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Effects of Lake Erie Habitat Variation and Digestion Rate on Feeding in Freshwater Fishes

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Effects of Lake Erie Habitat Variation and Digestion Rate on Feeding in Freshwater Fishes

By

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Declaration of Co-Authorship / Previous Publication

I. Co-Authorship Declaration

This thesis also incorporates the outcome of a joint research undertaken in collaboration with Stuart Ludsin (The Ohio State University) and Jeff Tyson (Ohio Department of Natural Resources) under the supervision of Timothy Johnson (Ontario Ministry of Natural Resources) and Daniel Heath (University of Windsor). 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 and through assistance from research collaborators.

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II. Declaration of Previous Publication

This thesis includes two original papers that have been previously, or will be, submitted for publication in peer reviewed journals, as follows:

Thesis Chapter	Publication title/full citation	Publication status
Chapter 1	Legler, N. D., T. B. Johnson, D. D. Heath, and S. A. Ludsin. Effects of water temperature, prey mass, and species on digestion of larval fish.	Manuscript submitted to Transactions of the American Fisheries Society: November 2008.
Chapter 2	Legler, N. D., T. B. Johnson, S. A. Ludsin, and D. D. Heath. Influence of river plumes on predator feeding and diet in Lake Erie.	Manuscript to be submitted to Canadian Journal of Fisheries and Aquatic Sciences.

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Abstract

My research was designed to evaluate predator-prey relationships in Lake Erie and the effects of watersheds, through river inputs, on prey consumption. I analyzed stomach contents of fishes collected from two distinct river plumes in Lake Erie's western basin to see if elevated turbidity in one river plume reduced predation mortality of larval fishes. I found that quantifying larval fish predation mortality is a difficult task; only 16 of 3,467 stomachs analyzed contained larval prey. I used laboratory experiments to evaluate digestion rates of larval fishes and found that both the complete breakdown of larvae in predator stomachs and the loss of morphological characters needed to identify larvae occurred rapidly, suggesting that conventional diet analyses are inadequate for quantifying larval predation mortality. My diet analyses did reveal spatial and temporal differences in prey consumption between river plumes, which are likely being driven by bottom-up and top-down effects associated with inputs of nutrients and sediments from tributary streams. Collectively, my results will allow managers to quantify the likelihood of detecting larval fishes during stomach content analyses and to better understand how tributary inputs influence predator-prey interactions.

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1.0 General Introduction

As part of a larger study designed to examine potential mechanisms influencing yellow perch *Perca flavescens* recruitment in Lake Erie, I evaluated the effects of river discharge on prey consumption by fishes in Lake Erie's western basin. My research was multi-faceted; I used laboratory experiments to evaluate the limitations of traditional diet analysis techniques and a field study to compare diets of fishes from two river plumes. Collectively, my results help identify the challenges in quantifying diets consisting of prey with differential digestion rates with a focus on larval fish and the importance of watershed-scale approaches to fisheries management.

Forecasting fish recruitment (defined as the addition of new individuals, or often breeding individuals, to a population by reproduction; Ricklefs 2007) and abundance are important tasks for fisheries management agencies. Unfortunately, attaining these predictive capabilities has been difficult in most systems due to large scale, stochastic, variability in recruitment (e.g., Atlantic cod *Gadus morhua L.* and haddock *Melanogrammus aeglefinus* recruitment; Fogarty 1993; Beaugrand et al. 2003) and a limited understanding of the mechanisms driving recruitment variability. These difficulties exist largely because there are numerous factors that simultaneously influence fish population dynamics. For example, growth and survival of larvae fishes are influenced by prey availability (i.e., phytoplankton and zooplankton), which is in turn dependent on nutrient concentrations (Freeberg et al. 1990; Graeb et al. 2004). In addition to prey availability, foraging success of both larval and adult fishes can be influenced by factors such as turbidity, which limits visual acuity, and inter- and intra-

specific competition for limited food resources (Abrahams and Kattenfeld 1997; De Robertis et al. 2003; Pekcan-Hekim and Lappalainen 2006).

Although there are many uncertainties and questions surrounding fish recruitment and abundance variability, it is generally accepted that recruitment is set during early life stages (egg, larvae, juvenile) and the extent of mortality during early life is expected to greatly influence the number of fish recruiting to the adult population (Hjort 1914, 1926; Anderson 1988; Govoni 2005). This idea is widely accepted simply because the number of eggs spawned by most fishes is much greater than the number of fish surviving to age 1 (Winemiller and Rose 1993). Specific hypotheses explaining fish recruitment variability and early life mortality include: 1) the critical period and match-mismatch hypotheses, which suggest that year-class strength is largely determined by survival during the transition from the yolk-sac stage to active first-feeding and that survival during this "critical period" is influenced by matching of spatial and temporal patterns in food availability and larvae in nursery areas; 2) the predation hypotheses, which suggests that predation is a major cause of mortality for larvae fishes, especially during the yolk-sac stage when starvation is ruled out because of energy reserves in the yolk; and 3) the bigger-is-better hypotheses, which suggests that rates of predation mortality decrease as larvae grow, and therefore predation, growth, and food availability are all closely related (Hjort 1914, 1926; Anderson 1988; Govoni 2005).

In Lake Erie, yellow perch recruitment and abundance are highly variable (YPTG 2007; OMNR 2008), likely due to a complex of continually changing conditions throughout the lake. Government regulated phosphorous abatement programs and the invasion of dreissenid mussels have led to the recent oligotrophication of Lake Erie, as

indicated by reduced phytoplankton and zooplankton biomass, increased water clarity, recovery of benthic macroinvertebrates, and changes in fish community composition (e.g., Regier and Hartman 1973; Makarewicz and Bertram 1991; Nicholls and Hopkins 1993; Sieney 1993; Madenjian et al. 1998; Nicholls et al. 1999; Johannsson et al. 2000; Ludsin et al. 2001). Since this recent oligotrophication, river inputs have played a major role in determining Lake Erie's total phosphorous load; precipitation driven river discharge events provide 60-70% of the lakes total phosphorous input (Curl 1959; Dolan 1993; Richards et al. 2001; Baker and Richards 2002). Since Lake Erie became increasingly oligotrophic, a positive correlation has existed between springtime (March-May) Maumee River discharge and yellow perch recruitment (S. A. Ludsin, The Ohio State University, unpublished data).

The mechanisms behind this relationship between Lake Erie Maumee River discharge and yellow perch recruitment are unknown. It is however possible that Maumee River discharge is influencing recruitment by affecting survival of yellow perch during early life stages. The Maumee River drains a largely agricultural watershed and is therefore rich in nutrients and sediments (Herbert 1959; Richards et al. 2001, 2002). Inputs of phosphorous from the Maumee River are known to create inter-annual variation in Lake Erie's total phosphorous levels and are positively correlated with copepod zooplankton abundance during spring-early summer (S. A. Ludsin, The Ohio State University, unpublished data). Maumee River discharge may therefore be impacting yellow perch recruitment via: 1) bottom-up control of food production for larvae (i.e., phosphorous inputs enhance phytoplankton and zooplankton abundance) and 2) enhanced

turbidity that reduces larval predation mortality (S. A. Ludsin, The Ohio State University, personal communication).

1.1 'Larger Study' Objectives

As part of a larger study designed to examine the effects of starvation and predation of larval yellow perch in Lake Erie, my research project was designed to evaluate the effects of turbidity (created by Maumee River discharge) on larval predation mortality. To evaluate this hypothesis, predatory fishes were collected for diet analyses during April-June of 2006 and 2007 from the turbid Maumee River plume, as well as the Detroit River plume (Figure 1.1). The Detroit River plume was expected to be clear compared to the Maumee River plume, because the Detroit River is fed by oligotrophic water from the upper Great Lakes (Herbert 1959; Richards et al. 2001, 2002). Since turbidity limits visibility and reduces predator-prey reaction distances (e.g., Snickars et al. 2004; Lehtiniemi et al. 2005), I expected to find more larval yellow perch in stomachs of fishes collected form the clear Detroit River plume. Instead, I found that almost all stomachs (from both the Maumee and Detroit River plumes) contained no larval fishes. Of 3,467 stomachs analyzed (Table 1.1) only 16 (Table 1.2) contained morphologically identifiable larval fish remains. These results are consistent with many previous studies (e.g., Crowder 1980; Tanabe 2001; Takasuka et al. 2003) which have also found it difficult to quantify larval fish predation mortality using stomach content analyses.

Figure 1.1 Satellite photo of western Lake Erie showing the Maumee and Detroit Rivers and each river's corresponding plume.

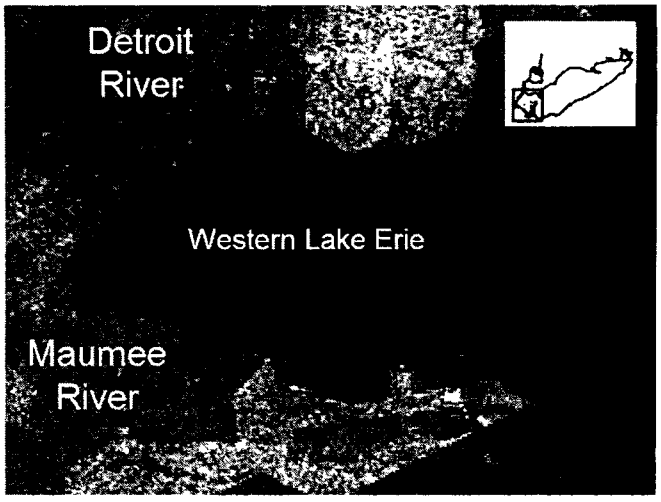

Table 1.1 Summary of the total numbers of stomach samples collected (using bottom trawls and gillnets) from the Maumee and Detroit River plumes in the western basin of Lake Erie during 2006 and 2007 and the total numbers of stomachs analyzed. Analysis included morphological identification of individual prey taxa and quantification by volumetric displacement and counts.

