Journal of Great Lakes Research 39 (2013) 295–302

Contents lists available at SciVerse ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Effects of water clarity on the length and abundance of age-0 yellow perch in the Western Basin of Lake Erie

Nathan F. Manning [a,*], Christine M. Mayer [a], Jonathan M. Bossenbroek [a], Jeff T. Tyson [b]

[a] *Department of Environmental Sciences & Lake Erie Center, University of Toledo, 6200 Bayshore Rd., Oregon, OH 43616, USA*
[b] *Sandusky Fisheries Research Unit, Ohio Department of Natural Resources, Division of Wildlife, 305 East Shoreline Drive, Sandusky, OH 44870, USA*

ARTICLE INFO

Article history:
Received 19 September 2012
Accepted 21 March 2013
Available online 4 May 2013

Communicated by Edward Rutherford

Keywords:
Lake Erie
Water clarity
Yellow perch
Generalized additive models

ABSTRACT

Water clarity is an important environmental variable that may affect fish populations by altering the visual environment. Effects can change feeding ability, as well as alter predation risk. The western basin of Lake Erie provides a valuable model system for studying the effects of transparency because the two main tributaries, the Maumee and Detroit rivers, differ substantially in clarity. We used Generalized Additive Models (GAMs) to quantify the relationship between transparency and the observed abundance and length of age-0 yellow perch (*Perca flavescens*) in August, based on surveys from 1986 to 2006. Secchi data from June to August were included in the models that best explained the variation in yellow perch abundance and length. August values for bottom oxygen and bottom temperature also increased model fit for abundance, whereas only bottom temperature improved model fit for length. Our models indicate that transparency was positively related to the August length while abundance of age-0 yellow perch was inversely related to transparency. Highest abundance was observed in areas with the lowest transparency, with peak abundances observed in areas with less than 1 m of Secchi depth. This is in contrast to August length, which increased as transparency increased, to an asymptote at around 3 m of Secchi depth. The split nature of water clarity conditions in the western basin of Lake Erie has resulted in areas with higher growth potential, versus areas with higher apparent survival.

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 (Harvey and Brown, 2004; Mayer et al., 2000; Mills et al., 1986; Miner and Stein, 1993; Wellington et al., 2010) and, in turn, the growth, recruitment, and subsequent year class strength of a population (Crecco and Savoy, 1985; Noble, 1975; Reichert et al., 2010; Tyson and Knight, 2001).

Multiple factors mediate the effect of water clarity on fish foraging, including fish species (DeRobertis et al., 2003; Rowe and Dean, 1998), developmental stage (Boehlert 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 (*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 (Chiu and Abrahams, 2010; DeRobertis et al., 2003; Diehl, 1988; Hartman and Margraf, 1993; Wahl et al., 1993) 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 (Clapp and Detmers, 2004; Hargeby et al., 2007; Hoffman et al., 2001; Olson et al., 2001; Paukert and Willis, 2001) 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 (Heisler et al., 2008; Nichols and Hopkins, 1993). These anthropogenically driven sediment plumes and algal blooms have become wide spread in coastal

---

[*] Corresponding author. Tel.: +1 419 530 8372.
E-mail address: nathan.manning@utoledo.edu (N.F. Manning).

0380-1330/$ – see front matter © 2013 International Association for Great Lakes Research. Published by Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.jglr.2013.03.010

systems that are often important nursery areas for age-0 fish (Jones et al., 2003; Nack et al., 1993). 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). While the Maumee River contributes less than 15% of the total water that flows into the western basin of Lake Erie, it contributes more than half of the suspended sediments input, and more than 2240 t of phosphorus annually (Moorhead et al., 2003) influencing sediment plumes (Paul et al., 1982) and algal blooms in the western basin (Correll, 1998; Smith, 1982). The Detroit River discharge averages 5324 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 we 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.

We 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, we hypothesize that water clarity will be more important than other physical factors in explaining variability in age-0 yellow perch size and abundance. We 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.

