River Plume Effects on Yellow Perch Growth, Survival, and Recruitment in Lake Erie

Julie Reichert
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RIVER PLUME EFFECTS ON YELLOW PERCH GROWTH, SURVIVAL, AND RECRUITMENT IN LAKE ERIE

By

Julie Marie Reichert

A Thesis Submitted to the Faculty of Graduate Studies through the Great Lakes Institute for Environmental Research in Partial Fulfilment of the Requirements for the Degree of Master of Science at the University of Windsor

Windsor, Ontario, Canada

2009

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RIVER PLUME EFFECTS ON YELLOW PERCH GROWTH, SURVIVAL, AND RECRUITMENT IN LAKE ERIE

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DECLARATION OF CO-AUTHORSHIP / PREVIOUS PUBLICATION

I. Co-Authorship Declaration

This thesis incorporates material that is a result of a joint research effort with the following collaborators: Timothy Johnson (Ontario Ministry of Natural Resources), Jeff Tyson (Ohio Department of Natural Resources), Brian Fryer (University of Windsor), and Kevin Pangle, Alison Drellich and Stuart Ludsin (The Ohio State University). In all cases, the key ideas, primary contributions, experimental designs, data analysis, and interpretation were performed by the author, and the contribution of co-authors was primarily in an advisory capacity.

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<td>Reichert, J.M., Ludsin, S.A., Fryer, B.J., Johnson, T.B., Tyson, J.T., Pangle, K.L., and Drellich, A.B. Watershed-derived habitat heterogeneity during early life influences recruitment success of a freshwater fish</td>
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ABSTRACT

Western Lake Erie receives tributary inputs that form open-lake plumes with distinct chemical, physical, and biological properties. I explored their importance to yellow perch (*Perca flavescens*) recruitment by testing two related hypotheses: 1) survival of larvae would be greater in the nutrient-rich Maumee River plume versus non-plume waters; and 2) warm temperature and high zooplankton (prey) that lead to fast larval growth would underlie survivorship differences. As expected, larval survival was higher in Maumee River plume versus non-Maumee waters during 2006 and 2007. This survival difference, however, was unexpectedly unrelated to zooplankton availability or temperature (i.e., bottom-up effects were unimportant). Instead, I suggest that high turbidity in the Maumee River plume offered a survival advantage over non-plume waters by reducing predation mortality on larvae (i.e., top-down effects appear important). These findings should help fisheries management agencies better understand and forecast yellow perch recruitment variation in Lake Erie.
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INTRODUCTION TO THESIS

Accurately predicting fish recruitment has long been a key goal of fisheries managers. In the context of fisheries management, recruitment is defined as the number of new individuals that survive to the exploitable population. However, predicting recruitment has proven difficult because most fishes exhibit high inter-annual variation in growth and survival, owing to the complex simultaneous effects of physical, chemical, and biological variables (Houde 1987, Miller et al. 1988; Leggett and DeBlois 1994; Bradford and Cabana 1997). For instance, variations in temperature, body size, and growth rates during the larval stage of fish were shown to significantly influence mortality, and therefore, recruitment levels (Houde 1987, 1994; Miller et al. 1988; Pepin 1991).

Both starvation and predation of larval fish are considered to be major factors regulating recruitment variation (Hunter 1981, Houde 1987, Leggett and Deblois 1994). Starvation can cause direct mortality (if no food is available then fish simply die) or indirect mortality by reducing growth rates, which could cause larval fish to become more vulnerable to size-selective predation (Shepherd and Cushing 1980; Miller et al. 1988). According to the ‘bigger is better’ and the ‘stage duration’ hypotheses, larvae that reach a larger body size (i.e., by means of faster growth) and metamorphose at an earlier age will be less vulnerable to starvation and predation mortality than slower-growing larvae (a detailed discussion of these two hypotheses can be found in Leggett and Deblois 1994).

While many hypotheses involving bottom-up effects (food availability, foraging and growth rates of larvae) and top-down effects (predation on larvae) have been
developed and tested, recruitment variation is still not well understood, owing to conflicting results between studies and the inability to relate results from lab experiments to field studies (Leggett and Deblois 1994). However, due to growing awareness and acceptance that recruitment is influenced by forcing factors external to the aquatic system (e.g., watershed, climate; Ludsin 2001; Koslow et al. 2002; Salen-Picard et al. 2002; Le Pape et al. 2003; MacKenzie and Koster 2004) and advancements in microchemical (Campana 1999, Thresher 1999) and genetic (Asahida et al. 1997; Rosel and Kocher 2002) techniques, researchers are moving closer to identifying and determining factors that drive recruitment dynamics of fishes.

To date, watershed influences on population dynamics have been more extensively studied in marine coastal systems than in freshwater systems, including the Mississippi River in the Gulf of Mexico (Grimes and Finucane 1991), the Rhone River in the Mediterranean (Lloret et al. 2001 and Salen-Picard et al. 2002), Botany Bay in southeast Australia (Rissik and Suthers 1996), the River Guadalquivir in the Gulf of Cadiz (Garcia-Isarch et al. 2006), and the Bio-Bio and Itata Rivers in central-south Chile (Quinones and Montes 2001). In aquatic ecosystems, river discharge leads to the formation of plumes or fronts in the lake or ocean because of density differences due to temperature and/or salinity (Largier 1993; Grimes and Kingsford 1996). River plumes and fronts typically differ in their chemical (e.g., phosphorus-inputs), physical (e.g., temperature, suspended sediments), and biological (e.g., primary production) attributes from the main body of water because of influences from the surrounding watershed (e.g., agricultural runoff, development). This habitat heterogeneity could result in bottom-up (e.g., enhanced prey availability that increases growth) and/or top-down (e.g., enhanced
turbidity that reduces predation mortality) controls, in turn, influencing survival, and ultimately fish recruitment.

Otolith microchemistry has made it possible to examine differential habitat-use of fish from chemically different aquatic environments. Otoliths are metabolically inert structures located in the inner ears of fish that incrementally grow throughout life (Campana and Neilson 1985), while incorporating trace elements from the surrounding water as they grow (Campana 1999; Campana and Thorrold 2001). These properties have been used to determine age, growth rates, natal origins, habitat-use, migration histories, and population structure and connectivity of fish (Thorrold et al. 1998; Thresher 1999; Gillanders and Kingsford 2000; Secor et al. 2001; Thorrold et al. 2001; Patterson et al. 2004; Crook and Gillanders 2006; Clarke et al. 2007). While most otolith chemistry studies have focused on marine systems, recent work by Brazner et al. (2004) and Ludsin et al. (2006) demonstrated that otoliths can also be used to discriminate between spawning locations in freshwater systems.

Recent research in Lake Erie has demonstrated a strong positive relationship between springtime Maumee River discharge and yellow perch *Perca flavescens* recruitment at age-two in the western basin (Ludsin 2000). This empirical model suggests that variation in recruitment is related to tributary outflows from the Maumee River into Lake Erie just before and during the larval yellow perch production period during spring (Ludsin 2000), supporting the need to understand mechanisms influencing early life dynamics. As part of a larger Great Lakes Fishery Commission project designed to examine bottom-up and top-down mechanisms influencing yellow perch recruitment in western Lake Erie, I sought to accomplish the following objectives:
i. determine if discrete otolith elemental “signatures” exist for the Maumee River plume and non-Maumee River plume areas of the basin;

ii. determine if yellow perch occupying the Maumee River plume and non-Maumee River plume habitats exhibit differential survival to the juvenile stage (~3 months of age, which is when recruitment is set for yellow perch in Lake Erie); and

iii. assess whether nutrient-rich river plumes offer a more suitable habitat for fast growth (e.g., greater zooplankton biomass/productivity, warmer temperatures) than less productive surrounding waters.

My main hypothesis is that high phosphorus-inputs from the Maumee River, relative to other areas of Lake Erie, increases prey (zooplankton) availability, which in turn, provides a more suitable habitat for larval yellow perch growth, survival, and ultimately, recruitment to the new year-class. Chapter II addresses the above objectives in manuscript format and Chapter III expands on the results from Chapter II.
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INTRODUCTION

Watersheds cause habitat heterogeneity in aquatic systems such as estuaries, coastal oceans, and large lakes through inputs of allochthonous materials from tributaries, which form plumes and fronts (hereafter referred to as “plumes”) in open waters. These tributary-derived plumes often differ from the surrounding water in terms of their chemical (e.g., dissolved nutrients), physical (e.g., temperature, suspended sediments), and biological (e.g., lower trophic level biomass/production) attributes (Grimes and Finucane 1991; Salen-Picard et al. 2002; Morgan et al. 2005; Vanderploeg et al. 2007). Although the degree of difference in physicochemical and biological properties depends heavily on the geology, topography, watershed land use, and the magnitude and frequency of river inputs, river plumes generally have higher levels of lower trophic-level production and turbidity (cloudiness) than surrounding waters, owing to the influx of nutrient- and sediment-laden water (Grimes and Kingsford 1996; Mallin et al. 2005). In turn, these nutrient-rich plumes could potentially provide a more favourable environment for growth and survival of fish—especially during planktivorous larval stages—than surrounding nutrient-poorer, less productive waters (e.g., ocean, open lake).
Understanding the relationship between such watershed-derived habitat heterogeneity and early-life growth and survival could be crucial to efforts aimed at understanding and forecasting fish recruitment variation and population dynamics. High, non-uniform mortality frequently occurs during early life stages (e.g., egg, larval, juvenile) of fish that provide no parental care, which can lead to variable recruitment dynamics (Houde 1987; Miller et al. 1988; Bradford and Cabana 1997). Owing to their small size, weak swimming capabilities, and dependence on small-sized planktonic prey, pelagic larvae are especially susceptible to mortality through both direct and indirect effects of abiotic (e.g., temperature, turbidity) and biotic (e.g., prey availability, growth, predation) factors (Shepherd and Cushing 1980; Houde 1987; Bailey and Houde 1989; Pepin 1991; Leggett and Deblois 1994). Consequently, the formation of biologically productive, turbid river plumes could influence fish population dynamics and future recruitment through bottom-up (e.g., increased prey availability resulting in faster growth and higher survival; Houde 1987; Ludsin and DeVries 1997) and/or top-down (e.g., enhanced turbidity reducing size-selective predation mortality; Rice et al. 1993; De Robertis et al. 2003) effects on larvae.

Although the influence of river plumes on fish population dynamics has received little attention in freshwater systems, a growing body of research exists in coastal marine systems worldwide (earlier works reviewed by Grimes and Kingsford 1996; Le Pape et al. 2003a, 2003b; Brodeur et al. 2005; De Robertis et al. 2005; Rowell 2005; Garcia-Ibarsarch et al. 2006). In general, these studies have demonstrated that heterogeneous environments (plumes) formed by nutrient-rich river water have higher zooplankton and larval fish biomass/densities (Grimes and Finucane 1991; Kingsford and Suthers 1996;
Garcia-Isarch et al. 2006) than non-plume waters, and for some species, higher levels of feeding (Rissik and Suthers 1996). Further, several studies have found a positive relationship between tributary discharge and fish recruitment, hypothesizing the importance of watershed-derived inputs and/or river plume formation on larval fish feeding, growth, and survival (Scarnecchia 1981; Ludsins 2000; Lloret et al. 2001; Salen-Picard et al. 2002; Le Pape et al. 2003). However, I am unaware of any study that has definitively (mechanistically) linked watershed-derived habitat heterogeneity (i.e., river plume formation) to recruitment success.