Year	Genus / Species	Common Name	Bottom Trawl				Gillnet			
			Collected		Analyzed		Collected		Analyzed	
			Maumee	Detroit	Maumee	Detroit	Maumee	Detroit	Maumee	Detroit
2006	*Alosa pseudoharengus*	Alewife	0	0	0	0	0	3	0	2
	Ambloplites rupestris	Rock Bass	0	4	0	4	0	2	0	2
	Aplodinotus grunniens	Freshwater Drum	46	9	46	9	0	59	0	44
	Catostomus commersoni	White Sucker	0	0	0	0	1	3	0	3
	Dorosoma cepedianum	Gizzard Shad	0	0	0	0	0	116	0	70
	Hiodon tergisus	Mooneye	0	0	0	0	0	1	0	0
	Hybopsis storeriana	Silver Chub	0	0	0	0	0	49	0	36
	Ictalurus nebulosus	Brown Bullhead	1	0	1	0	0	0	0	0
	Ictalurus punctatus	Channel Catfish	2	0	2	0	0	2	0	0
	Micropterus dolomieui	Smallmouth Bass	0	2	0	2	0	8	0	6
	Morone americana	White Perch	121	150	121	150	244	368	178	220
	Morone chrysops	White Bass	77	165	77	134	73	135	39	90
	Moxostoma anisurum	Silver Redhorse	0	0	0	0	0	2	0	2
	Moxostoma erythrurum	Golden Redhorse	0	0	0	0	0	2	0	1
	Notropis hudsonius	Spottail Shiner	0	0	0	0	0	5	0	3
	Perca flavescens	Yellow Perch	137	93	137	89	287	222	191	120
	Sander vitreus	Walleye	37	89	37	89	141	106	51	80
2007	*Alosa pseudoharengus*	Alewife	0	1	0	0	0	0	0	0
	Ambloplites rupestris	Rock Bass	0	7	0	0	0	4	0	4
	Aplodinotus grunniens	Freshwater Drum	46	46	0	0	61	130	0	39
	Dorosoma cepedianum	Gizzard Shad	0	0	0	0	0	1	0	1
	Hybopsis storeriana	Silver Chub	0	13	0	0	0	0	0	0
	Ictalurus punctatus	Channel Catfish	23	1	0	0	22	9	0	2
	Micropterus dolomieui	Smallmouth Bass	0	7	0	0	1	9	1	2
	Morone americana	White Perch	119	158	119	158	323	499	100	213
	Morone chrysops	White Bass	31	128	30	128	97	360	30	106
	Notropis atherinoides	Emerald Shiner	0	0	0	0	5	0	0	0
	Perca flavescens	Yellow Perch	92	105	91	104	204	159	58	101
	Sander vitreus	Walleye	14	13	14	13	120	205	45	72

Table 1.2 Summary of the 16 stomachs (of 3,467 stomachs analyzed) that contained morphologically identifiable larval fish remains. Summary information includes when (year, data), where (plume), and how (gear) each predator (genus/species, common name, total length, weight) was collected. N is the total number of larval fishes found in each stomach (Ukn means there were larval fish remains, but an accurate count was not possible due to excessive digestion).

Year	Date	Plume	Gear	Genus / Species	Common Name	TL (mm)	W (g)	N
2006	2-May	Detroit	Gillnet	*Perca flavescens*	Yellow Perch	172	53	1
2006	8-May	Detroit	Gillnet	*Aplodinotus grunniens*	Freshwater Drum	327	363	1
2006	5-Jun	Maumee	Bottom Trawl	*Morone americana*	White Perch	149	48	Ukn
2006	5-Jun	Maumee	Bottom Trawl	*Morone americana*	White Perch	142	39	115
2006	14-Jun	Detroit	Bottom Trawl	*Morone chrysops*	White Bass	138	29	2
2006	14-Jun	Detroit	Bottom Trawl	*Morone chrysops*	White Bass	168	56	1
2007	24-Apr	Maumee	Gillnet	*Morone americana*	White Perch	200	127	3
2007	8-May	Detroit	Gillnet	*Morone americana*	White Perch	232	199	1
2007	6-Jun	Detroit	Bottom Trawl	*Morone americana*	White Perch	235	201	1
2007	6-Jun	Detroit	Bottom Trawl	*Morone chrysops*	White Bass	225	134	14
2007	12-Jun	Detroit	Gillnet	*Morone americana*	White Perch	228	179	1
2007	12-Jun	Detroit	Gillnet	*Morone americana*	White Perch	234	215	1
2007	12-Jun	Detroit	Gillnet	*Morone americana*	White Perch	243	237	3
2007	12-Jun	Detroit	Gillnet	*Morone americana*	White Perch	252	236	7
2007	12-Jun	Detroit	Gillnet	*Morone americana*	White Perch	245	232	1
2007	12-Jun	Detroit	Gillnet	*Morone americana*	White Perch	199	90	1

1.2 Quantifying Larval Fish Predation

Since most diet studies (including mine) have been unable to reliably identify fish larvae in stomach contents of predatory fishes, the extent of larval fish predation mortality is largely unknown, despite the fact that predation is widely accepted as a major cause of mortality for larval fishes (Hjort 1914, 1926; Anderson 1988; Govoni 2005). Rapid digestion rates likely explain why larvae are rarely found in stomach contents, yet a quantification of digestion rates of larvae is generally lacking, especially in freshwater systems. Using a series of laboratory experiments, I quantified the effects of temperature and larval fish (prey) size on digestion rates. I also evaluated if species type (of both predator and prey) influences digestion rate, described the morphological breakdown of larval fishes during digestion, and report the probability of identifying digested larvae using traditional stomach content analyses techniques. Quantifying the time required for

larval fishes to digest and become morphologically unidentifiable in a predators stomach is an important step towards quantifying larval fish predation mortality. Ultimately, my findings should help researchers quantify the likelihood of detecting larval fishes in stomach contents of field-caught predators when using conventional diet analyses techniques.

1.3 Effects of Habitat Variability on Diet Composition

Spatial and temporal habitat heterogeneity can greatly influence fish population dynamics, including foraging behaviours (e.g., Hayes & Rutledge 1991). Tributary streams (through inputs of freshwater, nutrients, sediments, etc.) can be major sources of habitat heterogeneity in aquatic systems, and such interactions have been studied in many coastal marine systems (e.g., Dauvin and Dodson 1990; Grimes and Finucane 1991; Sirois and Dodson 2000; North and Houde 2001; Roman et al. 2001). I evaluated how watersheds, through river inputs, influence prey consumption of freshwater fishes by comparing stomach contents of white perch *Morone American, y*ellow perch, white bass *Morone chrysops, and* walleye *Sander vitreus* collected from the Maumee and Detroit River plumes during 2006 and 2007. Habitat heterogeneity associated with inputs of nutrient and sediment rich water from the Maumee River, and comparatively nutrient poor, clear water from the Detroit River, were expected to influence foraging behaviours through bottom-up and top-down effects on prey availability and visual acuity. A better understanding of how tributary plume dynamics influence prey consumption of Lake Erie fishes will facilitate further development of management practices that incorporate watershed-scale approaches.

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2.0 Effects of Water Temperature, Prey Mass, and Species on Digestion of Larval Fish

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Transactions of the American Fisheries Society
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2.1 Introduction

Predation is widely accepted as a major source of mortality for fishes during early life, despite difficulties associated with quantifying such mortality (Hjort 1914, 1926; Brandt et al. 1987; Houde 1989; Tsou and Collie 2001; Munk 2002). Newly hatched fish are vulnerable to predation because of their small size and poorly developed sensory and motor systems (Tonn et al. 1992). In an extensive literature review, based on 25 species of larvae from a wide geographic region, Almany and Webster (2006) estimated that fish predators can consume between 6% and 100% (mean = 56%) of newly hatched larvae within 48 hours of hatch. However, such predation rate estimates have proven difficult to obtain and are often underestimated because of the difficulties associated with detecting larvae in stomach contents of predators (Crowder and William 1982; Tanabe 2001; Takasuka et al. 2003).

After ingestion, larval fish undergo rapid digestion which can inhibit detection during conventional stomach content analyses and thereby prevent accurate estimates of larval predation mortality rates (Crowder 1980; Brandt et al. 1987). Rapid digestion is expected because larval fish are small, soft bodied organisms that lack or have poorly developed protective scales and resistant hard body parts. The few studies that have reported fish larvae in predator stomachs often indicate that larvae are highly digested and identification is difficult (Tanabe 2001; Takasuka et al. 2003). For example, the

number of juvenile cod *Gadus morhua* stomachs needed to positively identify one yolk sac cod larvae using morphological features (i.e., remnants of skin, skull remains, fin structures) was estimated to be between 29 and 1,700 at 10°C (Folkvord 1993). Most certainly, estimates of the time required for larval fishes to break down during digestion, and the influence of water temperature and prey size on digestion rates, would enable researchers to more accurately assess the likelihood of finding larval prey during diet studies. Such information also would allow an assessment of the magnitude of predation on larval mortality rates.

Herein, I conducted a series of laboratory experiments to evaluate the digestion process of larval fishes in stomachs of fish predators, relating digestion time to prey (larval fish) size, water temperature, and prey/predator species. I also described the morphological breakdown of larval fish during digestion and report the probability of identifying digested larvae during stomach content analyses. Measuring the time required for a larval fishes to become morphologically unrecognisable during diet analysis will provide insight for diet studies designed to estimate larval predation mortality.

