day<64,(0.3594*NTU11+86.975),
      (-0.3594*NTU12+86.975)))))

T4 = ifelse(init$day<71,(-0.4594*NTU13+35.975),
      ifelse(init$day<78,(-0.4594*NTU14+35.975),
      ifelse(init$day<85,(-0.4594*NTU15+35.975),
      (-0.4594*NTU16+86.975)))))

###prey item masses

prey1 = 2.87
prey2 = 12.800
prey3 = 32.520

###select 12 hourly ingestions for each individual
hourly=rnorm(12,T1,40)
hourly2=rnorm(12,T2,60)
hourly3=rnorm(12,T3,50)
hourly4=rnorm(12,T4,70)

##convert hourly ingestions to mass
mass=hourly*prey1
mass2=((hourly2*.7)*prey3)+((hourly2*.2)*prey1)+((hourly2*.1)*prey2)
mass3=((hourly3*.7)*prey3)+((hourly3*.2)*prey1)+((hourly3*.1)*prey2)
mass4=((hourly4*.7)*prey3)+((hourly4*.2)*prey1)+((hourly4*.1)*prey2)

##temperature equations and parameters
Tm=35
To=32
Q=2.1
T=25
Y=(log(Q))*(Tm-To+2)
W=(log(Q))*(Tm-To)
X=(W^2*(1+(1+40/Y)^.5)^2)/400
V=ifelse(init$day<8,(Tm-temp1)/(Tm-To),
  ifelse(init$day<15,(Tm-temp2)/(Tm-To),
  ifelse(init$day<22,(Tm-temp3)/(Tm-To),
  ifelse(init$day<29,(Tm-temp4)/(Tm-To),
  ifelse(init$day<36,(Tm-temp5)/(Tm-To),
  ifelse(init$day<43,(Tm-temp6)/(Tm-To),


ifelse(init$day<50, (Tm-temp7)/(Tm-To),
ifelse(init$day<57, (Tm-temp8)/(Tm-To),
ifelse(init$day<64, (Tm-temp9)/(Tm-To),
ifelse(init$day<71, (Tm-temp10)/(Tm-To),
ifelse(init$day<78, (Tm-temp11)/(Tm-To),
ifelse(init$day<85, (Tm-temp12)/(Tm-To),
ifelse(init$day<92, (Tm-temp13)/(Tm-To),
ifelse(init$day<99, (Tm-temp14)/(Tm-To),
ifelse(init$day<106, (Tm-temp15)/(Tm-To),
(Tm-temp16)/(Tm-To)))))
)rR=(V^X)*(exp(X*(1-V)))

##define CMAX

CMAX = 2.875*init$wght^0.8496

##define hourly mass consumption based on length or day

cx = ifelse(init$len<30, sum(mass),
ifelse(init$day<43, sum(mass2),
ifelse(init$day<90, sum(mass3),
sum(mass4))))

##define I

I = ifelse(cx>CMAX, CMAX, cx)

##Bioenergetics parameters

AE = 0.8*(1-(0.25*2.71828^(-0.0002*(init$wght-10))))
RM = ((0.172*init$wght)^(-0.216))*rR
TC = (RM + (4.4 * .5) + I*(0.3))

###apply growth to each individual

Growth = ifelse(init$day<4,(1.5*init$wght),(I*AE)-TC)

print(mean(Growth))

init$wght<-init$wght+Growth

init$len <- (init$wght/ 0.519)^(1/3.293)

init$maxwght<-apply(cbind(init$wght,init$maxwght),1,max)

###starvation threshold

Wfin <- Thresh * init$maxwght

init$wfin<-Wfin

ifelse (init$wght < Wfin, init$dead <- 1, init$dead<-0)

d1 <- 1

init$day <- init$day + d1

init

}

}

}

###predation equations (Not used)

die = function(init,parms){

    with(parms, {

        RD = 0.5*(200)
        RA = (RD)^2*pi*0.5
        SS = 0.776 * (200)^1.07
        
    })

}
SV = SS * RA

Encounter = (SV*.15*0.5417)/2370

ifelse(init$wght<6800,init$dead <- rbinom(length(init$len),1,0.075),init$dead <-
  rbinom(length(init$len),1,0.001))

init<-init[init[,4]==0,]

init

}),

##define other parameters not defined in equation list
parms = list(
  Light = 0.5417,
  AssimMax = 0.8,
  AssimSh = 0.002,
  MetabNum = 4500,
  MetabDen = 45000,
  SDAE = 0.3,
  ActMetab = 2.5,
  Thresh = 0
),

##apply growth and dead to initial data frame and update for next day
init = data.frame(len=length, wght=weight, maxwght=weight, dead=0, wfin=0, day=0),
times = c(from=0, to=124, by=1),
solver = "iteration"

## observer function to visualize or output data to an outside data frame
observer(newrun) <- function(state, time, i, out, y) {

## numerical output to the screen
cat("index =", i,
    ", time =", time,
    ", length =", mean(state$len),
    ", remaining =", length(state$dead),
    ", sd len =", sd(state$len),
    ", sd wght =", sd(state$wght), "\n"
    
    #, file="Oneida2011.csv", sep=",", append=T
}

## animation
par(mfrow = c(4, 2))
plot(state$len, state$wght, xlab = "len", ylab = "wght", pch = 16,
    col = "red", xlim = c(0, 100))
plot(i, length(state$dead), xlab = "time", ylab = "survivors", , pch = 16,
    col = "red", xlim = c(0, 110))
hist(state$len)
hist(state$wght)

if (is.matrix(out)) # important because out may be NULL for the first call
matplot(out[,1], out[,1]) # dynamic graph of sd in both directions

## return a vector with summary information

#highalout<- c(times = time, sdlen=sd(state$len), sdwght=sd(state$wght))

#write.table(state$len, file = 'latest.csv',sep="",)

}

##run new simulation

obstest <- sim(best)