One likely impediment to determining the influence of river plumes on fish recruitment has been an inability to determine past habitat-use of larvae or juveniles. Fortunately, advances in the field of otolith microchemistry (Campana 1999; Thresher 1999; Campana and Thorrold 2001) are now affording a means to identify past habitat-use patterns of juvenile and adult recruits in both freshwater and marine systems (reviewed by Elsdon et al. 2008), taking advantage of chemical differences in the ambient water in which the fish reside that are recorded in otoliths.

Herein, I used otolith microchemistry as a tool to determine the past larval habitat-use of Lake Erie yellow perch *Perca flavescens* juveniles collected in western Lake Erie during August of their first year of life, which is when recruitment to the fishery is set (i.e., juvenile abundance is a strong predictor of future recruitment to the fishery at age-2; Ludsin 2000; Yellow Perch Task Group Report 2007). In so doing, I ultimately sought to test two related hypotheses concerning fish recruitment: 1) survivorship to the juvenile stage is higher for larvae that use nutrient-rich river-plume waters (i.e., the Maumee River plume; see Study Area and Species in Materials and
Methods) versus nutrient-poorer waters of Lake Erie’s west basin (i.e., non-Maumee River plume); and 2) differences in larval fish growth rates, as influenced by temperature and zooplankton (prey) availability (i.e., bottom-up effects), would underlie survivorship differences between habitats (i.e., larval fish growth rates would be faster in the Maumee River plume versus non-Maumee River plume waters, owing to higher temperatures and prey availability). To test these hypotheses, I quantified differences in the Maumee River plume versus non-Maumee River plume waters during 2006 and 2007 in terms of temperature, zooplankton biomass/productivity, larval yellow perch growth rate, and survivorship to the juvenile stage. I also quantified differences in turbidity between habitats to address the alternative top-down mechanism that enhanced turbidity reduces predation mortality of larvae.

**MATERIALS AND METHODS**

*Study Area and Species*

Lake Erie (USA-Canada) is the southernmost, shallowest, and most biologically productive of the Laurentian Great Lakes. It has three lake basins—western, central, and eastern—that predictably differ in their physical, chemical, and biological properties, including temperature, nutrients (phosphorus, the element most limiting to productivity in Lake Erie; Vollenweider 1976; DiToro and Connolly 1980; DePinto 1986), and primary (phytoplankton) and secondary (zooplankton, fish) production; all attributes tend to decrease from west to east, the same direction that water flows (Makarewicz 1993a, 1993b). My study area was the shallow western basin (mean depth = 7.4 m), which
included waters west of an imaginary line extending from Point Pelee, Ontario, Canada to Huron, Ohio, USA (Figure 1).

The Detroit River and the Maumee River, Lake Erie’s two largest tributaries, flow into the western basin, respectively contributing ~80% and ~5% of the total annual water (Bolsenga and Herdendorf 1993). Despite the large contribution of water from the Detroit River annually, inter-annual total phosphorus loading variation in Lake Erie’s western basin has been strongly positively related to total phosphorus inputs from the Maumee River in recent decades ($r = 0.84, p < 0.0001$), which contributes ~ 35% of the annual phosphorus load to the west basin (see Baker and Richards 2002; Dolan and McGunagle 2005 for raw data; S. Ludsin, P. Richards, and D. Dolan, unpub. data). Importantly, variation in phosphorus inputs from the Maumee River into western Lake Erie has been shown to be highly dependent on precipitation-driven discharge from the Maumee River (Baker and Richards 2002).

Maumee River discharge results in an observable river plume in Lake Erie’s western basin (Figure 1), which I refer to as the Maumee River plume (MRP). The area of the basin not influenced by the Maumee River, I refer to as the non-Maumee River plume (non-MRP), which includes waters more influenced by the Detroit River. Habitat heterogeneity caused by Maumee River inputs is common in western Lake Erie. Historically, the MRP and non-MRP areas of the basin have differed in temperature (higher in the MRP than non-MRP), water clarity (lower in the MRP than non-MRP), and dissolved oxygen (lower in the MRP than non-MRP) based on annual inter-agency monitoring data collected during August 1987-2004 (J. Tyson, Ohio Department of Natural Resources, and T. Johnson, Ontario Ministry of Natural Resources, unpub. data).
Additionally, total phosphorus concentrations and chlorophyll $a$ have been shown to be higher in the MRP than the non-MRP during both study years (T. Johengen, University of Michigan, and S. Ludsin, unpub. data).

Production of larval yellow perch is high in the west basin, occurring during late April through early June (Goodyear et al. 1982; Ludsin et al. 1997). Yellow perch are pelagic as larvae, becoming demersal during their habitat shift to the juvenile stage at about 20 – 25 mm in total length (TL) (Gopalan et al. 1998; Ludsin 2000). While the degree of movement of yellow perch between lake basins is unknown, Lake Erie fishery management agencies currently manage the west basin as a discrete stock (Yellow Perch Task Group Report 2007). Further, yellow perch recruitment to the fishery at age-2 has been shown to be strongly, positively correlated with Maumee River discharge during spring (March-May), just before and during the larval production period (Ludsin 2000; S. Ludsin, unpub. data), suggesting the potential importance of Maumee watershed inputs to this species.

**Sampling Design and Field Collections**

**Site selection.** Extensive sampling of west basin habitat was conducted in daylight hours during late April through June 2006 and 2007 (Table 1), a time period that encompassed the entire larval yellow perch production period (Ludsin et al. 1997). Remote-sensing via Moderate-Resolution Imaging Spectoradiometer (MODIS) 250-m resolution, true color, near real-time imagery from the Terra and Aqua satellites ([http://coastwatch.glerl.noaa.gov/](http://coastwatch.glerl.noaa.gov/)) was used to map and track the MRP during each sampling week (Figure 1). This approach was similar to the one used during the Episodic
Events Great Lakes Experiment (EEGLE) project, which monitored the initiation, development, and decay of coastal plumes in Lake Michigan (Eadie et al. 1996; Schwab and Beletsky 2001). Eight fixed sites and four random sites were sampled weekly within the MRP and northerly non-MRP. Sampling designs were similar during 2006 and 2007 (Figure 2), with the exception of the number and type of sites sampled in the middle of the basin (2006: n = 6 random sites; 2007: n = 1 fixed site). Fixed sampling sites were selected using historical limnological data (water temperature, Secchi depth, oxygen) from August 1987-2004 (J. Tyson and T. Johnson, unpub. data). Random sampling sites were selected each week using satellite images void of any obstructions (e.g., clouds) with ArcMap software. To maximize spatial coverage, random sites had to be at least 2 km from any fixed site. Table 2 lists the number of weeks each fixed site was sampled and Figure 2 depicts the overall sampling design and number of random sites sampled during 2006 and 2007.

Physical attributes. Limnological sampling was conducted at each site. Vertical casts of an instrument package consisting of a SeaBird SBE19 CTD and transmissometer (5-cm path) were used to measure conductivity, temperature, depth, and transmissometry (proxy for turbidity, $r = 0.98$, $p < 0.0001$) throughout the water column ($n = 1$ cast per site). For analyses, I integrated across all depths, given that the water column was unstratified and larvae were sampled throughout most of the water column. Surface water samples (1 to 2 m depth) were filtered through 0.45-µm nylon filters for trace-elemental analysis. These samples were acidified with nitric acid (1% of the total volume of water; 0.6 ml acid to 60 ml of water) with the resulting solution analyzed by inductively coupled plasma mass spectrometry (ICP-MS). Temperature, conductivity,
transmissometry, and elemental concentrations in the water were used to 1) discriminate sites as belonging to either MRP or non-MRP waters, 2) relate water chemistry to otolith chemistry, and 3) quantify differences in water-mass attributes.

**Zooplankton collections.** Replicate vertical (1 m from bottom to surface) zooplankton tows were conducted with a metered 0.3-m diameter net with 64-µm mesh. Upon collection, zooplankton were immediately preserved in a 10% buffered sugar formalin solution. Replicates from each site were brought to equal volumes and a 50% subsample from each was combined. The composite sample was then well mixed and subsampled using a wide-bore pipette. Adult and juvenile zooplankton were identified to species and genus, respectively. Subsampling continued until 100 individuals for each major group were enumerated or 20% of the entire sample volume was processed. Major groups included cladocerans, adult copepods, juvenile copepods (including nauplii), and *Dreissena* veligers, which constitute the diet of larval yellow perch in Lake Erie (Ludsin 2000; S. Ludsin, unpub. data).

Zooplankton biomass and productivity were quantified for both MRP and non-MRP water masses. Estimates only included groups commonly consumed by larval yellow perch in western Lake Erie (cladocerans, calanoids, and cyclopoids) (Ludsin 2000). Zooplankton length (nearest 0.01 mm) was measured using a program created by Russell R. Hopcroft, Department of Zoology, University of Guelph. Individual zooplankter biomass density was then calculated, using length-weight regressions (see Hillbricht-Illkowska and Stanczykowska 1969; Downing and Rigler 1984) and volume estimates from flowmeter readings. I followed the procedure of Shuter and Ing (1997) to calculate zooplankton productivity (mg m\(^{-3}\) day\(^{-1}\)) (P), using the following formula:
\[
\ln(P/B) = \alpha + \beta T
\]

where \( \alpha = -1.725 \) (Cladocera), -1.766 (Cyclopoida), or -2.458 (Calanoida); \( \beta = 0.044 \) (Cladocera), 0.040 (Cyclopoida), or 0.050 (Calanoida); \( B = \) biomass (mg m\(^{-3}\)); and \( T = \) temperature (°C).

**Fish collections.** Larval yellow perch were collected using oblique tows (beginning 2 m from bottom to the surface; average tow duration = ~8 min.) with paired, metered bongo nets (1-m diameter), one with 500-µm mesh and the other with 1000-µm mesh. Collections for larval fish were preserved in 100% ethanol. In the laboratory, larval yellow perch were identified (Auer 1982) and enumerated in the entire sample, or until at least 100 individuals were counted from a 50% (by mass) subsample. Abundance was estimated using 500-µm mesh net collections only, given that small larvae may not have been retained in the 1000-µm mesh and no differences in catchabilities of large larvae were evident between mesh sizes (J. Reichert, unpub. data). Larvae were measured to the nearest 0.01 mm total length (TL) using an image analysis system (ImagePro® Plus software, MediaCybernetics, Inc., Bethesda, MD).