2.2 Methods

Due to an inability to get wild-caught fish to feed in captivity, I used hatchery-reared bluegill sunfish *Lepomis macrochirus* and yellow perch *Perca flavescens* (Table 2.1) as predators for this study because these fish were pre-conditioned to feeding in a captive environment. All predators were held in 475-L aerated tanks supplied with a continuous flow of dechlorinated water at 19°C. During acclimation and holding, fish

were maintained on a diet of commercial fish feed Prior to feeding experiments, predators were transferred to individual 32-L experimental chambers and acclimated to experimental temperatures (range: 7-22°C) for 48 hours during which time they were fasted to ensure empty stomachs

Table 2.1 Experimental factors considered in larval fish digestion-rate experiments. Means (± standard deviation), ranges, and sample sizes of each independent variable are included.

	Treatment Classes/Levels	Mean	Range	N
Prey species	Guppy *Poecilia* spp	0 011 ± 009 g	0 003 – 0 048 g	55
	Rainbow trout *Oncorhynchus mykiss*	0 061 ± 014 g	0 029 – 0 099 g	119
	Yellow perch *Perca flavescens*	0 179 ± 051 g	0 098 – 0 355 g	68
Predator species	Bluegill sunfish *Lepomis macrochirus*	56 ± 31 g	15 – 176 g	222
	Yellow perch *Perca flavescens*	79 ± 19 g	43 – 101 g	20
Water temperature	Continuous variable	15 ± 5 °C	7 – 22 °C	242
Time	Continuous variable	4 7 ± 4 5 hr	0 05 – 20 hr	242

Larval fish prey were obtained from a variety of sources. 1) newly hatched guppies *Poecilia* spp. were obtained from a pet store; 2) rainbow trout *Oncorhynchus mykiss* sac fry were obtained from Fraser Valley trout hatchery in Abbotsford, British Columbia; and 3) young-of-year yellow perch were obtained from Lake Erie (Table 2 1) Larval rainbow trout and yellow perch were frozen and subsequently thawed prior to being fed to predators, whereas guppies were fed live to predators Each feeding trial consisted of feeding one larva to each predator after measuring individual larval length

and mass. Excess moisture was removed prior to measuring larvae by blotting with a paper towel.

Initially, predators were allowed to feed *ad libitum* while being observed for time of ingestion. However, this procedure was abandoned due to the often lengthy delay before feeding actually occurred. Instead, I opted to force-feed predators, whereby a larval fish was carefully injected into the stomach by gently pushing an open ended syringe down the oesophagus. Predators were examined briefly (for < 1 minute) in a recovery bucket to ensure larvae were not regurgitated before being transferred back into their experimental tanks.

Predators were removed from aquaria at predetermined time intervals (0-20 hours after ingestion) and euthanised using an overdose of clove oil (approximately 3-ml clove oil: 25-ml 95% ethanol: 4-L water). Once stage IV anaesthesia was reached (medullary collapse, no opercular movement), stomachs were immediately removed and examined under a dissecting microscope. Stomach contents were classified as being identifiable or unidentifiable fish remains, described for presence or absence of six morphometric traits (i.e., pigmentation, presence of head, caudal fin, anal fin, dorsal fin, pectoral fin), and weighed. Digestion was considered complete when stomachs were devoid of measurable larval fish remains.

Degree of digestion (DD) was calculated as:

$$DD = \left(1 - \left(\frac{mass_t}{mass_0}\right)\right) * 100$$

where $mass_t$ is the mass (g) upon dissection, and $mass_0$ is the pre-feeding mass (g). The influence of prey mass, water temperature, and time from ingestion on DD was evaluated using a multiple regression approach. To find the most parsimonious multiple regression

model that explained the most variation with the least number of variables, I evaluated the full complement of all 1-, 2-, and 3-variable models using Akaike's Information Criterion (Burnham and Anderson 1998). Analysis of covariance was used to test for differences in degree of digestion among prey and predator species. Logistic regression was used to determine the probability of positively identifying stomach contents as a larval fish and recognizing morphological traits. All statistical analyses were completed using SYSTAT version 11.0, with statistical significance assigned at $p < 0.05$.

2.3 Results

Individual feeding experiments (N = 242) Were conducted using three larval fish species as prey, two species of predator, and temperatures ranging from 7 to 22°C (Table 2.1). Across all species of prey and predator, digestion rate increased with water temperature and decreased with prey body mass (Figure 2.1). My AIC analysis revealed that the 3-variable multiple regression model, $DD = -136.70M + 2.78T + 5.20H$, was the most parsimonious (ANOVA, $F_{3,239} = 401.2$, $p < 0.001$, $R^2 = 0.83$), where DD is the degree of digestion (%), M is larval fish prey mass (g), T is water temperature (°C), and H is time since ingestion (hr) (Table 2.2). Although the next best model, $DD = 2.34T + 4.23H$ (ANOVA, $F_{2,240} = 525.5$, $p < 0.001$), had a relative AIC value of 26 when compared to the "best" 3-variable model, it also explained nearly an identical amount of variation in the data ($R^2 = 0.81$) as my 3-variable model, signifying that temperature and time since digestion are the most important factors in explaining variation in the DD. Additionally, analysis of partial correlation coefficients indicates that temperature (T; partial $R^2 = .34$) is more important than time (H; partial $R^2 = .19$) (Table 2.2).

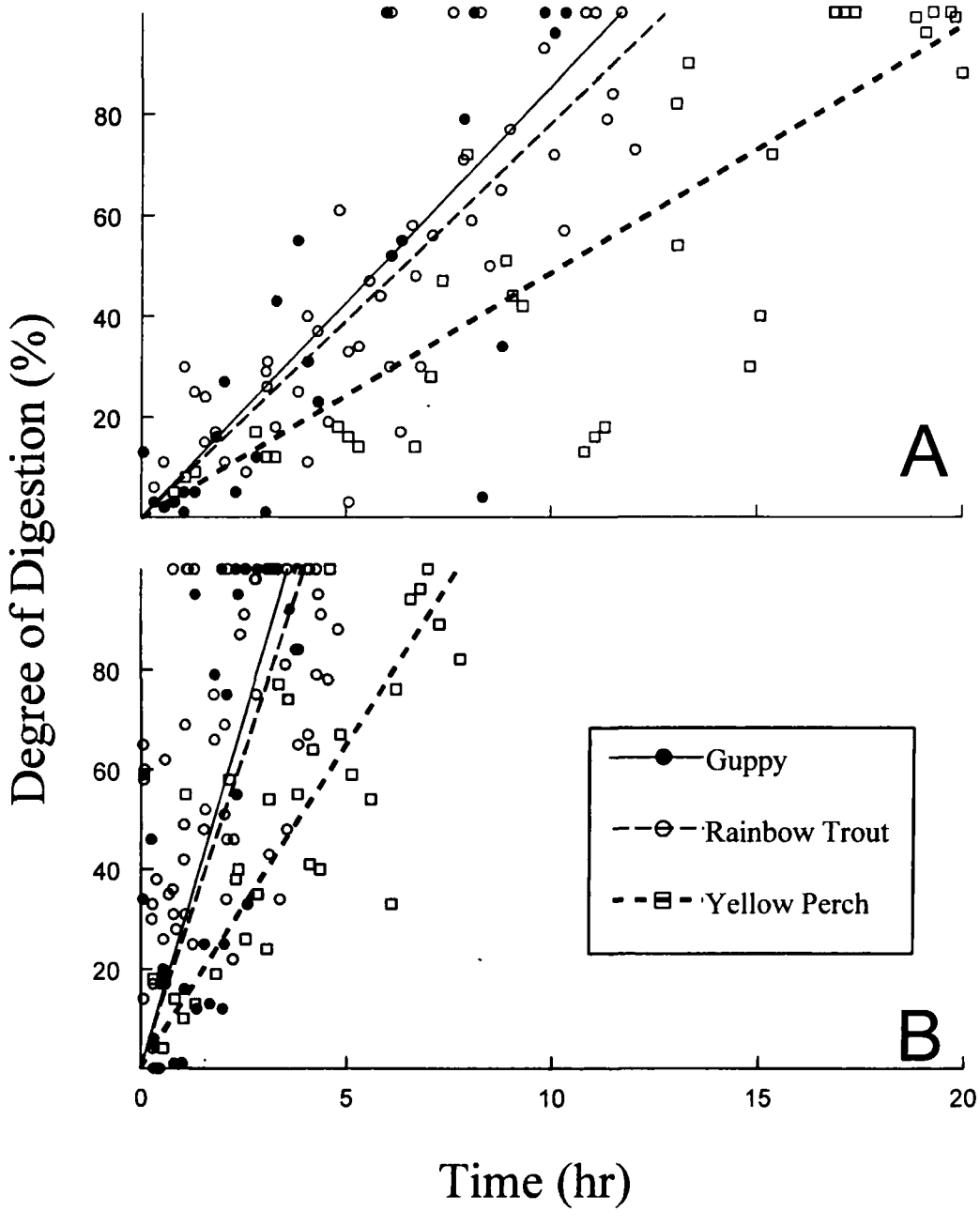

Figure 2.1 Degree of digestion of three larval fish (prey) species by bluegill sunfish and yellow perch predators. Degree of digestion was calculated as: $100-(mass_t/mass_0*100)$ where $mass_t$ is the mass (g) upon dissection, and $mass_0$ is the pre-feeding mass (g). Data are categorized by temperature as A) range: 7-13°C, mean ± SD: 10 ± 1 and B) range: 16-22 °C, mean ± SD: 19 ± 1. The y intercept was set to 0 for all linear regressions.

Table 2.2 Statistics for multiple regression models (n=7 models), and each models independent variables, relating degree of digestion (DD) to larval fish mass (M, g), water temperature (T, °C), and time since ingestion (H, hr). Akaike's Information Criterion (AIC) was used to rank models, with the most parsimonious one having a relative AIC = 0.