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 our analyses, while only fish data from August were considered because this is when age-0 yellow perch have become demersal and are first 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, we 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 (Johnson 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, we tested our length, CPUE and Secchi depth locations for spatial autocorrelation using the method describe in Kaluzny et al. (1998). First we used General Linear Models to remove the trends in the data using the general equation: $f(x) = Latitude + Longitude$. Semi-variograms 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 our 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, we 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. 1A). 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 we 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). GAMs 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. A 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. We used the *gam* function of the mgcv package (Wood, 2006) in R (v. 11.1 R core team, 2012), 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

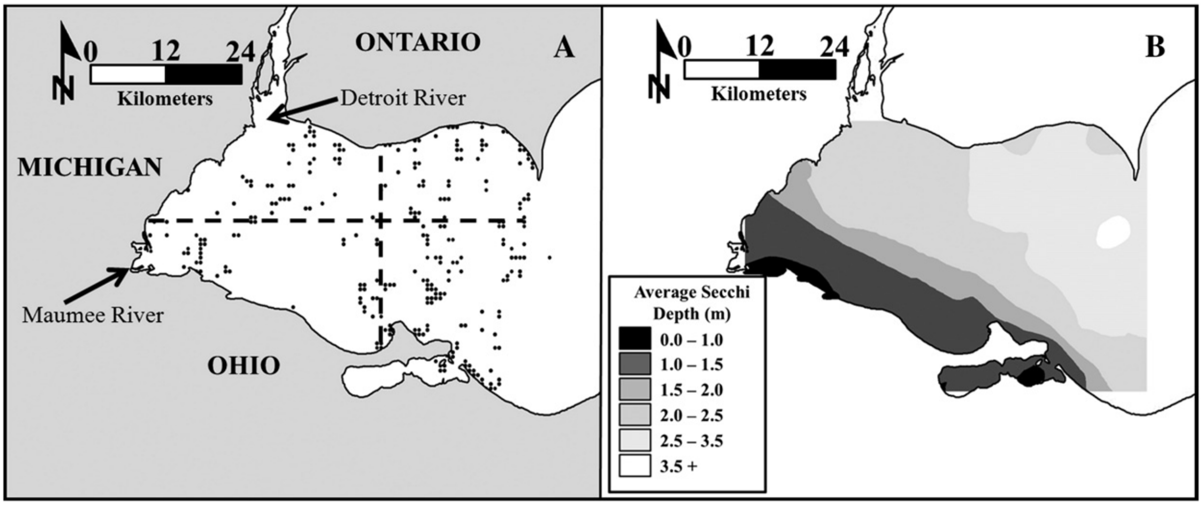

Fig. 1. Maps of the western basin of Lake Erie showing: (A) Approximate distribution of sample locations. The dotted lines indicate the approximate divisions used to separate the four sections of the basin. (B) Kriging map of average August Secchi disk depth in the Western basin of Lake Erie, 1986–2006.

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).

We 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 Fig. 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.

We constructed ten candidate models to predict relative CPUE and length of the age-0 yellow perch in August (Table 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 we assume that growth and abundance are a result of both past and current conditions. We 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 our "dynamic" factors, as their values can change from sample to sample. We 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 1
Model structure for the candidate models for predicting yellow perch metrics and the respective AIC and ΔAIC values. Model number is indicated on the left. An X indicates 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.

Static factors				Dynamic factors													
Model	Depth	Latitude	Longitude	Secchi depth			Bottom oxygen		Bottom temperature								
				Jun	Jul	Aug	Jul	Aug	Jun	Jul	Aug	Aug abundance AIC	Aug abundance ΔAIC	% deviance explained	Aug length AIC	Aug length ΔAIC	% deviance explained
Base						X						416.64	89.27	34.2	427.64	52.07	21.9
1						X		X			X	385.73	58.36	35.7	410.12	34.55	29.4
2	X	X	X			X		X			X	385.83	58.46	37.6	409.80	34.23	33.3
3	X	X	X	X	X	X						396.21	68.84	37.1	399.37	23.80	28.2
4	X	X	X				X	X				652.04	324.67	30.1	518.87	143.30	13.6
5	X	X	X						X	X	X	590.09	262.72	32.4	479.81	104.24	38.7
6	X	X	X	X	X	X	X	X				371.12	43.75	45.7	395.27	19.70	44.8
7	X	X	X	X	X	X			X	X	X	362.63	35.26	46.3	375.57	0	59.7
8	X	X	X				X	X	X	X	X	561.15	233.78	54.2	462.59	24.02	46.1
9	X	X	X	X	X		X		X	X		367.82	40.45	56.1	399.65	24.08	51.1
10	X	X	X	X	X	X		X			X	327.37	0	73.6	387.89	12.32	50.2
Full	X	X	X	X	X	X	X	X	X	X	X	352.16	24.79	74.1	379.33	3.76	60.3

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 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, we 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). Two of the models (7 and 14) included in this set of supplemental models were also included in the a priori model suite.