During late August 2006 and 2007, yellow perch juveniles were collected via bottom trawling (10.7-m headrope; 13-mm cod-end liner; 3 km/hr tow-speed) by the Ontario Ministry of Natural Resources (R/V *Keenosay*) and the Ohio Department of Natural Resources (R/V *Explorer*) as part of annual assessment surveys (Yellow Perch Task Group Report 2007). During each year, ~75 sites were sampled within the western
basin. A paired trawling exercise indicated that no corrections were required to account for different vessels collecting juvenile yellow perch (Tyson et al. 2006).

Maumee River Plume Identification

To test whether the MRP positively influenced survival, I first had to differentiate the MRP from the non-MRP area. The outer boundary of the average MRP during the larval yellow perch production period during 2006 and 2007 was determined using kriging and forward and backward step-wise linear discriminant function (LDF) analyses. However, because backward step-wise analyses produced the same results as the forward step-wise analyses, only results from the forward step-wise models are reported. To define the average MRP, I used only fixed sites during weeks in which larval yellow perch were collected (Table 1). Fixed sites allowed quantification of both spatial and temporal variation in water-mass attributes because they were sampled weekly. In contrast, random sites only provided a “snapshot” of a specific area during a particular week, and thus could not be used to define the average MRP. Potential water-mass discriminators during both years included conductivity, temperature, and transmissometry data. For the 2007 model, I also evaluated weekly water strontium (Sr), barium (Ba), and magnesium (Mg) to calcium ratios (Sr:Ca, Ba:Ca, and Mg:Ca), given that these elements were shown to be potentially important discriminators among yellow perch spawning locations in Lake Erie (Ludsin et al. 2006). No water chemistry data were collected during 2006.

To satisfy the normality assumption, temperature was log$_{10}$ transformed, and Sr:Ca ratios and transmissometry values were reciprocally transformed, whereas all other
variables were normally distributed (Kolmogorov-Smirnov normality test: \( p > 0.05 \)), and therefore, not transformed. Only variables with an F-value \( \geq 10 \) were included in the LDF analysis models used to classify sample sites.

For the first LDF analysis, \textit{a priori} assignments of fixed sites (MRP versus non-MRP) were based on the fixed historical MRP location (determined from previous analysis of temperature, Secchi disk, and dissolved oxygen data from August 1987-2004). Classifications using a jackknife procedure from the first LDF analysis were then used to reclassify sites as either MRP or non-MRP. Analyses were carried out until all new site groupings had at least 50\% of their sampling events correctly classified; two LDF analyses were required to achieve this end goal. Kriging of the average MRP posterior probabilities from the final “best grouped” water mass LDF analysis was used to locate the outer boundary of the MRP each year, which was set at the 50\% contour line. Fixed and random sites below (south or west of) this boundary were considered MRP and fixed and random sites above (north or east of) it were considered non-MRP. These site assignments were used for all subsequent analyses. The accuracy of these assignments was tested using classification functions from the “best grouped” water mass LDF analyses. Since random sites were not used to develop the classification functions, they served as an independent means to test how well the model discriminated between the MRP and non-MRP areas of the basin.

\textit{Survivorship and Larval Habitat-use of Juvenile Recruits}

To determine the past average larval habitat-use of juvenile yellow perch recruits (survivors), I developed characteristic otolith elemental signatures, using laser-ablation
(LA-) ICP-MS, for both MRP and non-MRP waters by quantifying otolith elemental concentrations from larvae captured in each water mass (2006: MRP = 20 larvae, non-MRP = 27 larvae; 2007: MRP = 38 larvae, non-MRP = 75 larvae). Owing to difficulties in handling and cleaning otoliths from the smallest larvae, I only used larvae that were at least 8 mm TL (> ~15 days of age). With water mass-specific signatures developed, I quantified otolith elemental concentrations within the region corresponding to the larval stage of age-0 juvenile recruits collected during August to determine their past “average” larval habitat-use (see Estimating elemental concentrations for details).

Larval fish preparation. Sagittal otoliths from larval yellow perch were prepared and analyzed using LA-ICP-MS following the procedures of Ludsin et al. (2006). Briefly, sagittal otoliths were removed using acid-washed glass probes under a Class 100 clean laminar flow cabinet. After removal, otoliths were immediately sonicated for ~3 min in ultrapure water and then rinsed three times in separate pools of ultrapure water to remove any adhering organic and/or inorganic contamination. These otoliths were then placed on top of double-sided tape attached to a petrographic slide. I omitted cleaning steps involving NaOCl because Ludsin et al. (2006) found it to be unnecessary. The second sagittal otolith was later mounted in Crystalbond® thermoplastic cement to determine yellow perch age, otolith radius, and growth rates (see Growth Rates of Larvae).

Juvenile fish preparation. To clean the juvenile otoliths, I first soaked them in 3% hydrogen peroxide for ~10 min, sonicated them in ultrapure water for 5 min, and then pulled off any remaining tissue with plastic forceps. After the otoliths dried for 24 hours, I mounted and polished them following procedures of Stevenson and Campana (Campana...
1992), with slight modifications. Instead of mounting the otoliths directly to a
microscope slide, they were first mounted sulcus side up to a piece of transparency film
with Superglue. Otoliths were polished until the core was visible (i.e., at the surface)
using 25x magnification. I did not polish the other side. Otoliths (still attached to
transparency film) were mounted with Superglue to a petrographic slide (13-15 per slide),
sonicated for 5 min, and rinsed 3 times with ultrapure water.

ICP-MS processing. A Thermo Elemental X7 ICPMS, equipped with a
Continuum solid-state ND:YAG laser (wavelength: 266 nm; power: ~1.15 V; pulse rate:
20 Hz; beam width: ~15 μm; speed: ~3-4 μm s⁻¹) was used to quantify lithium (Li),
magnesium (Mg), manganese (Mn), zinc (Zn), strontium (Sr), barium (Ba), lead (Pb)
concentrations across LA-transects of larval and juvenile otoliths. Calcium (Ca), the
internal standard, and mass 120 of tin (Sn), a contamination indicator (Ludsin et al.
2006), also were quantified. Otolith transects on larvae spanned from the outer edge,
through the core, to the opposite edge of the entire otolith. The double-sided tape was
ablated before and after each larval yellow perch otolith, producing Sn spikes
(representing a carbon-molecular ion from the tape) that allowed me to locate when the
ablation of the otolith began and ended, as well as if I accidentally burned through the
otolith (Ludsin et al. 2006). The time at which the laser passed through the core was
noted for each otolith. Otoliths from the MRP and non-MRP were ablated in an
alternating fashion for both years.

Transects ablated on juvenile otoliths began 168 μm (~56 days of life at ~3 μm
per day) before the core, crossed through the core, and then continued 168 μm on the
other side of the core (in the direction of the longest otolith axis). My goal was to ablate
a transect that included at least 28 days of life (majority of the larval period; see
Estimating elemental concentrations) from both sides of the core. By doubling the
estimated 28 day transects, I ensured collection of elemental concentration data for the
entire larval period. Manganese and Ba peaks sometimes occurred at the core in both the
larval and juvenile otoliths, which helped identify the exact location of the core (Ludsin
et al. 2006). Since finding the core in some juvenile otoliths was difficult, owing to a
lack of Mg and Ba peaks, the distance from the start of ablation to the core was later
measured using an image analysis system (ImagePro Plus® software, MediaCybernetics,
Inc., Bethesda, MD).

**Estimating elemental concentrations.** Calcium was used as the internal standard
to correct for ablation-yield differences. A glass standard (NIST 610) was analyzed twice
before and after every 16 samples to correct for drift and estimate the precision (coefficient
of variation, CV) of the instrument between runs (Ludsin et al. 2006). The Argon carrier
gas was analyzed 60 s before every sample to determine instrument background levels,
which was used later to estimate the limits of detection (LOD) of individual samples
(Ludsin et al. 2006).

To obtain average elemental concentrations, I integrated otolith transect data
using the ICP-MS PlasmaLab software (from Thermo Electron Corporation).
Background subtractions and NIST 610 and Ca standardizations were done with an Excel
macro program modeled after LAMTRACE (Jackson 2001). For larvae, integrated
regions included most of the ablated transect, except for 5-10 s at the start and end of the
signal to avoid carryover contamination from the mounting tape. For juvenile otoliths, I
integrated the larval portion of the signal before and after the core, which was estimated
using the lower average otolith radius length of 28 day old larvae (total of 4 weeks of life) collected earlier in the year from either the MRP or non-MRP. During 2006, the average radius length used was 90 µm (average of MRP individuals: non-MRP individuals = 112 µm) and during 2007, it was 110 µm (average of non-MRP individuals: MRP individuals = 120 µm). I used the lower mean because it still represented the majority of the larval life stage, but decreased the chance of incorporating part of the juvenile signal into the larval habitat-use signature. I chose 28 day old larvae because that age best represented the majority of the oldest larvae caught from both water masses in both years (mode, 2006: MRP = 30 days old; non-MRP = 26 days old; 2007: MRP = 33 days old; non-MRP = 27 days old). If one side of the otolith elemental signal showed a sudden drop in Ca due to ablating a noticeable crack or high contamination (indicated by an increase in Sn), then I only integrated from the core to edge of the uncontaminated side.

**Water-mass otolith elemental signatures.** LDF analysis was used to differentiate between MRP and non-MRP otolith elemental signatures for each year. For elements to be considered, I followed the criteria of Ludsin et al. (2006); concentrations had to be above the LOD for 90% of the samples within a water mass (MRP and non-MRP) and the glass standard CV had to be < 10.5%. For the MRP signature, I only used larvae that were collected from sites that had ≥ 80% of their sampling events classified as MRP, according to the “best grouped” water mass LDF analysis (per above; Table 2). For the non-MRP signature, I only used larvae captured from sites that were in the northerly non-MRP because sites located in the middle of the basin may have included individuals exposed to
both water masses. Two of 29 larvae during 2006 and 16 of 91 larvae from the non-MRP were excluded.