Model	Overall Model					Individual Model Variables				
	R^2	Std Error	p	F	Rel AIC	Variable	Std Error	Partial R^2	t	p
DD = -136 70M + 2 78T + 5 20H	0 83	25 79	< 0 001	401 23	0	M	25 29	0 06	5 41	< 0 001
						T	0 15	0 47	18 13	< 0 001
						H	0 36	0 29	14 51	< 0 001
DD = 2 34T + 4 23H	0 81	27 26	< 0 001	525 46	26	T	0 14	0 34	17 07	< 0 001
						H	0 33	0 19	12 90	< 0 001
DD = 47 29M + 3 11T	0 69	35 29	< 0 001	265 23	151	M	29 94	0 01	1 58	0 116
						T	0 208	0 59	14 96	< 0 001
DD = 3 34T	0 69	35 39	< 0 001	524 71	151	T	0 146	0 69	22 91	< 0 001
DD = 109 66M + 6 15H	0 61	39 65	< 0 001	185 03	207	M	32 80	0 04	3 34	0 001
						H	0 55	0 40	11 28	< 0 001
DD = 7 42H	0 59	40 48	< 0 001	344 35	216	H	0 40	0 59	18 56	< 0 001
DD = 367 11M	0 40	48 95	< 0 001	159 28	308	M	29 09	0 40	12 62	< 0 001

No effects of prey or predator species were observed. In a comparison of digestion rates of guppies and rainbow trout, which were similar sized prey, I found no differences between species when fed to bluegill sunfish at similar temperatures (16 to 21 °C; $F_{1,78} = 1.031$, $p = 0.31$; Figure 2.1). Likewise, no difference in digestion rates were found between bluegill sunfish and yellow perch when fed rainbow trout at similar temperatures (16 to 22 °C; $F_{1,68} = 2.59$, $p = 0.11$; Figure 2.2).

As larval fish were digested, morphological characteristics that could be used to confirm the prey items as fish and distinguish between prey species were rapidly lost (Figure 2.3, 2.4). Logistical regression analyses indicated that rainbow trout could be identified as fish prey with 95% confidence when the degree of digestion was $\leq$ 36%, whereas yellow perch and guppies could only be digested $\leq$ 24% before the ability to identify species was lost (Table 2.3). Similar patterns of loss of traits over time were observed among all larval fish prey (Figure 2.4). Fins were lost first, with pectoral, dorsal, and anal fins only being detected < 50% of the time, even when digestion was not

far advanced (0-24%) (Table 2.3). The head was lost next, whereas pigmentation remained evident even on highly digested prey (Table 2.3).

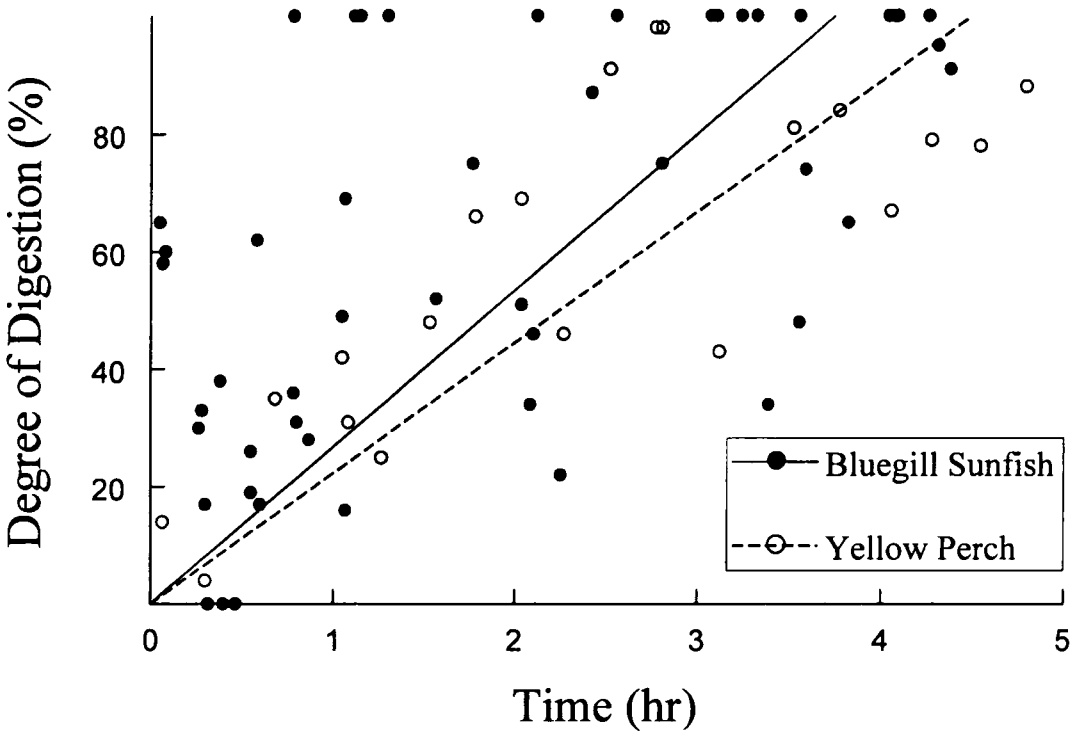

Figure 2.2 Degree of digestion of rainbow trout prey by sunfish and yellow perch predators at warm temperatures (range: 16-22 °C, mean ± SD: 19 ±2). Data are categorized by predator species. The y intercept was set to 0 for all linear regressions.

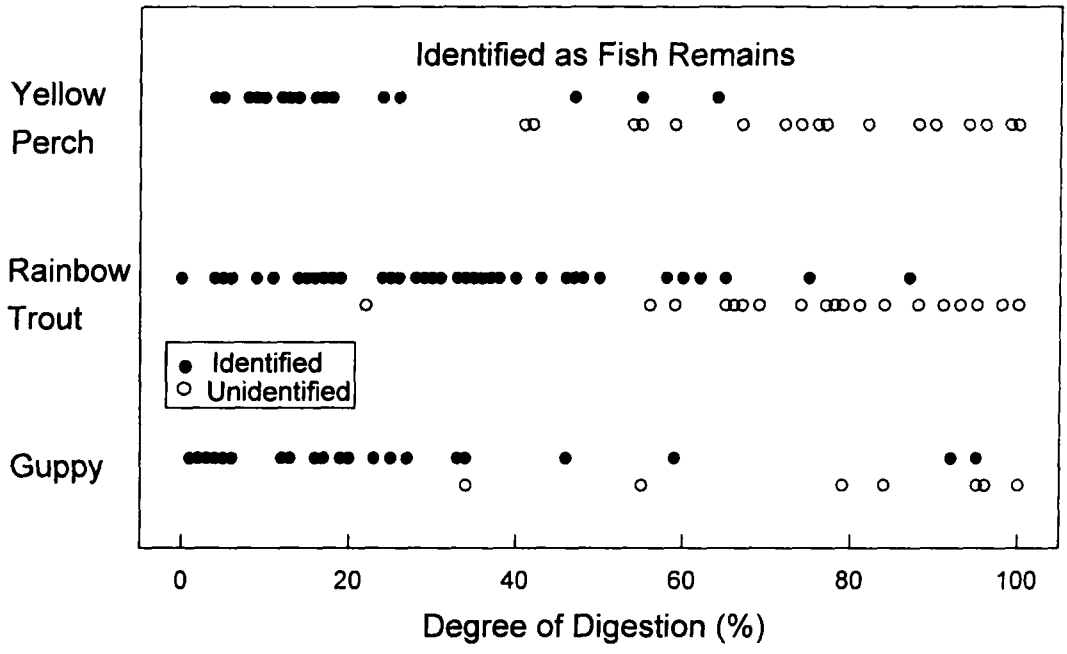

Figure 2.3 Classification of individual larval fish prey recovered from predator stomachs as recognizable fish remains. Results are summarized by prey species and degree of digestion.