Results

Data visualization and basin comparison

Preliminary exploration of our data indicated that Secchi depth was consistently lower (indicating low transparency) along the south and southeastern shore of the western basin (Fig. 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). 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 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).

Abundance in August model

Our 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. 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 1). This best-fit model explained 73.6% of the deviance observed in the data (Table 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 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. 3 A). 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.

Table 2
Model structure for the supplemental models on the effect of the time of capture and their respective AIC and ΔAIC values. Model number is indicated on the left. An X indicates 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.

Static factors				Dynamic factors								
Model	Depth	Latitude	Longitude	Secchi depth	Bottom oxygen	Bottom temperature						
				Aug	Aug	Aug	Aug abundance AIC	Aug abundance ΔAIC	% deviance explained	Aug length AIC	Aug length ΔAIC	% deviance explained
1				X			212.45	20.52	11.9	266.54	42.67	10.1
2					X		304.18	112.25	5.2	279.41	55.54	4.3
3						X	282.43	90.50	6.9	274.11	50.24	6.7
4				X	X		227.92	35.99	14.9	262.75	38.88	14.2
5				X		X	209.77	17.84	16.5	261.87	38.00	17.5
6					X	X	231.04	39.11	13.2	264.82	40.95	17.1
7				X	X	X	191.93	0	34.7	225.31	1.44	33.6
8	X	X	X	X			213.84	21.91	23.4	236.02	12.15	26.4
9	X	X	X		X		218.88	26.95	15.2	257.12	33.25	20.1
10	X	X	X			X	216.13	24.20	25.7	240.93	17.06	21.1
11	X	X	X	X	X		198.10	6.17	33.1	235.26	11.39	31.6
12	X	X	X	X		X	195.43	3.50	31.5	228.76	4.89	32.1
13	X	X	X		X	X	203.67	12.37	29.9	236.07	12.2	31.6
14	X	X	X	X	X	X	191.93	0	35.1	223.87	0	34.3

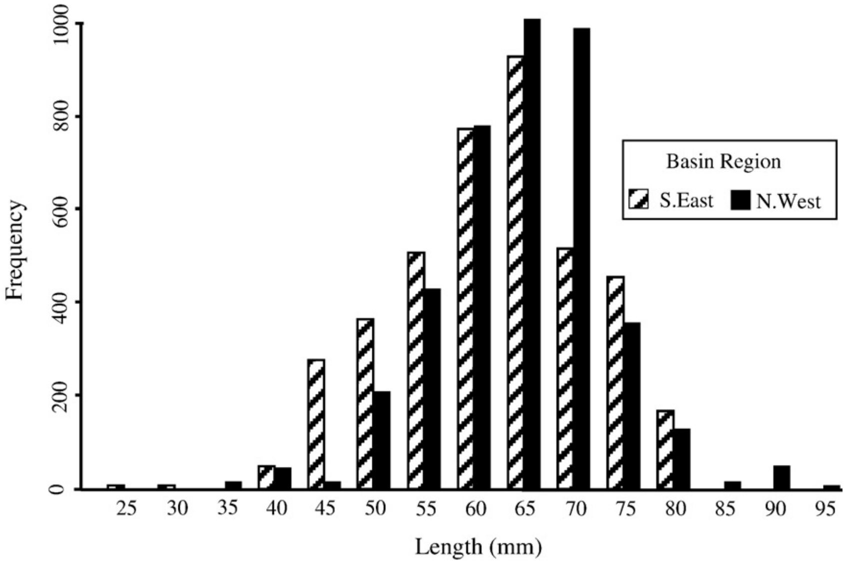

Fig. 2. Length-frequency distributions of age-0 yellow perch for the northwestern and southeastern portions of the western basin of Lake Erie. Distributions are significantly different (K–S test, $p < 0.001$) between the two areas, with larger fish occurring in the northwestern portion of the basin.