Because larval yellow perch TL between the MRP (average ± 1 SE, 2006: 9.7 ± 0.3 mm; 2007: 9.5 ± 0.3 mm) and non-MRP (2006: 12.6 ± 0.3 mm; 2007: 11.2 ± 0.2 mm) differed during both years (t-test, 2006: t = 2.01; 2007: t = 1.98; both years: p = <0.0001), I needed to account for potential effects of fish size on otolith microchemistry (see Thorrold et al. 1998). Briefly, I used analysis of covariance (ANCOVA) to determine if a significant interaction between fish size and otolith concentration existed between water masses during both years. Elements with a significant interaction effect were not included in subsequent analyses (Thorrold et al. 1998). Afterwards, the ANCOVA was repeated without the interaction term (in cases where the term was not significant) to determine if a fish size effect existed. Otolith radius (along the longest axis) was highly correlated with fish TL for larvae collected across both water masses and years ($r = 0.96$, $p < 0.001$, $n = 154$ larvae). Therefore, otolith radius was used as a measure of fish size rather than TL because the results could be directly applied to the otolith chemistry of juveniles, which had a fixed larval radius of 90 µm in 2006 and 110 µm in 2007 (per above). I used the otolith radius-TL relationship to estimate missing values ($n = 24$ otoliths). Those elements that were significantly related to otolith radius were detrended (to remove the effect of fish size), using the slope of the relationship between elemental concentration and otolith radius (Thorrold et al. 1998; Campana et al. 2000). Analysis of variance (ANOVA) was then used to test for differences in MRP and non-MRP otolith (and water from 2007) elemental concentrations retained from the ANCOVA. Strontium otolith concentrations were log-transformed, water Sr:Ca ratios were reciprocally
transformed, and *water* Ba:Ca ratios and otolith Ba concentrations did not need a transformation to meet normality assumptions (Kolmogorov-Smirnov normality test, all p > 0.05). Results were considered significant at an α-level = 0.05. For larvae to be included in the final otolith LDF analysis models, both the water and otolith elemental concentrations had to significantly differ in the same direction (from ANOVA) between water masses and F-values had to be ≥ 10.

The final LDF analysis used a jackknife procedure to classify larvae, based on their otolith elemental signatures, as either MRP or non-MRP, allowing me to test the model’s ability to correctly classify larvae to their water mass of collection. While I did not focus on quantifying fish movement between water masses, I did look for it in otoliths that were misclassified in the LDF analysis (i.e., in fish where the otolith elemental signature did not match the water mass to which it was assigned; 2006: n = 2; 2007: n = 12). Specifically, I was concerned about defining water masses using larvae that may have moved between water masses before capture. To assess potential movement, I qualitatively inspected elemental concentrations of larval yellow perch otoliths across ablated transects (core- to edge, binning data into 0.5-µm intervals that represented < 1 day of life). Misclassified larvae that demonstrated possible movement between water masses before capture (as evidenced by apparent changes in Sr concentrations between core and edge) were individually evaluated.

**Survival assessment.** Classification functions derived from larval otolith elemental signatures were used to determine the past (first 28 days of life) larval habitat-use of new juvenile recruits (2006: n = 100; 2007: n= 165). The number of individuals from each collection site used in the classification was proportional to the abundance
(catch per unit effort) of juvenile yellow perch at each site during each year. In so doing, I could relate past larval habitat-use to recruitment at the juvenile stage. Posterior probabilities of assignment to the MRP or non-MRP were assessed afterwards to determine reliability in past larval habitat-use determinations.

To assess differences in survival from the larval stage to the juvenile stage, I used a $\chi^2$ goodness-of-fit test. If survival of larvae was equal between water masses, I expected the ratio of the average peak larval abundance between the MRP and non-MRP to remain constant when assessing past habitat-use of juveniles (i.e., the ratio of juvenile survivors that used the MRP versus non-MRP would be identical to the ratio of average peak larval abundances). If not, this would suggest differential survivorship between water masses. Peak larval abundance (the highest weekly average larval yellow perch density in a water mass during a year) was assumed to represent total larval fish production of a water mass in a given year (Donovan et al. 1997).

_Growth Rates of Larvae_

Age and growth rates of yellow perch larvae were estimated by counting and measuring daily growth increments (rings) of sagittal otoliths not used for microchemical analysis (following Campana 1992, Ludsin 2000). Formation of daily increments was validated for laboratory-reared yellow perch up to 63 days of age (Ludsin 2000). All otoliths were aged and measured—along the longest readable transect—at least twice by different readers under 50-100x magnification (depending on the size of the otolith) immersed in oil, with the date, location, and knowledge of previous reads being unknown to readers.
Individual otolith ring widths used in analyses were measured with an image analysis system. Distance from the otolith nucleus to the hatch check (designated as the first apparent dark check near core when focusing from above the incremental plane) was measured as a single entity, given difficulties distinguishing rings prior to the hatch check. Individual rings were measured from the outer edge of the hatch check to the outer edge of the otolith, with otolith radius representing the sum of the pre- and post-hatch check measurements. Ages were determined by summing the total number of daily increments measured after the hatch check. If the first two reads were within 3 days of one another, I used the oldest age (highest count) as the final age to provide a more conservative measure of growth rate (Ludsin and Devries 1997). If the first two ages differed by > 3 days, the otolith was re-read (and re-measured) once more. If no two ages differed by ≤ 3 days, then only the measurements from the readable portion was used, and the age remained unknown (2006: n = 4 fish; 2007: n = 8 fish). If no increments were visible, then the otolith was discarded (n = 1 fish in 2006). Increment measurements were averaged over 7-day intervals to determine the average growth rate for the first four weeks of life of each individual. The periphery (last ring) was not included in the weekly growth rate estimates because it was not a complete day of life. Any weekly (7-day) interval with three or less increment measurements was discarded from analysis (e.g., a growth rate for a 23-day old individual during the fourth week of life would not be included).

Mechanisms of Survival

To help understand mechanisms underlying differences in survivorship between water masses, I contrasted differences in temperature and zooplankton (prey) availability
through the sampling season during 2006 and 2007. I also evaluated turbidity (transmissometry) as a potential variable that could support a top-down mechanism by reducing predation risk on larvae. Individual two-way ANOVAs (with Tukey’s unequal n HSD post hoc tests) were used to determine the water mass (MRP versus non-MRP), sampling week, and water mass * sampling week effects for temperature, zooplankton biomass, and zooplankton productivity (bottom-up attributes), as well as transmissometry (top-down attribute).

Two-way ANOVAs (with Tukey’s unequal n HSD post hoc tests) also were used to evaluate larval growth rate differences between water masses across the first four weeks of life (mean 7-day intervals from hatch check) during both years. Because otolith radius (along the longest axis) was highly correlated with fish TL for larvae collected across both water masses and years ($r = 0.96$, $p < 0.001$, $n = 154$ larvae), I was able to use otolith radius as a surrogate measurement for yellow perch length. Also, I only used larvae $\geq 8$ mm in TL ($\geq 15$ days of age), given that smaller individuals tended to still have a yolk sac and likely were feeding endogenously (Ludsin 2000; J. Reichert, unpub. data).

Sample sizes used in these analyses are provided in Table 6. Samples (from fixed and random sites) were included in these analyses as long as they fell inside the average plume based on the “best grouped” water mass LDF analysis (Figure 2). To achieve normality (Kolmogorov-Smirnov normality test, all $p > 0.05$), temperature, zooplankton biomass, and zooplankton productivity data were $\log_{10}$ transformed, whereas a reciprocal transformation was used for transmissometry (turbidity) data. Larval yellow perch
growth rates did not require any transformation. Two-way ANOVAs were considered significant at $\alpha$-level $= 0.05$.

**RESULTS**

*Maumee River Plume Identification*

During both 2006 and 2007, discrimination between the MRP and non-MRP areas of Lake Erie’s western basin was quite high. Conductivity was the only discriminator included in the 2006 model (“best grouped” water mass LDF analysis: $F_{1,77} = 120.3$; Wilk’s lambda, $p < 0.0001$), resulting in a 94% average classification accuracy of sites in the “best grouped” water mass model (MRP = 84% for 25 sampling events; non-MRP = 98% for 54 sampling events). Based on this analysis, five fixed sites were classified as MRP (A, B, C, E, and M), and the remaining 11 sites were classified as non-MRP (Table 2, Figure 2). Sites D, F, and N, which were originally hypothesized to be representative of the MRP (based on historical limnological sampling conducted in the west basin during August 1987-2003; J. Tyson and T. Johnson, unpub. data), were more characteristic of the non-MRP. No non-MRP sites were changed to MRP during 2006 (Table 2).

Both water chemistry (not available during 2006) and limnological (temperature, conductivity, transmissometry) data were evaluated as discriminators during 2007. This LDF analysis resulted in a two-variable model that included a strong predictor, Sr:Ca ($F_{1,100} = 246.6$; Wilk’s lambda, $p < 0.0001$), and a weak predictor, Mg:Ca ($F_{1,100} = 12.9$). In fact, classification accuracies were nearly identical with (MRP = 91% for 44 sampling events; non-MRP = 95% for 61 sampling events) or without (MRP = 89% for 44 sampling events; non-MRP = 95% for 61 sampling events) inclusion of Mg:Ca in the
model. Further, only 1 of 105 sampling events was classified differently when Mg:Ca was not included in the model, and this one event had a borderline MRP posterior probability of 60% (i.e., it could have easily been classified as either MRP or non-MRP). All other potential discriminators (Ba:Ca, conductivity, temperature, and transmissometry) were found unimportant (F-value < 10.0).

Importantly, conductivity (S/m) was positively correlated with Sr:Ca (ppm) across sampling sites during 2007 (conductivity = 0.0083 + 3.3522 * Sr:Ca; r = 0.92, p < 0.0001; n = 101 sites), suggesting that conductivity was not included in the LDF analysis model because it co-varied with Sr:Ca. Indeed, when Sr:Ca was removed from the model, conductivity became the most influential variable (F_{1,100} = 136.8), producing nearly identical classification results as the model with Sr:Ca. Therefore, to remain consistent with 2006, I only used conductivity to define the MRP during 2007. Missing conductivity values (n = 4 sites during 2007) were predicted using the relationship between conductivity and Sr:Ca (see above).

The 2007 “best grouped” water mass LDF analysis model (using conductivity; F_{1,106} = 135.8; Wilk’s lambda, p < 0.0001) resulted in an average classification accuracy of 92% (MRP = 87% for 46 sampling events; non-MRP = 95% for 62 sampling events). These resultant classifications led to one site, F, which was originally hypothesized to be representative of the MRP, to be classified as a non-MRP site (Table 2, Figure 2). Similar to 2006, no non-MRP sites were changed to MRP (Table 2).

I used kriged MRP posterior probabilities associated with classification of the “best grouped” sites to depict the average size of the MRP during both years. These
results indicate that the MRP was about twice as large during 2007 than during 2006 (Figure 2).

Overall, the classification accuracy of random sampling events in the average MRP and non-MRP were high and consistent within water masses during 2006 and 2007 (all > 75%; Table 3), validating the location of the average MRP based on the “best grouped” water mass LDF analysis models. The classification accuracy in the non-MRP was ~12% higher than the MRP during both years, suggesting the MRP is more dynamic than the non-MRP.

Survivorship and Larval Habitat-use of Juvenile Recruits

Water mass signatures. During both 2006 and 2007, Sr and Ba otolith concentrations met my criteria to be included in analyses, and during 2007, Mg and Mn also met my criteria (Table 4). However, I only included Sr and Ba because these elements consistently had a %LOD (maximum percentage of otoliths above LOD) > 90% for the MRP and non-MRP during both years. The inconsistencies of Mg and Mn can be understood, given that both elements are physiologically regulated (Campana 1999, Thresher 1999).