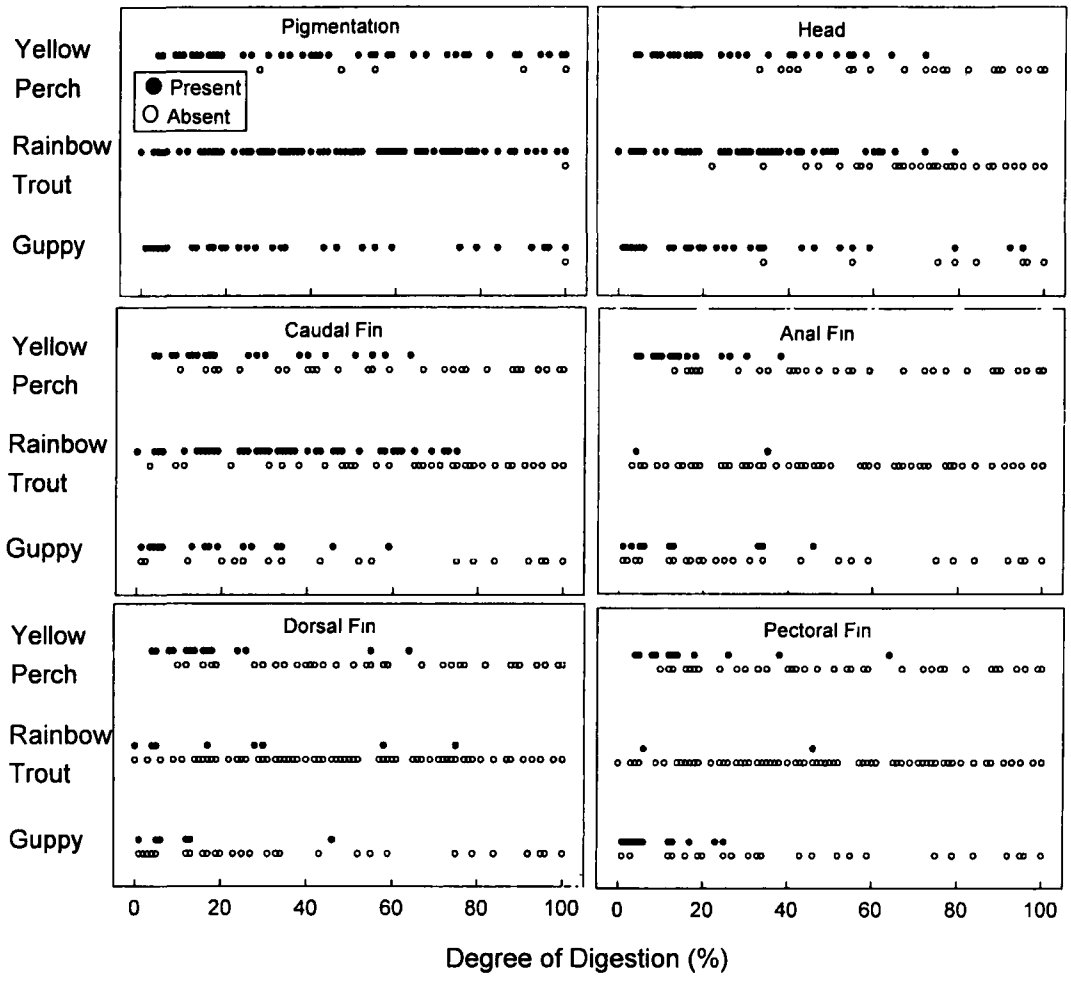

Figure 2.4 Presence / absence of individual morphometric traits of larval fish prey recovered from predator stomachs. Results are summarized by prey species and degree of digestion.

Table 2.3 Logistic regression coefficients and selected probabilities (50, 75, 95, and 99%) of classifying individual larval fish recovered from predator stomachs as recognizable fish remains and detecting individual prey morphometric traits at a specified degree of digestion. Degree of digestion was calculated as: $100-(mass_t/mass_0*100)$ where $mass_t$ is the mass (g) upon dissection, and $mass_0$ is the pre-feeding mass (g).

Trait	Species	Constant	PerDig	50%	75%	95%	99%
Recognizable	Perch	5 692	-0 119	48	38	23	9
Recognizable	Trout	6 909	-0 111	62	52	36	21
Recognizable	Guppy	4 693	-0 072	65	50	24	1
Pigmentation	Perch	3 394	-0 017	100	100	26	0
Pigmentation	Trout	335 775	-3 352	100	100	99	99
Pigmentation	Guppy	205 732	-2 055	100	100	99	98
Head	Perch	4 989	-0 094	53	41	0	4
Head	Trout	6 110	-0 106	58	47	30	14
Head	Guppy	5 358	-0 076	71	56	32	10
Caudal Fin	Perch	2 278	-0 064	36	18	0	0
Caudal Fin	Trout	3 469	-0 062	56	38	8	0
Caudal Fin	Guppy	1 500	-0 056	27	7	0	0
Anal Fin	Perch	3 182	-0 131	24	16	2	0
Anal Fin	Trout	0 064	-0 129	0	0	0	0
Anal Fin	Guppy	-0 205	-0 043	0	0	0	0
Dorsal Fin	Perch	2 011	-0 084	24	11	0	0
Dorsal Fin	Trout	-1 116	-0 037	0	0	0	0
Dorsal Fin	Guppy	-0 854	-0 045	0	0	0	0
Pectoral Fin	Perch	1 111	-0 076	15	0	0	0
Pectoral Fin	Trout	-2 618	-0 037	0	0	0	0
Pectoral Fin	Guppy	1 628	-0 126	13	4	0	0

2.4 Discussion

My experiments confirm that researchers will have a low likelihood of finding recently hatched larval fishes in the stomachs of field-caught predators because larvae digest rapidly and quickly become unidentifiable. My results suggest only a 50% probability of confirming the presence of larval fish prey during stomach content analyses after as little as 2-4 hours post-ingestion, and a 95% probability after 1-2 hours depending on water temperature and larval fish size. Similar low detection rates have been reported for larval capelin *Mallotus villosus* (50% probability of recognition after 2h 19min for 19.9 mm larvae; Hallfredsson et al. 2007) and larval cod (recognizable until 15-90 min post-ingestion for 4-10 mm larvae at 6-15°C; Folkvord 1993).

My results are consistent with expectations and previous conclusions regarding the effects of prey size, temperature, and time on digestion (Windell et al. 1976; Folkvord 1993; Knutsen and Salvanes 1999; Vinagre et al. 2007; Yamamoto et al. 2007). Large larvae were expected to digest slower then small larvae because, as fish grow, 1) surface area per unit mass decreases, resulting in reduced exposure to digestive enzymes, and 2) scale and hard structure development progresses, providing greater resistance to breakdown. Fish scales provide resistance to digestion similar to chitinized exoskeletons, which delay digestion of aquatic invertebrates and zooplankton (Hess and Rainwater 1939; Kionka and Windell 1972; Hallfredsson et al. 2007). I expected digestion rate to be higher at warmer temperatures because of increases in metabolic rate and enzyme activity (Evans 1984; Clarke and Johnston 1999; Galarowicz and Wahl 2003).

Rate of digestion did not differ by prey species (guppy vs. rainbow trout) likely because early larvae are similar (i.e., small, soft-bodied) regardless of species. Digestion

rates similar to what I observed were reported for capelin and cod of sizes similar to my larval prey (Folkvord 1993; Hallfredsson et al. 2007), further supporting the notion of a prey species-independent rate of digestion. Yellow perch digested slower then guppies and rainbow trout, but this was likely because yellow perch were larger and further developed, not because of species-dependent effects; the average mass of yellow perch prey (0.179 g) was almost four times greater than guppy and rainbow trout prey (0.045 g) and yellow perch were beginning to develop scales. Additionally, rate of digestion did not differ by predator species (bluegill sunfish vs. yellow perch) likely because of similar feeding mode and physiology (e.g., Fish 1960; Hofer and Schiemer 1981; Hidalgo et al. 1999). In contrast, digestion rates differed among species in gar *Lepisosteus platyrhlncus*, warmouth *Chaeaobryttus gulosus*, and largemouth bass *Micropterus salmoides*, but such differences were attributed to behavioural differences among predators (Hunt 1960). My digestion rate estimates should therefore be comparable across most species of early stage larval fishes being digested by predators with feeding behaviours and physiology similar to bluegill sunfish and yellow perch. The quantitative tools I used - multiple regression and logistic models - will enable researchers to assess the likelihood of detecting larvae in stomach contents when water temperature and prey size are known for a wide range of temperate prey and predator species and systems.

The rapid digestion of larval fishes across a range of sizes and temperatures will pose challenges for researchers hoping to quantify larval predation rates in natural systems. This will hamper testing the hypothesis that predation mortality of young fishes is a significant factor affecting recruitment (Hjort 1914, 1926; Brandt et al 1987; Houde 1989; Tsou and Collie 2001; Munk 2002). Conventional stomach content analysis

techniques are expected to be ineffective for quantifying larval mortality, so alternative approaches must be considered. Traditional diet analyses techniques rely on morphological characters to identify larvae and often use predator capture techniques, such as gillnets, that allow digestion to progress long after predators are captured. Alternative approaches for quantifying larval mortality may involve using bioenergetics models to estimate mortality rates (e.g., Hartman and Margraf 1993), genetic techniques to identifying highly digested stomach contents (e.g., Rosel and Kocher 2002), and predator capture techniques that minimize digestion time (e.g., bottom trawls, electrofishing, short-set gillnets).

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3.0 Influence of River Plumes on Predator Feeding and Diet in Lake Erie

To be submitted to
Canadian Journal of Fisheries and Aquatic Sciences

3.1 Introduction

Natural and anthropogenic factors create spatial and temporal heterogeneity in aquatic ecosystems that can greatly influence fish population dynamics. These factors vary in magnitude and duration; examples include climate change, storm events, eutrophication, and pollution. Changes in the physical, chemical, and biological attributes of aquatic ecosystems can influence survival and growth rates of resident organisms, in part by impacting foraging behaviours, feeding efficiency, and food availability. Unfortunately, it is difficult to study the events that drive environmental variability because they are often short-lived and difficult to detect and predict.

Conversely, tributaries and their associated plumes are relatively straightforward to study because they are persistent and predictable. Tributaries create spatial variability in lake and ocean ecosystems that can have significant impacts on resident organisms and communities. Such interactions have been characterized in many marine systems. For example, in the Gulf of Mexico, concentrations of ichthyoplankton, chlorophyll a, and macrozooplankton are all elevated in waters associated with the Mississippi River discharge plume (Grimes and Finucane 1991). Additionally, areas of increased turbidity due to river discharge are present in Chesapeake Bay and the Gulf of St. Lawrence (Dauvin and Dodson 1990; Sirois and Dodson 2000; North and Houde 2001; Roman et al. 2001). Many of these studies focused on evaluating the effects of river plumes on larval fishes in marine systems, with expectations that inputs of nutrients and sediments

will improve larval fish survival by improving prey availability and reducing predation risk (Dauvin and Dodson 1990; Grimes and Finucane 1991; Sirois and Dodson 2000; North and Houde 2001; Roman et al. 2001). In freshwater systems, the ecological impacts of river plumes remain largely unknown, but effects similar to those observed in coastal marine systems may be reasonably expected.