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 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. 4). 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

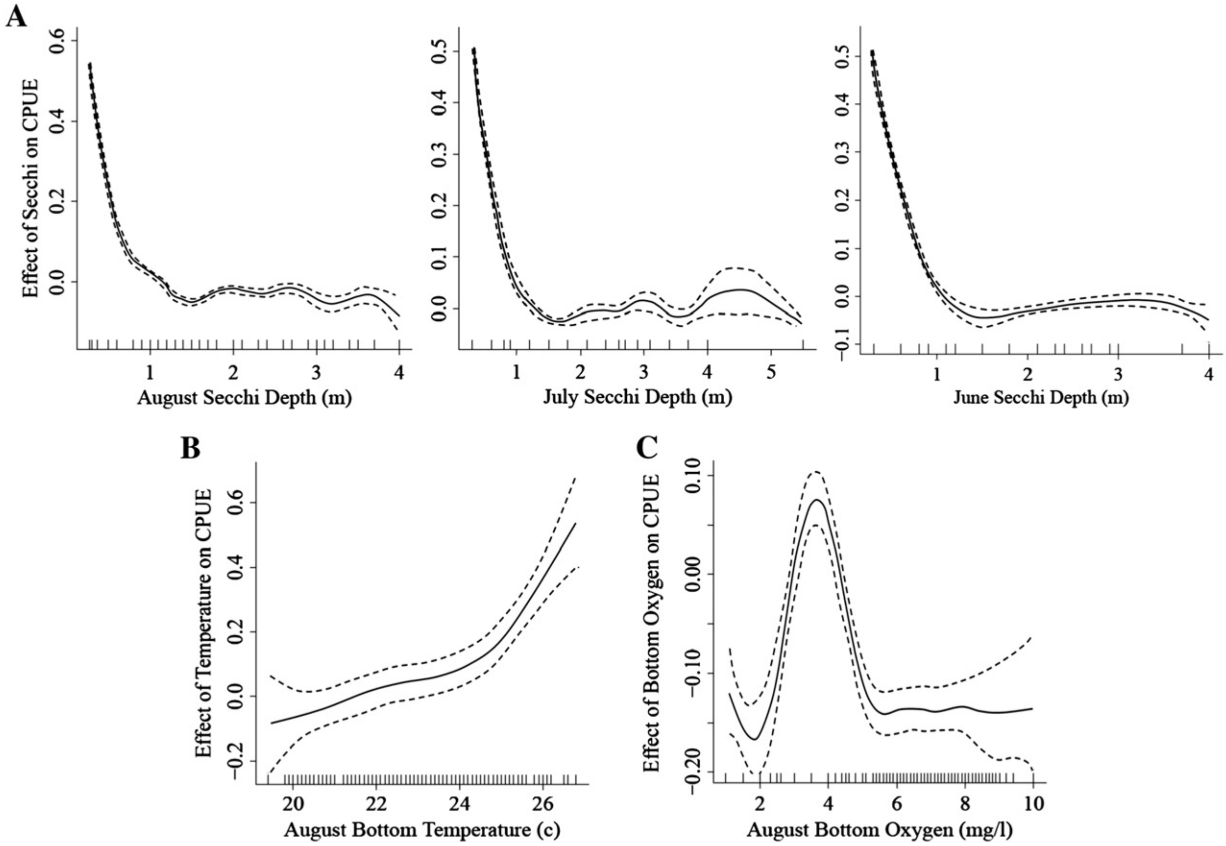

Fig. 3. Relationship between August abundance, measured as standardized trawl CPUE, and the smoothing functions for (A) Secchi depth, (B) bottom temperature, and (C) bottom oxygen. The solid line is the predicted value of the dependent variable as a function of the x-axis. The small lines along the x-axis show 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.

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. 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) show that the inclusion of prior conditions significantly increased the deviance explained by the models for both length and abundance (Tables 1 and 2). For abundance, the best-fit time of capture models, model 7 and model 14, had a Δ 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.

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 our 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 positively related to fish length but negatively 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 our 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 the 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 Magnuson, 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 (DeRobertis et al., 2003; Diehl, 1988). 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). Our 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.