Concentrations of Sr and Ba in larval yellow perch otoliths differed between the MRP and non-MRP during both 2006 and 2007. However, because larval size varied between water masses (per above), and both Sr and Ba concentrations in otoliths were negatively related to the otolith radius (proxy for fish TL) (ANCOVA: all p < 0.01), I detrended the data to minimize any confounding effects of fish size. Because no water mass * otolith radius interaction effect was found for Sr during either year (ANCOVA:
interaction term > 0.05), I detrended Sr during both years, using slope estimates from the ANCOVA (2006: slope\textsubscript{Sr} = -0.0013; 2007: slope\textsubscript{Sr} = -0.0016) to provide a more conservative comparison between water masses. Although no interaction effect was found for Ba during 2006, I found a significant water mass * otolith radius interaction for Ba during 2007 ($F_{1,111} = 30.25$, $p < 0.01$). As such, I removed this element from 2007 analyses (Thorrold et al. 1998), and detrended Ba during 2006 (slope\textsubscript{Ba} = -0.3403).

Even after detrending, otolith Sr and Ba concentrations differed between water masses (one-way ANOVA: 2006 Sr, $F_{1,45} = 157.4$, $p < 0.0001$; Ba, $F_{1,45} = 90.0$, $p < 0.0001$; 2007 Sr, $F_{1,111} = 127.6$, $p < 0.0001$). I also found differences in the Sr:Ca and Ba:Ca ratios in the water during 2007 (one-way ANOVA: Sr:Ca, $F_{1,161} = 344.1$, $p < .0001$; Ba:Ca, $F_{1,161} = 19.2$, $p < .0001$). During both 2006 and 2007, Sr was greater in MRP otoliths (detrended mean ± 1 SE: 2006, 1,062 ± 48; 2007, 1,207 ± 63) and water (untransformed mean Sr:Ca ± 1 SE: 2007, 0.006189 ± 0.001242) than the non-MRP (otoliths: 2006, 625 ± 14; 2007, 781 ± 10; water: 2007, 0.003931 ± 0.000604). By contrast, differences in Ba were inconsistent. During 2006 and 2007, the average Ba otolith concentration was greater in the non-MRP (detrended mean ± 1 SE: 2006, 138 ± 6; mean ± 1 SE: 2007, 142 ± 27) than the MRP (2006, 52 ± 6; 2007, 38 ± 7), whereas the opposite occurred in the water during 2007—the average Ba:Ca was greater in the MRP (mean ± 1 SE: 0.000495 ± 0.000034) than the non-MRP (mean ± 1 SE: 0.000473 ± 0.000029). Since Ba concentrations in otoliths did not reflect Ba in water, I did not include Ba in LDF analyses used to determine past larval habitat-use of juvenile recruits.

Even though a single element (Sr) in larval yellow perch otoliths was used to discriminate between the MRP and non-MRP during both years, average classification
accuracies of larvae to their water mass of capture were quite high (Table 5). During 2006, 96% and 95% of the MRP and non-MRP individuals were classified correctly (LDF analysis: $F = 157.4$; Wilk’s lambda, $p < 0.0001$). During 2007, larvae from the non-MRP were classified with equal success as 2006; however, accuracy in the MRP dropped slightly, to 79% ($F = 127.6$; Wilk’s lambda, $p < 0.0001$; Table 5).

I examined otolith elemental concentrations of misclassified larvae to determine if movement between water masses during the larval stage (before capture) might have caused the misclassification. All 2006 and 2007 larvae caught in the MRP that were misclassified as non-MRP individuals (Table 5; Figure 3) had consistent low Sr signals from core to edge, suggesting no movement had occurred. All 2006 and 2007 larvae caught in the non-MRP that were misclassified as MRP individuals (Table 5; Figure 3) had higher Sr concentrations in the core than the edge, suggesting movement from the MRP to the non-MRP. However, because these larvae were captured near the north shore of the west basin, just east of the Detroit River mouth, I doubted that these larvae originated in the MRP; the signals most likely reflect sub-plume environments within the MRP and non-MRP, and not movement. As a conservative measure, I included all misclassified larvae in the final LDF analyses used to determine past larval habitat-use of juvenile recruits.

**Habitat-use.** Using classification functions derived from Sr concentrations in otoliths of larvae, I determined the likely water mass used by juvenile recruits as larvae (i.e., first 28 days of life). During 2006, I found that 34 of the juvenile recruits appeared to have used the MRP as larvae, whereas the remaining 66 juveniles were typed back to the non-MRP. During 2007, a near even split was obtained with 82 and 83 juvenile
recruits using the MRP and non-MRP as larvae, respectively. Investigation of posterior probabilities provided confidence in assignments of most individuals. During 2006, 32 of 34 juveniles typed back to the MRP and 64 of 66 individuals typed back to the non-MRP had a posterior probability assignment ≥ 70%. During 2007, classification confidence was lower than in 2006, with 68 of 82 (MRP) and 64 of 83 (non-MRP) juvenile otoliths having a posterior probability ≥ 70%.

**Survival assessment.** Average peak larval yellow perch abundance in the MRP and non-MRP occurred during the third and fourth sampling week of 2006 and 2007, respectively (Figure 4). Counter to my expectations, average peak larval yellow perch abundance was 10-fold less in the MRP versus non-MRP during 2006 (MRP:non-MRP ratio was 1:10) and 5-fold less during 2007 (MRP:non-MRP ratio was 3:15) (Figure 4). If survivorship to the juvenile stage was equivalent between the MRP and non-MRP, then these average peak larval abundance ratios should hold constant in juvenile recruits (survivors) to the new year-class in August. Therefore, the expected ratio of juvenile survivors that used the MRP versus the non-MRP was 9:91 in 2006 and 28:137 in 2007. By contrast, the observed ratio of juvenile recruits that used the MRP versus non-MRP as larvae was 34:66 during 2006 and 82:83 during 2007 (using a posterior probability of 0.50 to classify recruits as either using MRP or non-MRP as larvae). A comparison of these expected to observed ratios of MRP versus non-MRP individuals between the larval and juvenile stages suggest that survivorship differed between water masses, ($\chi^2$ test, 2006: $\chi^2 = 76.3$, $p < 0.0001$; 2007: $\chi^2 = 125.4$, $p < 0.0001$) (Figure 5).

To test the sensitivity of these results, I also evaluated survivorship only using juveniles with posterior probabilities ≥ 0.70 and ≥ 0.90 to calculate the observed
MRP:non-MRP frequencies. Observed frequencies of juveniles classified as MRP versus non-MRP did not change during 2006, although a slight increase in individuals classified as using the MRP as larvae occurred during 2007 (MRP frequencies = 50%, 52%, and 56% at ≥0.50, ≥0.70, and ≥0.90 posterior probabilities). Figure 6 spatially depicts the distribution of juvenile recruits (survivors) that used the MRP and non-MRP as larvae. While little correspondence between larval habitat-use and juvenile collection site was evident during 2006 (e.g., juveniles collected in the southern part of the west basin used the MRP or non-MRP as larvae), I found that juveniles tended to be captured in areas of the west basin that they used as larvae (e.g., juveniles captured along the north shore generally used non-MRP waters as larvae) during 2007.

**Mechanisms of Survival**

**Temperature.** Temperatures were higher in the MRP than the non-MRP during nearly all sampling weeks in both years (Figure 7A, 7D). During 2006, a significant water mass effect was observed with no water mass * week interaction (Table 7). In general, temperatures warmed from about 7°C during a span of 4 weeks in both plumes, with temperatures being about 1°C to 2°C higher in the MRP than the non-MRP (Figure 7A). A similar 2°C difference in temperature between plumes was observed during 2007 (Figure 7D), except in the third and fourth weeks when temperatures did not differ, leading to a significant interaction effect (Table 7).

**Zooplankton.** Unexpectedly, zooplankton biomass did not differ in any consistent manner between the MRP and non-MRP in either year, as indicated by a significant water mass * sampling week interaction (see Table 7) and no significant water mass difference
in any sampling week (Tukey’s unequal N hsd test; Figure 7B, 7E). By contrast, zooplankton productivity was consistently (i.e., no interaction effect) greater in the MRP than the non-MRP during both years (see Table 7) with the difference in productivity increasing through the sampling season (Figure 7C, 7F).

**Larval growth rate.** Larval yellow perch growth rates either did not vary between the MRP and non-MRP, or were opposite than expected. During 2006, a water mass * week of life interaction was observed (see Table 7), wherein growth rates did not vary between water masses during the first two weeks of larval life, but were significantly *higher* in the non-MRP than the MRP during the latter two weeks of life (Figure 8). During 2007, no growth rate differences were found between water masses during any week (Figure 8). Additionally, during both years, larval yellow perch growth rates tended to increase through time in both water masses (Figure 8), although the increase was greater in the non-MRP than the MRP during 2006.

**Turbidity.** Turbidity was higher in the MRP than the non-MRP during all sampling weeks in both 2006 and 2007, with no interactions (Table 7; Figure 9). Even so, turbidity levels varied through time, being generally higher in early sampling weeks (in the MRP) than later ones, especially during 2007, which was ~2 times higher than 2006 levels.

**DISCUSSION**

**Habitat identification.** Larvae from the MRP and non-MRP were clearly distinguishable by their otolith Sr concentrations. Barium was a less valuable discriminator, which was not expected because this element is typically used in otolith
studies (Thresher 1999). In fact, Ludsin et al. (2006) found Ba a good discriminator between spawning locations near the mouth of the Maumee River and Sandusky River (OH), located just outside the west basin. I found Ba in otoliths (from 2006 and 2007 samples) was negatively related to Ba in the water (from 2007 samples), a finding that was unexpected because Ba in the otoliths of marine fish was shown to be positively related to Ba in the water (Elsdon and Gillanders 2005). Because I alternated between MRP and non-MRP otoliths during LA-ICP-MS runs, and there were no noticeable “Sn” spikes (indicator that the laser burned through the otolith into the Ba-rich mounting slide; Ludsin et al. 2006), this finding is likely real and not due to contamination or instrument bias. Interestingly, Melancon et al. (2009) demonstrated differential otolith uptake rates of Ba from Lake Erie water for two different freshwater species, lake trout (Salvelinus namaycush) and burbot (Lota lota), despite similar Sr uptake. Ultimately, Melancon et al. (2009) result suggests that a different crystallization process is influencing the uptake of Ba into the otolith of freshwater fish versus marine fish, which may be species- or system-specific. Therefore, the use of Ba to discriminate fish in freshwater systems should be carefully evaluated.