In Lake Erie, two river plumes are created in the lake's western basin by discharge from the Maumee and Detroit Rivers (Figure 3.1). The physical, chemical, and biological conditions of the Maumee and Detroit Rivers are distinct and driven largely by watershed-scale influences. The Maumee River is rich in nutrients and sediments, derived from its largely agricultural watershed, whereas the Detroit River is comparatively clear and nutrient poor because it is fed by water from the upper Great Lakes (Herbert 1959; Richards et al. 2001, 2002). Maumee River discharge is known to create inter-annual variation in Lake Erie's total and west basin phosphorous levels, is positively correlated with copepod zooplankton abundance during spring-early summer, and increases turbidity through inputs of suspended materials (S. A. Ludsin, The Ohio State University, unpublished data).

Foraging behaviours of fishes in western Lake Erie are expected to be influenced by habitat differences created by the Maumee and Detroit Rivers. Yellow perch *Perca flavescens,* walleye *Sander vitreus*, white bass *Morone chrysops*, and white perch *Morone americana* are all common fishes of western Lake Erie that support important recreational and commercial fisheries (Hushak et al. 1988; YPTG 2007; OMNR 2008). They also play major roles in the food web and collectively represent numerous trophic guilds, including planktivore / omnivore (white perch), omnivore / benthivore (yellow

perch), omnivore / piscivore (white bass), and piscivore (walleye) (Ludsin et al. 2001; Zhu et al. 2008). An analysis of how plume dynamics influence foraging behaviours of these fishes will provide a better understanding of the role tributary plumes play in large freshwater lakes, as will as enable managers to more effectively evaluate growth and biomass production of important Lake Erie fisheries.

I examined stomach contents of white perch, yellow perch, white bass, and walleye collected from the Detroit and Maumee River plumes in western Lake Erie as part of a larger study of river-borne water mass influences on fish production. My objectives were to compare diets among species between plumes and years and to relate any differences to tributary plume influences. Particular interests were to compare consumption of zooplankton and forage fishes, given that, in the Maumee plume, zooplankton abundance was expected to be higher and enhanced turbidity was expected to reduce predation risk of forage fishes.

3.2 Methods

Fishes were collected for diet analysis in the Maumee and Detroit plumes (Figure 3.1) using a bottom trawl (7.6-m semi-balloon design, 13-mm stretched-mesh cod-end liner). Samples were collected throughout 24-hr periods in both plumes on: 5-7 June 2006, 12-14 June 2006, 21-23 May 2007, and 6-8 June 2007. A total of 52 trawls were conducted with an average tow time of 18 minutes (range: 5-31 minutes) at a boat speed of about 3-4 knots. Upon retrieval of the trawl, fishes were immediately euthanised using clove oil, stomachs were injected with 100% ethanol to halt digestion, and whole fish

were frozen for future analysis. In the lab, each fish was thawed, measured (total length, mm), weighed (g), sexed, and stomachs were removed for diet analysis.

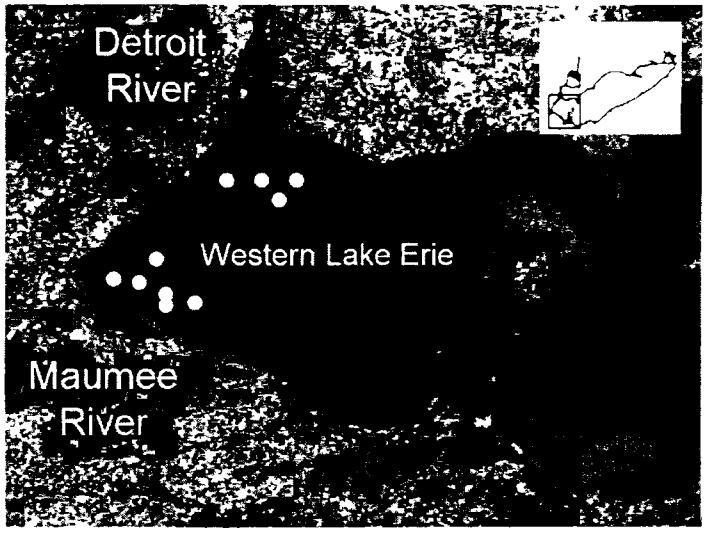


Figure 3.1 Map of western Lake Erie showing locations of fish collection sites within the Maumee and Detroit River plumes. Fishes were collected using bottom trawls in 2006 and 2007.

Diet analyses involved separating prey items into major taxonomic groups, under a dissecting microscope. Individual prey items were counted and the mass of each prey taxa were determined using volumetric displacement assuming a density of 1 g / ml. When counting of individual prey was not feasible (due to large numbers of small prey, e.g., zooplankton) or highly digested prey (e.g., pieces of dreissenid shell), counts were estimated by multiplying the mass of all individuals per stomach by an average number of prey per gram (averages were determined using prey with a known mass & count). No mass corrections were applied for partially digested prey. Stomachs that were completely empty or contained only unidentifiable matter were excluded from all diet summaries.

For all analyses, predator diets were grouped by plume, predator species, and

predator size for each year. White perch, yellow perch, and white bass were assigned to two size categories (small and large) based on length frequency distributions (Figure 3.2), to account for possible ontogenetic diet shifts. Walleye were not broken into size groupings due to small sample sizes and because all individuals were overwhelmingly piscivorous. Predators were collected throughout the 24 hour period in each plume in both years (Figure 3.3) and therefore time of day was not used as a covariate in the analyses. Diets were summarized as mean percent composition by mass, mean percent composition by number, and frequency of occurrence (Bowen 1996) for each predator group and differences between plumes were evaluated for each size group and year.

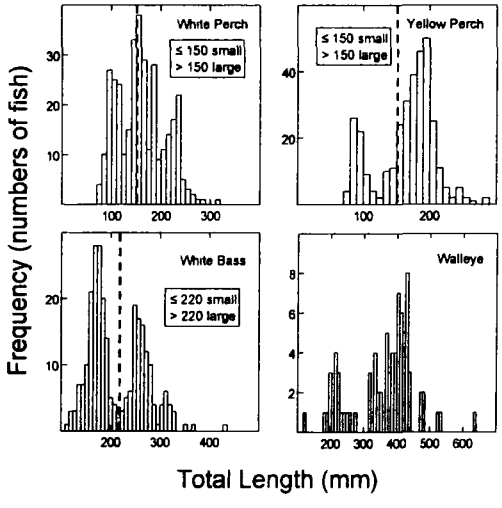
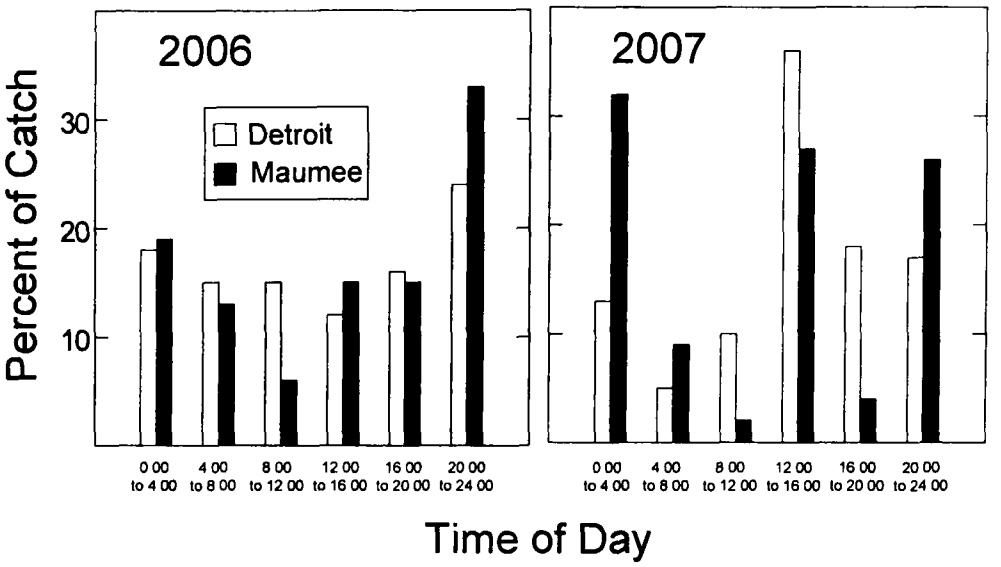


Figure 3.2 Length distributions, by species, of fishes collected in 2006 and 2007 from the Maumee and Detroit River plumes for stomach content analyses. Numbers within each figure (e.g., ≤ 150 small), and dashed lines, indicate the size groupings (total length, mm) that were assigned to each species to account for ontogenetic diet shifts when evaluating diets. Walleye were not broken into size groups.

Figure 3.3 Summary of catch presented as a percentage of the total catch for each time period, plume, and year.



A Kolmogorov-Smirnov test was used to evaluate differences in percent composition by weight, percent composition by number, and frequency of occurrence by comparing the cumulative distributions of dietary proportions between plumes.

Schoener's (1970) index

$$\alpha = 1 - 0.5 \sum_i |p_{x,i} - p_{y,i}|$$

was used to compare the degree of diet overlap between plumes using values of percent composition by weight, where $P_{x,i}$ is the proportion of food category *i* in diet of species *x*. Index values (α) range from 0.0 (no overlap) to 1.0 (complete overlap), with values < 0.6 representing significant differences between diets (Zaret and Rand 1971, Mathur 1977).

The G-statistic (Crow 1982)

$$G = 2 * \sum X_{i,j} \ln \frac{X_{i,j}}{(X_i X_j)/N}$$

was used to compare proportions of diet items between plumes using values of percent composition by number, where X_{ij} is the number of prey of the i^{th} prey taxon consumed by predators in the j^{th} predator category, X_i is the total number of prey of the i^{th} prey category eaten by all predators, X_j is the total number of prey eaten by predators in the j^{th} predator category, and N is the total number of prey eaten by all predators. To evaluate differences in consumption of specific prey taxa (by mass and number) and absolute ration (i.e., g prey / g predator), two-sample Kolmogorov-Smirnov tests were computed in SYSTAT version 11.0 using continuous datasets. All statistical significance was assigned at $p < 0.05$.