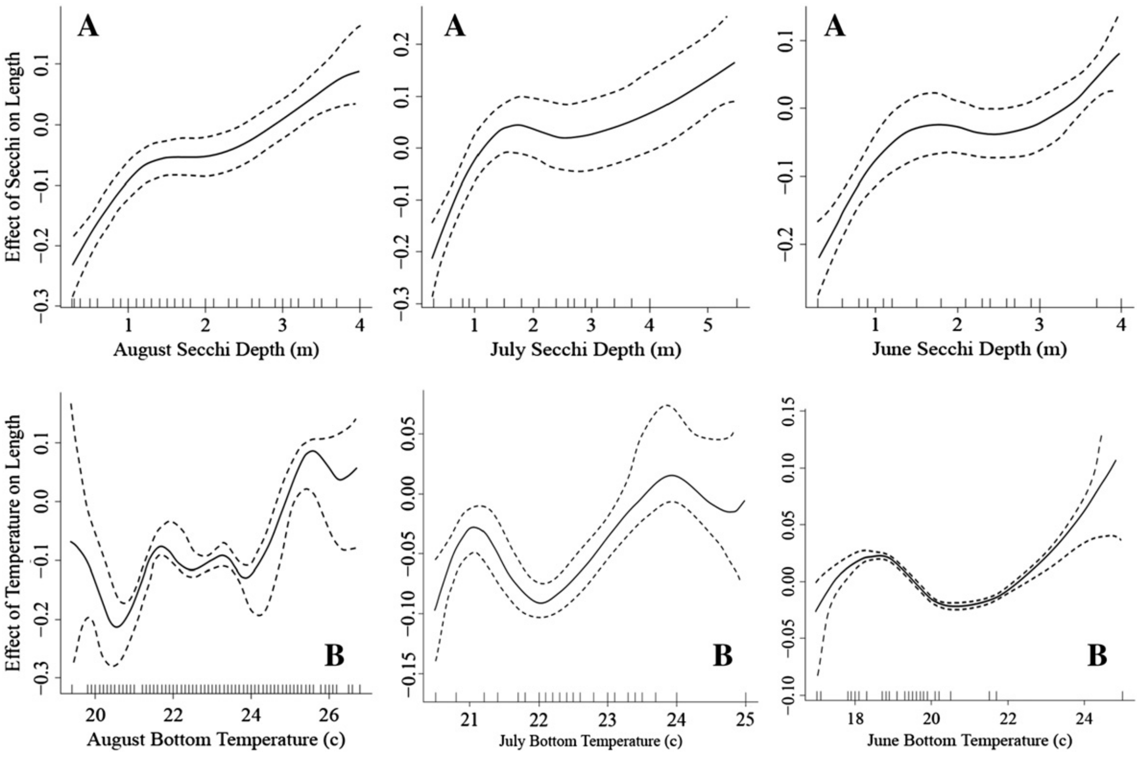

Fig. 4. Relationship between August length and the smoothing functions for (A) Secchi depth, and (B) bottom temperature. The solid line is the predicted value of the dependent variable as a function of the x-axis. The small lines along the x-axis show the value of individual observations. The y-axis 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.

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; Fulford et al., 2006; Parrish and Margraff, 1990; Post and Prankevicius, 1987). 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 as 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 (Breen and Ruetz, 2006; Hayward et al., 1989); 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 our 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, our 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.

Our 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 (Chaffin et al., 2011; Rinato-Kanto et al., 2005) and other coastal areas (Anderson et al., 2002; Backer and McGillicuddy, 2006; Hallegraeff, 1993) 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. Additional stresses on fish populations from introduced predators and competitors may mean that such turbid refugia remains important in maintaining the abundance of river-associated stocks.

Acknowledgments

The authors would like to thank the members of the Mayer and Bossenbroek labs at the University of Toledo, Department of Environmental Sciences. This work was supported by the Great Lakes Fishery Commission and the National Science Foundation grant #NSF DGE-0742395 to the University of Toledo's Lake Erie Center, “Graduate Learning Community at the Land-Lake Ecosystem Interface”. This is publication 2013–12 from the University of Toledo's Lake Erie Center.

References

Akaike, H., 1987. Factor analysis and AIC. Psychometrika 52 (3), 317–332.

Anderson, D.M., Gilbert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuar. Coasts 25 (4), 704–726.

Backer, L.C., McGillicuddy Jr., D.J., 2006. Harmful algal blooms. Oceanography 19 (2), 94–106.

Baker, D.B., Richards, R.P.R., 2002. Phosphorus budgets and riverine phosphorus export in northwest Ohio watersheds. J. Environ. Qual. 31 (1), 96–108.

Boehlert, G.W., Morgan, J.B., 1985. Turbidity enhances feeding abilities of larval Pacific herring, *Clupea harengus pallasi*. Hydrobiologia 123 (2), 161–170.

Brandt, S.B., Mason, D.M., Macneill, D.B., Coates, T., Gannon, J.E., 1987. Predation by alewives on larvae of yellow perch in Lake Ontario. Trans. Am. Fish. Soc. 116 (4), 641–645.

Brazner, J.C., 1997. Regional, habitat and human development influences on coastal wetland and beach fish assemblages in Green Bay, Lake Michigan. J. Great Lakes Res. 23 (1), 36.

Breen, M.J., Ruetz III, C.R., 2006. Gear bias in fyke netting: evaluating soak time, fish density, and predators. N. Am. J. Fish. Manag. 26 (1), 32–41.