Even though only one element (Sr) in larval yellow perch otoliths was found to be a valuable discriminator between water masses, high habitat-use classification accuracies for larvae collected during 2006 and 2007 (≥ 95%, except for the MRP during 2007, which was 79%) was achievable. The slight decrease in classification accuracy in the MRP during 2007 could be attributable to an area of low Sr concentration as a result of weekly plume dynamics. Schwab et al. (2009), using a high-resolution numerical circulation model, demonstrated high phosphorus variability along the southern and
western shores of Lake Erie during 1994, including an area of low phosphorus availability in the center of the western basin. Considering the strong, positive relationship between Maumee River discharge and western basin phosphorus inputs into western Lake Erie (Baker and Richards 2002; Dolan and McGunagle 2005; S. Ludsin, P. Richards, and D. Dolan, unpub. data), I suggest similar circulation patterns in western Lake Erie may drive variability in the distribution of Sr in the basin, including Sr entering from the Maumee River. Interestingly, the larvae from the MRP that misclassified as non-MRP during 2007 were collected within this region (see Figure 3). These findings demonstrate how circulation modeling could help researchers determine areas influenced by river plumes and uncover causes for discrepancies in misclassified fish, not to mention aiding researchers in understanding how physical processes (e.g., wind-driven circulation, river discharge) influence fish recruitment through habitat heterogeneity.

By classifying sites using conductivity data, I was able to distinguish the MRP from the non-MRP. The positive relationship between conductivity and water Sr:Ca ratios proved useful in identifying the average location of the MRP and relating it to otolith microchemistry (indicated by the high habitat-use classification accuracies of Sr in larval otoliths). Therefore, conductivity could assist researchers and fisheries managers in identifying habitats that can be differentiated using otolith microchemistry, particularly in instances where elemental inputs from a river differ from the open lake. Assuming strong relationships between water chemistry and conductivity are found (as was the case for Sr in my study), fishery managers and researchers may find it more cost-effective to use conductivity, which is typically measured as part of their routine water quality
monitoring programs, as a means to differentiate habitats, as opposed to analyzing the chemistry of the water.

**Survival assessment.** My results showed a potential survival advantage for larvae that used the MRP (a nutrient-rich, turbid river plume) versus non-MRP waters. In turn, a higher proportion of MRP versus non-MRP larvae recruited to the new year-class in August, which is a strong predictor of future recruitment to the fishery (Ludsin 2000; Yellow Perch Task Group Report 2007). However, this conclusion is based on two main assumptions: 1) the decrease in the proportion of non-MRP larvae that survive to the juvenile stage is due to mortality and not movement out of the west basin; and 2) juvenile recruits typed back to the MRP or non-MRP actually used these water masses as larvae and not other habitats with similar elemental (Sr) signatures.

Recent findings from marine systems suggest that movement out of the west basin is unlikely. While passive larval dispersal and “open populations” with plentiful exchange of larvae were dominant paradigms in marine systems during the late 20th century (Levin 2006), recent research now suggests that marine fish populations are more “closed” and the retention of larvae is more frequent than initially suspected (Cowen et al 2000; Levin 2006) due to the combination of larval fish behaviour and physical dynamics (Grimes and Kingsford 1996; Bradbury et al. 2006). Given that freshwater fishes such as yellow perch tend to be larger and have better swimming capabilities than marine fishes (Houde 1994; Miller et al. 1988), and zooplankton prey availability tends to be greater in the west basin than central basin during spring (Ludsin 2000; S. Ludsin, unpublished data), I feel it is unlikely that yellow perch larvae were passively transported or actively moved into the central basin.
If, however, the high constant flow rate of the Detroit River (Schwab et al. 2009) did indeed transport larvae from the non-MRP east to the central basin, it would not change the fact that yellow perch larvae residing in non-MRP waters are contributing disproportionately less to the west basin fishery than larvae residing in the MRP. Clearly, more research is required to determine if the disproportionate loss of non-MRP larvae is due to mortality or movement. Most notably, I would recommend using otolith microchemical (similar to those conducted here) or genetic approaches to determine if juvenile recruits in the central basin originated from the non-MRP waters of the west basin (indicating movement) or were produced locally.

While I do not have otolith microchemistry data from outside of the west basin to definitively know whether juvenile recruits typed back to the MRP as larvae actually did not emanate from other habitats with similar Sr concentrations as the MRP, I find it unlikely to be the case. First, otolith microchemical signatures from other regions of Lake Erie have been shown to be lower than the MRP for yellow perch and walleye Sander vitreus, with the exception of waters found in Sandusky Bay (Figure 1) (Hedges 2002; Ludsin et al. 2006; K. Pangle and S. Ludsin, unpub. data). In fact, Sr levels in otoliths of yellow perch and walleye larvae from Sandusky Bay have been shown to be consistently (and significantly) higher than those of Maumee Bay larvae (Hedges 2002; Ludsin et al. 2006). Second, larvae or juveniles produced in Sandusky Bay would more likely move west into the central basin, given that nutrient-rich water from the Sandusky River tends to flow east into the central basin. I also find it unlikely that juveniles classified as using the non-MRP as larvae originated from Lake St. Clair (Figure 1), given recent genetic evidence that the yellow perch population in the western basin is
genetically distinct from the population in Lake St. Clair (USA-Canada) (Osvaldo J. Sepulveda Villet and Carol A. Stepien, University of Toledo, unpub. data; see http://www.utoledo.edu/as/lec/fishery/perch/Perch5.html). However, I do recommend that future efforts aimed at determining origins of juvenile yellow perch recruits in the west basin also collect larvae from Sandusky Bay and Lake St. Clair for otolith microchemical analysis. Doing so could allow for a definitive assessment of contributions of larvae from the Sandusky Bay and Lake St. Clair to the west basin fishery.

Both MRP and non-MRP waters can be viewed as important contributors of recruits to the west basin fishery in Lake Erie, given that 66% and 50% of the survivors to the new year-class spent their larval life in the in the non-MRP (with others emanating from the MRP) during 2006 and 2007, respectively. While the exact spawning locations of yellow perch in western Lake Erie are not well known, my results indicate that spawning locations likely exist in both water masses, with more spawning potentially occurring in the non-MRP than has been previously documented (Goodyear et al. 1982).

**Recruitment mechanisms.** I hypothesized that survival from the MRP would be greater than the non-MRP, owing to bottom-up processes emanating from plume-driven differences in temperature and prey availability (i.e., zooplankton biomass and productivity). However, evidence that bottom-up effects were responsible for the differential survival was not obvious. Specifically, I found no real differences in zooplankton biomass during both years and weak evidence that zooplankton productivity was higher in the MRP than the non-MRP during 2006. Only during 2007 did differences in prey availability seem substantial (zooplankton productivity in the MRP
was clearly significantly higher than the non-MRP). However, during both years, enhanced zooplankton productivity did not equate to faster larval growth rates in the MRP than non-MRP waters. Instead, growth differences were either equal between water masses (2007) or the opposite of what I expected (i.e., faster growth rates were observed in the non-MRP water mass than the MRP during 2006). Furthermore, temperature differences between plumes were relatively minor (<2°C in both years, across the sampling season). Given this suite of findings, I propose that bottom-up effects are not the principal cause for survival differences between water masses, which was hypothesized for similar river plumes in marine systems (Grimes and Finucane 1991; Grimes and Kingsford 1996; Le Pape et al. 2003; Garcia-Isarch et al. 2006).

Yellow perch recruitment variation in Lake Erie is more likely influenced by top-down effects, involving increased turbidity enhancing the survival of larvae in plume waters relative to surrounding waters by reducing predation risk. While this mechanism has been hypothesized as an alternative means in which river plumes can positively influence recruitment (De Robertis 2003), I was unable to find any field studies that directly examined predation mortality differences in river plumes. This lack of field data is most likely attributed to difficulties in quantifying predation rates on larvae, owing to fast digestion rates in the stomach of predators (Legler 2009). However, other evidence supporting this top-down regulation of recruitment is growing. Fiksen et al. (2002), for example, used an individual-based model to quantify predation risk associated with visual-feeding planktivores in a prey-abundant environment. Their results suggested that turbid environments substantially reduced predation rates on fish larvae due to a shading effect from high phytoplankton concentrations, which led them to conclude that, in food
abundant environments, turbidity could be more important to larval survival than bottom-up controls.

Additionally, lab experiments by De Robertis et al. (2003) indicated that piscivorous feeding was more sensitive to elevated suspended sediments than planktivorous feeding, concluding that turbidity enhanced the survival of larvae by making them less vulnerable to predation, without decreasing their ability to feed. Therefore, it is possible that larvae inhabiting the MRP had a survival advantage over larvae using the less turbid non-MRP primarily because of reduced predation risk stemming from enhanced turbidity, with perhaps higher zooplankton productivity contributing secondarily.

Increased turbidity reducing predation risk could explain the unanticipated growth discrepancy between water masses during 2006. Conceivably, the faster average growth rate of larvae in the non-MRP may be due to predation on the slowest-growing larvae, and in turn, only individuals with moderate to fast growth rates survived. Such size-selective predation has been shown to be an important determinant of apparent growth rates (Rice et al. 1993). By contrast, enhanced turbidity in the MRP may have allowed all larvae, both slow and fast-growing individuals, to survive equally as well, thereby resulting in reduced average growth. While I do not have data to quantify predation rates on larvae to test this mechanism, I do feel it is worth exploring further.

Findings by Miner and Stein (1993) provide a potential alternative hypothesis concerning differences in larval growth rates between water masses. Miner and Stein (1993) found that larval bluegill (*Lepomis macrochirus*) selected smaller zooplankton prey at increased turbidity levels than at low turbidity levels (while holding light levels
consistently high). Therefore, slower larval growth in the more turbid MRP during the 3\textsuperscript{rd} and 4\textsuperscript{th} weeks of life may be due to selection of smaller (less energy per unit mass) zooplankton prey than in the non-MRP. However, this hypothesis did not hold during 2007, during which time, equal growth rates occurred in both the MRP and non-MRP. Therefore, larval yellow perch could just have been consuming less in the MRP during 2006 and the same during 2007. Stomach contents of larvae from both the MRP and non-MRP would be helpful in determining the relative importance of size-selective predation versus size-selective foraging on zooplankton to growth.

My results support the use of elemental concentrations in otoliths to directly quantify the recruitment contribution of distinct watershed-derived habitats to a fishery. Importantly, they also show that habitats with a proportionally high larval abundance may not produce a similar high proportion of juvenile recruits to the fishery, regardless of whether the loss of these potential recruits is due to mortality or movement out of the basin. My findings of higher survival and turbidity in the MRP than the non-MRP, coupled with the conflicting or absent larval growth rate response to increased prey availability in the MRP during 2006 and 2007, suggest that a top-down control of increased turbidity reducing predation risk during the larval stage may be the primary mechanism influencing recruitment variation of yellow perch in western Lake Erie.

Because of the dependence of fish population dynamics on watershed-derived inputs during early life and the clear differential use of the MRP and non-MRP by yellow perch larvae, Lake Erie fishery managers should consider ecosystem (watershed) management approaches, in addition to, managing yellow perch from the MRP and non-MRP as distinct stocks.
REFERENCES


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Le Pape, O., Chauvet, F., Désaunay, Y., and Guérald, D. 2003a. Relationship between interannual variations of the river plume and the extent of nursery grounds for the


Table 1.— Western Lake Erie water-mass sampling schedule during 2006 and 2007. Only bolded dates were used in analyses.