3.3 Results

In total, I examined 548 white perch, 421 yellow perch, 369 white bass, and 152 walleye stomachs. These four species represented 89% of the large bodied fish (i.e., not forage fish) collected in the trawls (Table 1.1). Comparable numbers of empty stomachs were found in each river plume for each fish species and there were few differences in absolute ration (g prey / g predator) (Table 3.1). Average diet compositions (i.e., percent composition by mass, percent composition by number, and frequency of occurrence) were almost always significantly different between plumes (Table 3.2).

Table 3.1 Summary statistics of sample size, percent empty stomachs, and ration for white perch, yellow perch, white bass, and walleye in the Maumee and Detroit River plumes of western Lake Erie during 2006 and 2007. A two-sample Kolmogorov-Smirnov test was calculated to compare ration between plumes. Significant differences are highlighted (♦) and were assigned as $p < 0.05$.

Predator	Size	Year	Number of Stomachs		Percent Empty		Ration (g prey / g predator)		
			Maumee	Detroit	Maumee	Detroit	Maumee	Detroit	p
white perch	small	2006	79	55	14	31	0 019	0 012	0 089
white perch	small	2007	27	41	48	20	0 005	0 009	0 059
white perch	large	2006	42	95	24	49	0 025	0 010	0 002♦
white perch	large	2007	92	117	55	43	0 003	0 006	0 003♦
yellow perch	small	2006	13	47	15	28	0 011	0 015	0 594
yellow perch	small	2007	7	47	57	11	0 008	0 016	0 863
yellow perch	large	2006	124	42	16	36	0 007	0 007	0 144
yellow perch	large	2007	84	57	24	19	0 007	0 008	0 142
white bass	small	2006	66	122	11	24	0 018	0 017	0 029♦
white bass	small	2007	1	3	100	33	N/A	0 007	N/A
white bass	large	2006	11	12	9	17	0 011	0 033	0 030♦
white bass	large	2007	29	125	45	39	0 014	0 008	0 965
walleye	all fish	2006	36	89	53	44	0 008	0 016	0 089
walleye	all fish	2007	14	13	43	38	0 005	0 007	0 187

Table 3.2 Statistics for intraspecific comparisons of diet between Maumee and Detroit River plume white perch, yellow perch, white bass, and walleye from western Lake Erie collected during 2006 and 2007. Comparisons were made between fishes of the same size group (small, large) and year. A Kolmogorov-Smirnov test was used to make comparisons of diets summarized as percent composition by mass, percent composition by number, and frequency of occurrence, Schoener's index of diet overlap was used to compare percent composition by mass, and the G-statistic was used to compare percent composition by number. Abbreviations are defined as follows: df = degrees of freedom, α = the Schoener's index value, which ranges form 0.0 (no diet overlap) to 1.0 (complete diet overlap), G = the G statistic value, used to assign significance with a chi-square distribution, ♦ indicates a significant difference between diets (i.e., $p < 0.05$ or $\alpha < 0.6$).

Comparison Maumee vs Detroit			Kolmogorov-Smirnov						Schoener's Index	G-Statistic		
			Volume		Number		Frequency			G	df	p
Predator	Size	Year	df	p	df	p	df	p	α			
white perch	small	2006	9	< 0 001♦	9	< 0 001♦	9	< 0 001♦	0 34♦	36 32	9	< 0 001♦
white perch	small	2007	8	< 0 001♦	8	< 0 001♦	8	< 0 001♦	0 56♦	10 96	8	< 0 25
white perch	large	2006	8	< 0 001♦	8	0 75	8	< 0 025♦	0 65	8 05	8	< 0 50
white perch	large	2007	10	< 0 001♦	10	0 975	10	< 0 001♦	0 59♦	3 18	10	< 0 99
yellow perch	small	2006	7	< 0 001♦	7	< 0 001♦	7	< 0 001♦	0 09♦	48 68	7	< 0 001♦
yellow perch	small	2007	6	< 0 005♦	6	< 0 001♦	6	< 0 001♦	0 36♦	10 40	6	< 0 25
yellow perch	large	2006	8	< 0 001♦	8	< 0 001♦	8	< 0 001♦	0 24♦	-10 39	8	1
yellow perch	large	2007	8	< 0 001♦	8	< 0 001♦	8	< 0 001♦	0 50♦	7 37	8	< 0 50
white bass	small	2006	8	< 0 001♦	8	0 10	8	< 0 001♦	0 23♦	7 18	8	< 0 75
white bass	small	2007	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
white bass	large	2006	3	< 0 001♦	3	< 0 001♦	3	< 0 001♦	0 40♦	33 11	3	< 0 001♦
white bass	large	2007	5	< 0 005♦	5	< 0 001♦	5	< 0 01♦	0 67	17 03	5	< 0 005♦
walleye	all sizes	2006	3	< 0 001♦	3	< 0 001♦	3	< 0 001♦	0 57♦	5 12	3	< 0 25
walleye	all sizes	2007	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

White Perch

White perch consumed mostly aquatic insects and zooplankton (Figures 3.4-3.6; Tables 3.3, 3.4). Diets were similar across years; however in 2006, Maumee plume white perch consumed more zooplankton and in 2007 Maumee plume white perch consumed more dreissenids.

Yellow Perch

Yellow perch consumed mostly aquatic insects and dreissenids (Figures 3.4-3.6; Tables 3.3, 3.4). Diets were similar across years, however in 2006, Maumee plume yellow perch

consumed more zooplankton. Maumee plume yellow perch generally consumed more dreissenids.

White Bass

White bass consumed mostly fish but aquatic insects and zooplankton were also taken in small amounts (Figures 3.4-3.6; Tables 3.3, 3.4). Diets were similar between years; however small sample sizes for small white bass in 2007 prevented statistical comparisons. Maumee plume white bass generally consumed more zooplankton while Detroit plume white bass generally consumed more fish.

Walleye

Walleye consumed fish almost exclusively; however, ephemeroptera were also consumed in the Maumee plume in 2006 (Figures 3.4-3.6; Tables 3.3, 3.4).

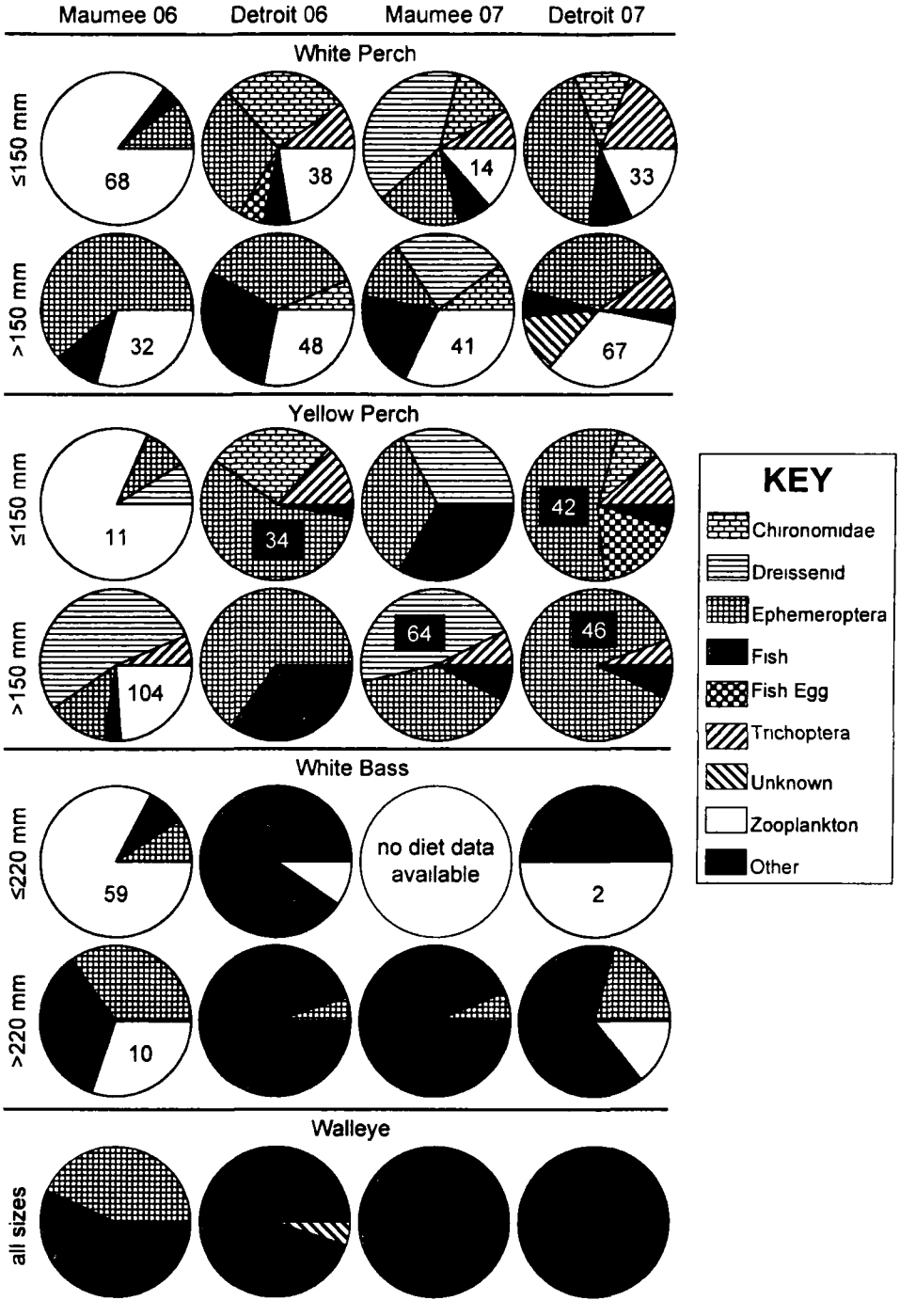


Figure 3.4 Diets summarized as mean percent composition by mass (g) for small (≤ 150 mm) and large (> 150 mm) white perch, yellow perch, white bass, and walleye from the Maumee and Detroit River plumes in western Lake Erie during 2006 and 2007. Individual prey taxa that made up ≤ 5% of the mean volume were summed and labelled as "other" Sample size is overlaid on each figure.