Bystrom, P.E., Garcia-Berthou, G., 1999. Density dependant growth and size specific competitive interactions in young fish. Oikos 86, 217–232.

Carton, A.G., 2005. The impact of light intensity and algal-induced turbidity on first-feeding *Seriola lalandi* larvae. Aquacult. Res. 36 (16), 1588–1594.

Chaffin, J.D., Bridgeman, T.B., Heckathorn, S.A., Mishra, S., 2011. Assessment of *Microcystis* growth rate potential and nutrient status across a trophic gradient in western Lake Erie. J. Great Lakes Res. 37 (1), 92–100.

Chiu, S., Abrahams, M.V., 2010. Effects of turbidity and risk of predation on habitat selection decisions by fathead minnows (*Pimephales promelas*). Environ. Biol. Fishes 87 (4), 309–316.

Clapp, D.F., Detmers, J.M., 2004. Yellow perch research and management in Lake Michigan: evaluating progress in a cooperative effort, 1997–2001. Fisheries 29 (11), 11–19.

Correll, D.L., 1998. The role of phosphorus in eutrophication of receiving waters: a review. J. Environ. Qual. 27, 261–266.

Crecco, V.A., Savoy, T.F., 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad in the Connecticut River. Can. J. Fish. Aquat. Sci. 42 (10), 1640–1648.

Crowl, T.A., 1989. Effects of crayfish size, orientation, and movement on the reactive distance of largemouth bass foraging in clear and turbid water. Hydrobiologia 183 (2), 133–140.

DeRobertis, A., Ryer, C.H., Veloza, A., Brodeur, R.D., 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Can. J. Fish. Aquat. Sci. 60 (12), 1517–1526.

Diehl, S., 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos 53 (2), 207–214.

Dorner, H., Wagner, A., Benndorf, J., 1999. Predation by piscivorous fish on age-0 fish: spatial and temporal variability in a biomanipulated lake (Bautzen Reservoir, Germany). Hydrobiologia 408, 39–46.

Enders, E.C., Boisclair, D., Boily, P., Magnan, P., 2006. Effects of body mass and water temperature on the standard metabolic rate of juvenile yellow perch, *Perca flavescens*. Environ. Biol. Fishes 76, 399–407.

Faraway, J., 2006. Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models. Chapman and Hall/CRC, Boca Raton, Florida.

Fisher, T.A., Harding Jr., L.W., Stanley, D.W., Ward, L.G., 1988. Phytoplankton, nutrients, and turbidity in the Chesapeake, Delaware, and Hudson Estuaries. Estuar. Coast. Shelf Sci. 27 (1), 61–93.

Forney, J.L., 1971. Development of dominant year classes in a yellow perch population. Trans. Am. Fish. Soc. 100 (4), 739–748.

Fulford, R.S., Rice, J.A., Miller, T.J., Binkowski, F.P., 2006. Elucidating patterns of size-dependent predation on larval yellow perch (*Perca flavescens*) in Lake Michigan: an experimental and modeling approach. Can. J. Fish. Aquat. Sci. 63 (1), 11–27.

Gitelson, A.A., Schalles, J.F., Hladik, C.M., 2007. Remote chlorophyll — a retrieval in turbid productive estuaries: Chesapeake Bay case study. Remote Sens. Environ. 109 (4), 464–472.

Granqvist, M., Mattila, J., 2004. The effects of turbidity and light intensity on the consumption of mysids by juvenile perch (*Perca fluviatilis* L.). Hydrobiologia 514 (1), 93–101.

Green, R.E., Bianchi, T.S., Dagg, M.J., Walker, N.D., Breed, G.A., 2006. An organic carbon budget for the Mississippi River turbidity plume and plume contributions to air–sea CO2 fluxes and bottom water hypoxia. Estuar. Coasts 29 (4), 579–597.

Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32 (2), 79–99.

Hargeby, A., Blindow, I., Andersson, G., 2007. Long-term patterns of shifts between clear and turbid states in Lake Krankesjon and Lake Takern. Ecosystems 10, 28–35.

Hartman, K.J., Margraf, F.J., 1993. Evidence of predatory control of yellow perch (*Perca flavescens*) recruitment in Lake Erie, U.S.A. J. Fish Biol. 43, 109–119.

Harvey, M.C., Brown, G.E., 2004. Dine or dash?: ontogenetic shift in the response of yellow perch to conspecific alarm cues. Environ. Biol. Fishes 70, 345–352.