<table>
<thead>
<tr>
<th>Sampling Week</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>26-28 April</td>
<td>24-27 April</td>
</tr>
<tr>
<td>2</td>
<td>1-4 May</td>
<td>30 Apr – 2 May</td>
</tr>
<tr>
<td>3</td>
<td>8-10 May</td>
<td>7-9 May</td>
</tr>
<tr>
<td>4</td>
<td>17 May</td>
<td>14-18 May</td>
</tr>
<tr>
<td>5</td>
<td>23-25 May</td>
<td>21-24 May</td>
</tr>
<tr>
<td>6</td>
<td>30 May – 1 June</td>
<td>29-31 May</td>
</tr>
<tr>
<td>7</td>
<td>5-8 June</td>
<td>4-7 June</td>
</tr>
<tr>
<td>8</td>
<td>12-15 June</td>
<td>11-13 June</td>
</tr>
</tbody>
</table>

Note: Sampling weeks 1, 4, and 8 were not used in 2006 analyses because of insufficient sampling in one or both plumes: 1) temperature, conductivity, and transmissometry data were not collected and only a total of 3 yellow perch larvae were caught during week 1; 2) the Maumee River plume was not sampled during week 4 due to boat maintenance; and 3) larval yellow perch samples were not preserved correctly during week 8. Week 1 was not used during 2007 analyses because no yellow perch larvae were caught during this week, suggesting that week 2 was the start of the larval yellow perch production period.
Table 2.—Average conductivity and classification results from “best grouped” water mass linear discriminant function analyses used to differentiate the Maumee River plume (MRP) from the non-Maumee River plume (non-MRP) area in western Lake Erie. The number of weeks sampled at each fixed site (n) during a given year is indicated. Sites A-F, N, and M were initially assigned to the MRP, whereas sites G-L, and O-Q were initially assigned to the non-MRP. Fixed sites were re-assigned to the MRP only if their “% MRP” was > 50% (bolded). A “% MRP” of 100 indicates that all sampling weeks for a site were classified as MRP, whereas a 0 indicates all sampling weeks were classified as non-MRP. Figure 2 shows the location of the fixed sites.

<table>
<thead>
<tr>
<th>Fixed Site</th>
<th>2006</th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Conductivity (S/m)</td>
</tr>
<tr>
<td>A</td>
<td>5</td>
<td>0.033</td>
</tr>
<tr>
<td>B</td>
<td>5</td>
<td>0.042</td>
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<td>C</td>
<td>5</td>
<td>0.034</td>
</tr>
<tr>
<td>D</td>
<td>5</td>
<td>0.024</td>
</tr>
<tr>
<td>E</td>
<td>5</td>
<td>0.030</td>
</tr>
<tr>
<td>F</td>
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</tr>
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<td>G</td>
<td>4</td>
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</tr>
<tr>
<td>H</td>
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</tr>
<tr>
<td>I</td>
<td>5</td>
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</tr>
<tr>
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<tr>
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<tr>
<td>M</td>
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<tr>
<td>N</td>
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</tr>
<tr>
<td>O</td>
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</tr>
<tr>
<td>P</td>
<td>5</td>
<td>0.021</td>
</tr>
<tr>
<td>Q</td>
<td>---</td>
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</tr>
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</table>
Table 3.—Classification results (% correct) for random sites located in the average Maumee River plume (MRP) (see Figure 2) and non-Maumee River plume (non-MRP) from the “best grouped” water mass linear discriminant function analyses, based on weekly differences in conductivity of fixed sampling sites in western Lake Erie during the larval yellow perch production period in 2006 and 2007. Sites were classified as either representing the Maumee River plume (MRP) or the non-Maumee River plume (non-MRP).

<table>
<thead>
<tr>
<th>Water Mass</th>
<th>Predicted habitat</th>
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</tr>
</thead>
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<tr>
<td></td>
<td>MRP</td>
<td>non-MRP</td>
<td>% correct</td>
</tr>
<tr>
<td>MRP</td>
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<td>3</td>
<td>77</td>
</tr>
<tr>
<td>non-MRP</td>
<td>5</td>
<td>42</td>
<td>89</td>
</tr>
<tr>
<td>Totals</td>
<td>15</td>
<td>47</td>
<td>83</td>
</tr>
</tbody>
</table>
Table 4.—Coefficient of variation (CV, %), mean limits of detection (LOD, ppm), and maximum percentage of otoliths above the LOD (“% > LOD”) for larval yellow perch otoliths used to determine the Maumee River plume (MRP) and the non-Maumee River plume (non-MRP) water mass signatures during 2006 and 2007 in western Lake Erie. Values in bold met my selection criteria.

<table>
<thead>
<tr>
<th>Isotope</th>
<th>2006</th>
<th></th>
<th></th>
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<tr>
<td></td>
<td></td>
<td>MRP</td>
<td>non-MRP</td>
<td></td>
<td>MRP</td>
<td>non-MRP</td>
</tr>
<tr>
<td></td>
<td>CV</td>
<td>LOD</td>
<td>%&gt;LOD</td>
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<tr>
<td>7 Li</td>
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</tr>
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<td>55 Mn</td>
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<td>138 Ba</td>
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<td>0.12</td>
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<tr>
<td>206 Pb</td>
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<td>0.06</td>
<td>60</td>
<td>0.06</td>
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</table>

MRP 2006 LOD 3.0 28.73 0 29.33 1
MRP 2007 LOD 1.7 18.00 100 18.48 100
non-MRP 2006 LOD 2.1 1.25 93 1.33 99
non-MRP 2007 LOD 4.5 2.59 84 2.73 88

Values in bold met my selection criteria.
Table 5.—Classification results (% correct) for the Maumee River plume (MRP) and non-Maumee River plume (non-MRP) from linear discriminant function analyses, based on differences in otolith strontium concentrations of larval yellow perch collected in western Lake Erie during 2006 and 2007. Larval yellow perch from collection sites used in analyses are shown in Figure 3.

<table>
<thead>
<tr>
<th>Water Mass</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td>MRP</td>
<td>19</td>
<td>30</td>
</tr>
<tr>
<td>non-MRP</td>
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<td>8</td>
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<tr>
<td>Totals</td>
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<td>34</td>
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</table>

<table>
<thead>
<tr>
<th>Predicted habitat</th>
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<th>2007</th>
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<tbody>
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<td>MRP</td>
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<td>4</td>
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<tr>
<td>non-MRP</td>
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<td>71</td>
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<tr>
<td>Totals</td>
<td>27</td>
<td>79</td>
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</table>

Table 6.—Sample sizes used in two-way ANOVAs to quantify differences in water-mass attributes (see Table 7) between the Maumee River plume (MRP) and non-Maumee River plume (non-MRP) in western Lake Erie, 2006 and 2007. The number of sites analyzed within each sampling week (dates listed in Table 1) is provided for temperature, turbidity (using transmissometry as a proxy), zooplankton biomass, and zooplankton productivity analyses. The numbers of larval yellow perch analyzed for their first four weeks of life are provided for larval growth rate analyses (using otolith increment widths as a proxy).

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Week</th>
<th>2006 MRP</th>
<th>2006 non-MRP</th>
<th>2007 MRP</th>
<th>2007 non-MRP</th>
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</thead>
<tbody>
<tr>
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<td>8</td>
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<td>6</td>
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<td>11</td>
<td>14</td>
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<td></td>
<td>4</td>
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<td>n/a</td>
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</tr>
<tr>
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<td>22</td>
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<td>11</td>
<td>13</td>
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<td>8</td>
<td>n/a</td>
<td>n/a</td>
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<td>14</td>
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<tr>
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Table 7.—Two-way ANOVA results for comparison of temperature (°C), zooplankton biomass (mg m\(^{-3}\)), zooplankton productivity (mg m\(^{-3}\) day\(^{-1}\)), larval yellow perch growth rate (using otolith increment widths as a proxy; µm day\(^{-1}\)), and turbidity (using transmissometry as a proxy) between the Maumee River plume and non-Maumee River plume in western Lake Erie, 2006 and 2007. Sample sizes are provided in Table 6. Significant P-values are in bold.

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<th>Attribute</th>
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<th>P</th>
<th>2007 df</th>
<th>F</th>
<th>P</th>
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<tr>
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<td>148</td>
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<td>148</td>
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</table>
FIGURE LEGENDS

Figure 1.—Satellite images depicting the Maumee River plume and the non-Maumee River plume (non-MRP) in the western basin of Lake Erie. Images were taken on April 22, 2006 and May 6, 2007.

Figure 2.—Location of sampling sites in the Maumee River plume (MRP) and non-Maumee River plume (non-MRP) during 2006 and 2007. Letters A-Q represent fixed sites (see Table 2) and triangles represent random sites from all sampling weeks (2006: MRP = 13 sites, non-MRP = 47 sites; 2007: MRP = 24 sites, non-MRP = 29 sites). Contour lines denote the outer boundary of the MRP during the larval production period, based on the “best grouped” water mass linear discriminant function analysis using conductivity measurements. Contours were estimated by kriging the MRP posterior classification probabilities of fixed sites (A-Q) sampled from 1 May to 8 Jun during 2006 (sampling weeks 2, 3, 5, 6, 7; see Table 1) and from 30 Apr to 13 Jun during 2007 (sampling weeks 2-8), respectively. Sites southwest of each contour were classified as MRP (characterized by high conductivity and high Sr concentrations with MRP posterior classification probabilities ≥ 50%). Sites northeast of each contour were classified non-MRP (characterized by low conductivity and low Sr concentrations with MRP posterior classification probabilities < 50%). These site classifications were later used to determine past larval habitat-use of juvenile survivors and to test for differences in water mass attributes.

Figure 3.—Location of larval yellow perch used in the linear discriminant function analyses to develop the 2006 and 2007 Maumee River plume (MRP) and non-Maumee River plume (non-MRP) “signatures” (model included mean Sr concentrations in otoliths). Fish that were correctly classified as MRP are represented by circles southwest of respective contours (outer edge of the MRP). Crosses northeast of respective contours were correctly classified as non-MRP.
Crosses within the MRP represent fish that were caught in MRP, but were misclassified as non-MRP. Circles outside the MRP represent fish caught in the non-MRP, but were misclassified as MRP. Symbol size reflects the number of fish used to develop the MRP and non-MRP otolith elemental signatures. For the 2006 and 2007 MRP and 2006 non-MRP signatures, otoliths of all caught larvae ≥ 8mm in total length (≥ ~15 days old) were analyzed. For the 2007 non-MRP signature, otoliths of all caught larvae ≥ 8mm in total length (≥ ~15 days old) from sample collections that had < 5 larvae and only 5-10 larvae from sample collections with ≥ 5 larvae were analyzed.

Figure 4.—Average larval yellow perch abundance (± 1 SE) in western Lake Erie during each sampling week (dates listed in Table 1), 2006 and 2007. Maumee River plume (MRP) and non-Maumee River plume (non-MRP) averages are provided.

Figure 5.—Expected (from peak larval abundance) and observed (from classifications based on Sr concentration in the larval region of juvenile otoliths) frequencies for age-0 yellow perch larval habitat-use in the Maumee River plume (MRP) and non-Maumee River plume (non-MRP) in 2006 (n=100) and 2007 (n=165).

Figure 6.—Classification results from LDF analyses (based on Sr concentrations in otoliths) of western Lake Erie yellow perch juvenile survivors (age-0) collected during August, 2006 and 2007. Crosses represent juveniles that used the non-Maumee River plume as larvae and circles represent juveniles that used the Maumee River plume as larvae. Symbol size proportionally reflects the number of fish caught.

Figure 7.—Weekly mean (untransformed) temperature, zooplankton biomass, and zooplankton productivity (± 1 SE) in the Maumee River plume (MRP) and the non-Maumee River plume (non-MRP) during 2006 (left panels) and 2007 (right panels). Tukey’s unequal N HSD post hoc test results from two-way ANOVAs (see Table 7) also are provided. Letters denote attributes that had significantly
consistent differences between the MRP and non-MRP (one water mass was always higher than the other) during all sampling weeks (i.e., the water mass * sampling week interaction effect was not significant). Sampling weeks with no letters in common are significantly different. Asterisks denote attributes that had inconsistent differences between the MRP and non-MRP (i.e., the water mass * sampling week interaction effect was significant). Sampling points with asterisks indicate a significant difference between the MRP and non-MRP. Non-significant differences are labelled “ns”. Sampling week dates are listed in Table 1 and sample sizes in Table 6.

**Figure 8.**— First four weeks of life mean larval yellow perch growth rates based on otolith increment widths (± 1 SE) in the Maumee River plume (MRP) and the non-Maumee River plume (non-MRP) during 2006 and 2007. Tukey’s unequal N HSD post hoc test results from two-way ANOVAs (see Table 7) are also provided (see Figure 7 for details). Sampling week dates are listed in Table 1 and sample sizes in Table 6.

**Figure 9.**—Weekly mean (untransformed) transmissometry (proxy for turbidity) in the Maumee River plume (MRP) and the non-Maumee River plume (non-MRP) during 2006 and 2007. Tukey’s unequal N HSD post hoc test results from two-way ANOVAs (see Table 7) are also provided (see Figure 7 for details). Sampling week dates are listed in Table 1 and sample sizes in Table 6.
Figure 1
Figure 2
Figure 3
Figure 4
Figure 5
Figure 6
Figure 7
Figure 8
Figure 9
GENERAL DISCUSSION

Recent research in marine systems has 1) demonstrated that allochthonous inputs from rivers can form plumes and fronts in open waters that differ from the surrounding water in their physicochemical and biological attributes and 2) has hypothesized that this habitat heterogeneity could result in bottom-up and/or top-down regulation of fish recruitment. Using these studies as a foundation, I sought to determine if formation of plumes by the Maumee River in western Lake Erie provided a more suitable habitat for faster growth of larval fish through enhanced zooplankton prey availability, in turn, producing more recruits to the fishery.

While plumes in marine systems typically have higher zooplankton and larval fish densities than the surrounding ocean water (Grimes and Finucane 1991; Kingsford and Suthers 1996; Garcia-Isarch et al. 2006), I found this not to be the case in western Lake Erie. Instead, I unexpectedly found that that the MRP had a lower abundance of yellow perch larvae relative to adjacent nutrient-poorer (non-MRP) waters during both years. Further, the differences in zooplankton (prey) availability between the MRP and non-MRP were marginal (i.e., no difference in biomass between habitats, with a slightly higher rate of production in the MRP). While I am uncertain as to the mechanisms underlying these disparities between my findings and those in marine systems, I propose that they are due to system-specific physicochemical differences. In marine systems, higher zooplankton and larval fish densities in plumes (relative to surrounding waters) have been attributed to passive accumulation through hydrodynamic convergence of frontal waters (the meeting of the freshwater river plume water with the saline main body of water) (Govoni et al. 1989; Grimes and Finucane 1991). Formation of such density
fronts may not occur as readily in western Lake Erie, owing to the small average temperature difference between the MRP and non-MRP (~2 °C), as well as the lack of a salinity gradient. In addition, freshwater larvae are generally larger than marine larvae (Miller et al. 1988; Houde 1994); thus, passive movement of larvae via wind-driven circulation into frontal areas is less likely in freshwater systems than marine systems.

Although my research suggests that differences in biological attributes between river plumes and their surrounding water may not be as pronounced in freshwater systems (western Lake Erie) as in marine systems, it does still support the (untested) conventional wisdom in marine systems that formation of plumes positively influences fish recruitment. Specifically, my research indicates that larval habitat-use of the MRP contributes a higher proportion of individuals than expected (based on average peak larval yellow perch abundance) to the west basin fishery than larvae that used non-MRP waters. However, the commonly viewed conception in marine systems that plume formation regulates recruitment through bottom-up effects on larval fish foraging, growth, and survival (e.g., Grimes and Finucane 1991; Grimes and Kingsford 1996; Kingsford and Suthers 1996; Rissik and Suthers 1996; Garcia-Isarch et al. 2006) may be less relevant than believed; my research does not support the notion that success of MRP larvae is due to bottom-up effects of prey availability or temperature that drive fish growth. Instead, I hypothesize that plume-driven habitat heterogeneity drives recruitment through inputs of sediments (or nutrients that cause reduced water clarity), which may promote larval yellow perch survival via reduced predation risk. To date, however, this mechanism has not been tested in this context in any system.
The importance of plume formation to the recruitment process is further highlighted by the fact that both the size of the MRP and strength of the new yellow perch year-class during August, which is when recruitment is set (Ludsin 2000; Yellow Perch Task Group 2007) doubled during 2007 relative to 2006. In addition, relative contributions of individuals to the new year-class from the MRP increased from 34% to 50% from 2006 to 2007. Thus, factors that influence the size, and perhaps timing, of the MRP may drive inter-annual recruitment variation.

Indeed, the timing, duration, and magnitude of discharge from the Maumee River differed during 2006 and 2007 (Figure 1). During 2007, river discharge was greater in magnitude and duration than during 2006, which most likely resulted in the 2-fold increase in turbidity in the MRP between years (Richards et al. 2008). While Maumee River discharge before the larval yellow perch production period (March-April) was higher during 2007 (mean ± SE: 385 ± 36 m$^3$ day$^{-1}$) than 2006 (mean ± SE: 157 ± 20 m$^3$ day$^{-1}$), interestingly, this was not the case during the larval production period; when larval yellow perch were present in the system (1 May-13 June), river discharge was lower in 2007 (mean ± SE: 82 ± 19 m$^3$ day$^{-1}$) than 2006 (mean ± SE: 237 ± 34 m$^3$ day$^{-1}$) (Figure 1). Perhaps the large discharge event during 2006 came too late to fully benefit all larval yellow perch cohorts, whereas the early (pre-larval production) arrival of pulsed inputs set in place conditions favourable for all larvae. In this way, high inputs of total dissolved phosphorus both before and during larval production period in 2007 (May mean ± 1 SD: 64 ± 30 ug l$^{-1}$, n = 3 dates; T. Johengen and S. Ludsin, unpub. data) may have promoted larval yellow perch survival during the entire larval yellow perch production period (even during periods of low sediment inputs during periods of low
river discharge) via phytoplankton shading that reduced predation mortality (sensu Fiksen et al. 2002). By contrast, inputs of total dissolved phosphorus were lower and occurred later in 2006 (27 ± 23 ug l\(^{-1}\), \(n = 2\) dates T. Johengen and S. Ludsin, unpub. data) than in 2007, which may only have afforded refuge from predators to late-hatched larvae. Alternatively, suspension of sediments could possibly be sustained by wind-driven circulation for weeks after a large river discharge event, which is indicated by the 2-fold increase in turbidity in the MRP from 2006 to 2007 during the beginning of the larval production period even though Maumee River discharge was lower during 2007 than 2006. Also, the average size of the MRP was bigger in 2007 than 2006. Clearly, more research is required to definitively tease apart the mechanism(s) by which discharge-driven inputs of allochthonous materials (e.g., nutrients, sediments) interact with wind-driven circulation to influence the extent of habitat heterogeneity, and ultimately larval fish survival to the new year-class.

CONCLUSIONS

Previous research has demonstrated a positive relationship between Maumee River discharge and recruitment to the west basin fishery for Lake Erie yellow perch (Ludsin 2000; S. Ludsin, unpub. data). However, the mechanisms underlying this relationship were unknown. My research suggests that Maumee River discharge may benefit yellow perch recruitment to the fishery in western Lake Erie by creating plumes in open waters of the west basin that promote survival of larvae. Although the exact mechanism underlying this relationship is still lacking, my findings discount the notion that zooplankton availability is responsible and instead provide some support for the
hypothesis that plumes may promote recruitment by reducing predation mortality on larvae. Therefore, a switch in focus from bottom-up effects to that of top-down effects seems warranted, not only in Lake Erie, but marine systems as well. Owing to the difficulty in quantifying predation rates on larvae (Legler 2008), advances using mitochondrial DNA and quantitative real-time PCR appear to be the most promising techniques to addressing this mechanism (Asahida et al. 1997; Rosel and Kocher 2002; Zabarovsky et al. 2003).

Given the growing recognition that fish population dynamics in both marine and freshwater systems appear dependent on watershed-derived inputs during early life, I fully endorse ecosystem (watershed) approaches for managing and sustaining fisheries in coastal settings. In addition, I fully promote the continued use of otolith microchemistry in tackling recruitment-related research problems. As my research has shown, this tool can provide invaluable insight toward understanding how external factors (i.e., nutrient- and sediment-inputs from tributaries) can influence recruitment dynamics through habitat heterogeneity. To date, few studies have used otolith microchemical techniques to address large-scale hypotheses concerning recruitment variation (Gillanders 2005; Hamilton et al. 2008; and Bradbury 2008). Of those studies, none have addressed top-down or bottom-up recruitment mechanisms associated with watershed influences (i.e., river plumes). Only through continued integration of research disciplines (i.e., researchers who study fish recruitment, otolith microchemistry, and watershed influences) will efforts aimed at unravelling the complexity of mechanisms that influence fish population dynamics prove successful, and in turn, managers will gain the capacity to understand and predict recruitment variation of valued fisheries.
REFERENCES


Figure 1.—Average Maumee River discharge (± 1 SE) during 2006 and 2007. Shaded area depicts the larval yellow perch production period in western Lake Erie. Maumee River flow data was downloaded from the United States Geological Survey website (http://waterdata.usgs.gov/usa/nwis/uv?site_no=04193500).
Vita Auctoris

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Date of Birth: 1981

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  1999-2004, BSc Biological Sciences
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  2006-2009, MSc Environmental Science