Hayward, R.S., Margraff, F.J., Knight, C.T., Glomski, D.J., 1989. Gear bias in field estimation of the amount of food consumed by fish. Can. J. Fish. Aquat. Sci. 46 (5), 874–876.

Heisler, J., Gilbert, P.M., Burkholder, J.M., et al., 2008. Eutrophication and harmful algal blooms: a scientific consensus. Harmful Algae 8 (1), 3–13.

Hilborn, R., Mangel, M., 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, New Jersey.

Hoffman, J.C., Smith, M.E., Lehman, J.T., 2001. Perch or plankton: top-down control of Daphnia by yellow perch (*Perca flavescens*) or *Bythotrephes cederstroemi* in an inland lake. Freshw. Biol. 46, 759–775.

Irwin, B.J., Rudstam, L.G., Jackson, J.R., VanDeValk, A.J., Forney, J.L., Fitzgerald, D.G., 2009. Depensatory mortality, density-dependent growth, and delayed compensation: disentangling the interplay of mortality, growth, and density during early life stages of yellow perch. Trans. Am. Fish. Soc. 138, 99–110.

Johnson, B.L., Richardson, W.B., Naimo, T.J., 1995. Past, present, and future concepts in large river ecology. Bioscience 45 (3), 134–141.

Johnston, K., VerHoef, J.M., Krivoruchko, K., Lucas, N., 2003. Using ArcGIS Geostatistical Analyst. ESRI Press.

Jones, N.E., Tonn, W.M., Scrimgeour, G.J., 2003. Selective feeding of age-0 arctic grayling in lake outlet streams of the Northwest Territories, Canada. Environ. Biol. Fishes 67 (2), 169–178.

Kaluzny, S.P., Vega, S.C., Cardoso, T.P., Shelly, A.A., 1998. S + SpatialStats: user's manual for Windows and UNIX. Springer.

Kramer, D.L., 1987. Dissolved oxygen and fish behavior. Environ. Biol. Fishes 18 (2), 81–92.

Ljunggren, L., Sandström, A., 2007. Influence of visual conditions on foraging and growth of juvenile fishes with dissimilar sensory physiology. J. Fish Biol. 70 (5), 1319–1334.

Ludsin, S.A., Kershner, M.W., Blocksom, K.A., Knight, R.L., Stien, R.A., 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. Ecol. Appl. 11 (3), 731–746.

Lyons, J., Magnuson, J.J., 1987. Effects of walleye predation on the population dynamics of small littoral zone fishes in a northern Wisconsin lake. Trans. Am. Fish. Soc. 116 (1), 29–39.

Mayer, C.M., VanDeValk, A., Forney, J.L., Rudstam, L.G., Mills, E.L., 2000. Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York, to the establishment of zebra mussels (*Dreissena polymorpha*). Can. J. Fish. Aquat. Sci. 57 (4), 742–754.

Metcalf, N.B., 1986. Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth. J. Fish Biol. 28 (5), 525–531.

Mills, E.L., Kretchmer, D.W., Confer, J.L., 1986. Zooplankton selection by young yellow perch: the influence of light, prey density, and predator size. Trans. Am. Fish. Soc. 115, 716–725.

Miner, J.G., Stein, R.A., 1993. Interactive influence of turbidity and light on larval bluegill (*Lepomis macrochirus*) foraging. Can. J. Fish. Aquat. Sci. 50 (4), 781–788.

Moorhead, D., Bridgeman, T., Morris, J., 2003. Changes in water quality of Maumee Bay 1928–2003. Ecovision World Monograph Series.

Nack, S.B., Bunnell, D., Green, D.M., Forney, J.L., 1993. Spawning and nursery habitats of largemouth bass in the tidal Hudson River. Trans. Am. Fish. Soc. 122 (2), 208–216.

Nichols, K.H., Hopkins, G.J., 1993. Recent changes in Lake Erie (North Shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. J. Great Lakes Res. 19 (4), 637–647.

Nielsen, L.A., 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 37 (1), 11–19.

Noble, R.L., 1975. Growth of young yellow perch in relation to zooplankton populations. Trans. Am. Fish. Soc. 104 (4), 731–741.

OEPA (Ohio Environmental Protection Agency), 2010. Ohio Lake Erie Phosphorus Task Force Final Report Executive Summary (Columbus, OH).

Olson, M.H., Green, D.M., Rudstam, L.G., 2001. Changes in yellow perch (*Perca flavescens*) growth associated with the establishment of a walleye (*Stizostedion vitreum*) population in Canadarago Lake, New York (USA). Ecol. Freshw. Fish 10, 11–20.

Ouyang, D., Bartholic, J., Selegean, J., 2005. Assessing sediment loading from agricultural croplands in the Great Lakes basin. J. Am. Sci. 1 (2), 14–21.

Parrish, D.L., Margraff, F.J., 1990. Interactions between white perch (*Morone americana*) and yellow perch (*Perca flavescens*) in Lake Erie as determined by feeding and growth. Can. J. Fish. Aquat. Sci. 47 (9), 1779–1787.

Paukert, C.P., Willis, D.W., 2001. Comparison of exploited and unexploited yellow perch (*Perca flavescens* (Mitchill)) populations in Nebraska Sandhill Lakes. Fish. Manag. Ecol. 8, 533–542.

Paul, J.F., Kasprzyk, R., Lick, W., 1982. Turbidity in the western basin of Lake Erie. J. Geophys. Res. 87 (C8), 5779–5784.

Post, J.R., Evans, D.O., 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. 46 (11), 1958–1968.

Post, J.R., McQueen, D.J., 1988. Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): a response to prey or predators? Can. J. Fish. Aquat. Sci. 45 (10), 1820–1826.

Post, J.R., Prankevicius, A.B., 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. 44 (11), 1840–1847.

Power, M., Van Den Heuvel, M.R., 1999. Age-0 yellow perch growth and its relationship to temperature. Trans. Am. Fish. Soc. 128 (4), 687–700.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Radke, R.J., Gaupisch, A., 2005. Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): possible implications for fish community structure in lakes. Naturwissenschaften 92 (2), 91–94.

Reichert, J.M., Fryer, B.J., Pangle, K.L., Johnson, T.B., Tyson, J.T., Drelich, A.B., Ludsin, S.A., 2010. River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. Can. J. Fish. Aquat. Sci. 67, 987–1004.

Ribeiro Jr., P.J., Diggle, P.J., 2001. geoR: a package for geostatistical analysis. R-News 1 (2) (ISSN 1609-3631).

Rinato-Kanto, J.M., Ouellette, A.J.A., Boyer, G.L., Twiss, M.R., Bridgeman, T.B., Wilhelm, S.W., 2005. Quantification of toxic *Mycrocystis* spp. during 2003 and 2004 blooms in western Lake Erie using quantitative real time PCR. Environ. Sci. Technol. 39 (11), 4198–4205.

Rowe, D.K., Dean, T.L., 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. N. Z. J. Mar. Freshw. Res. 32 (1), 21–29.

Smith, V.H., 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. Am. Soc. Limnol. Oceanogr. 27 (6), 1101–1112.

Tyson, J.T., Knight, R.L., 2001. Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. Trans. Am. Fish. Soc. 130 (5), 766–782.

Tyson, J.T., Johnson, T.B., Knight, C.T., Bur, M.T., 2006. Intercalibration of research vessels on Lake Erie. N. Am. J. Fish. Manag. 26 (3), 559–570.

Utne-Palm, A.C., 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar. Freshw. Behav. Physiol. 35 (1–2), 111–128.

Vanderploeg, H.A., Liebig, J.R., Carmichael, W.W., Agy, M.A., Johengen, T.H., Fahnenstiel, G.L., Nalepa, T.F., 2001. Zebra mussel selective filtration promoted toxic *Mycrocystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish. Aquat. Sci. 58, 1208–1221.

Wahl, C.M., Mills, E.L., McFarland, W.N., DeGisi, J.S., 1993. Ontogenic changes in prey selection and visual acuity of the yellow perch. Can. J. Fish. Aquat. Sci. 50 (4), 743–749.

Wellington, C.G., Mayer, C.M., Bossenbroek, J.M., Stroh, N.A., 2010. Effects of turbidity and prey density on the foraging success of age-0 yellow perch (*Perca flavescens*). J. Fish Biol. 76 (7), 1729–1741.

Williamson, C.E., Metzgar, S.L., Lovera, P.A., 1997. Solar ultraviolet radiation and the spawning habitat of yellow perch (*Perca flavescens*). Ecol. Appl. 7 (3), 1017–1023.

Wood, S.N., 2006. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

Wood, P.J., Armitage, P.D., 1997. Biological effects of fine sediment in the lotic environment. Environ. Manage. 21 (2), 203–217.

Yee, T.W., Mitchell, N.D., 1991. Generalized additive models in plant ecology. J. Veg. Sci. 2 (5), 587–602.