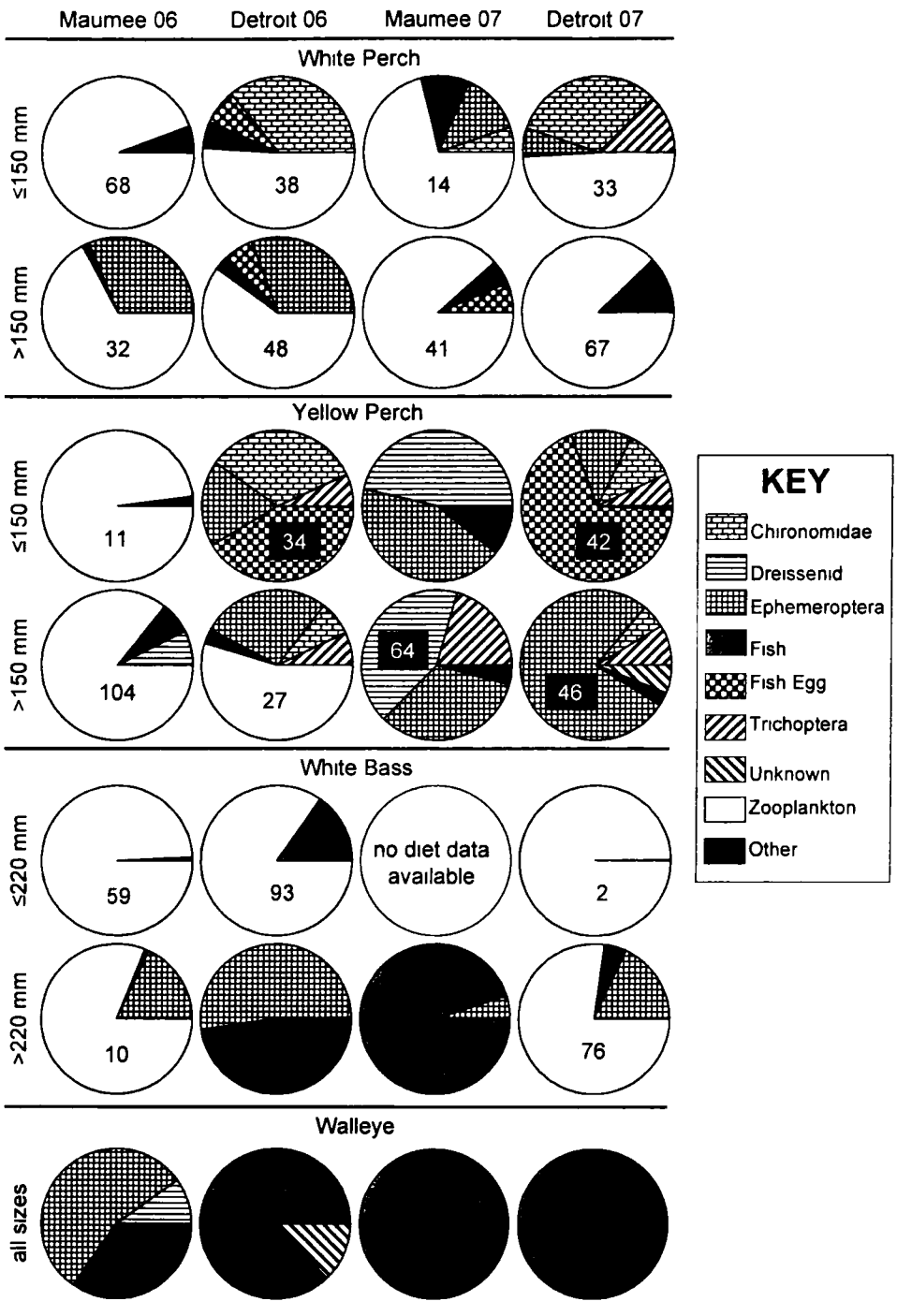


Figure 3.5 Diets summarized as mean percent composition by number for small (≤ 150 mm) and large (> 150 mm) white perch, yellow perch, white bass, and walleye from the Maumee and Detroit River plumes in western Lake Erie during 2006 and 2007. Individual prey taxa that made up ≤ 5% of the mean number were summed and labelled as "other" Sample size is overlaid on each figure.

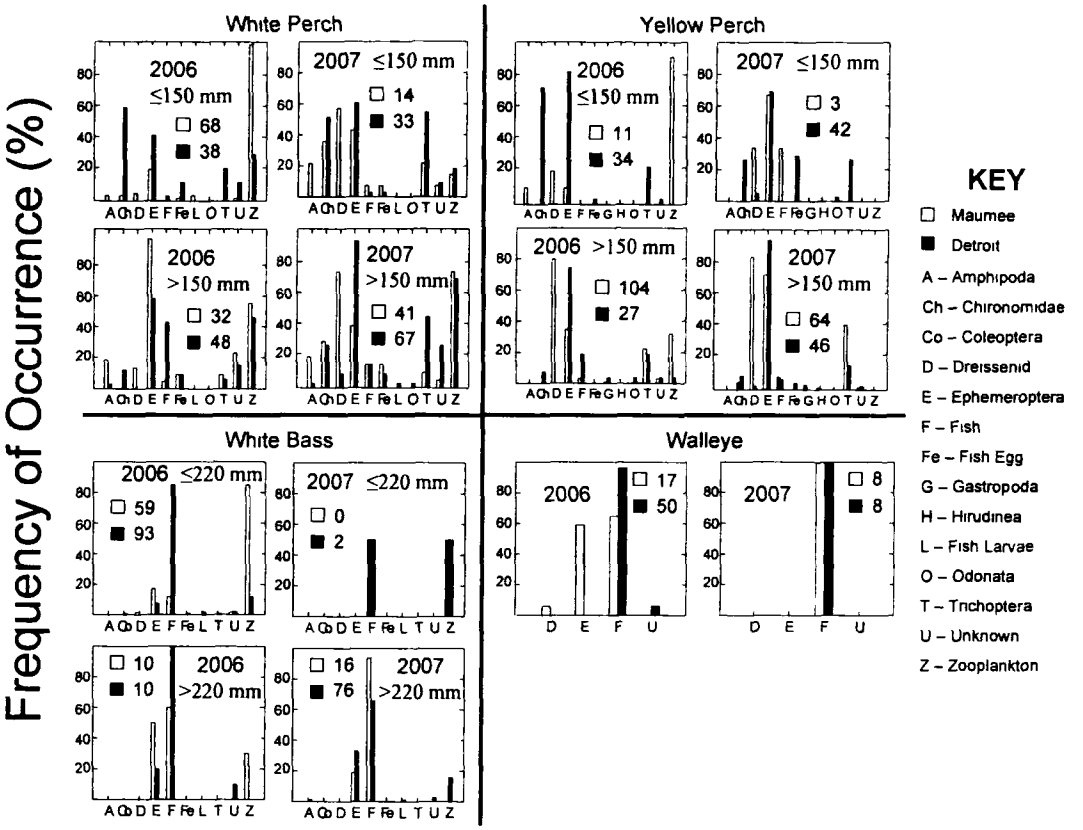


Figure 3.6 Diets summarized as frequency of occurrence (%) for small (≤ 150 mm) and large (> 150 mm) white perch, yellow perch, white bass, and walleye from the Maumee and Detroit River plumes in western Lake Erie during 2006 and 2007. Sample size is overlaid on each figure.

Table 3.3 Statistics for intraspecific comparisons of individual taxa consumption (g) between Maumee and Detroit River plume white perch, yellow perch, white bass, and walleye from western Lake Erie during 2006 and 2007. A two sample Kolmogorov-Smirnov test was used to make comparisons between fishes of the same size group (small, large) and year. Average consumptions (g) for Maumee (M) and Detroit (D) plume fishes are listed to facilitate interpretation of results. Significant differences are highlighted (♦) and were assigned as $p < 0.05$.

Predator	Size	Year	Zooplankton			Fish			Dreissenid			Ephemeroptera			Chironomid & Trichoptera		
			M (g)	D (g)	p	M (g)	D (g)	p	M (g)	D (g)	p	M (g)	D (g)	p	M (g)	D (g)	p
white perch	small	2006	0 28	0 05	0 000♦	0 00	0 04	0 000♦	0 00	0 00	1	0 03	0 04	0 392	0 00	0 04	0 000♦
white perch	small	2007	0 06	0 08	1	0 03	0 04	1	0 07	0 00	0 003♦	0 02	0 14	0 247	0 02	0 09	0 585
white perch	large	2006	0 29	0 09	0 126	0 01	0 59	1	0 00	0 00	0 000♦	2 77	0 69	0 000♦	0 01	0 01	1
white perch	large	2007	0 11	0 28	0 213	0 21	0 05	1	0 04	0 00	0 009♦	0 03	0 21	0 076	0 02	0 05	1
yellow perch	small	2006	0 13	0 00	0 000♦	0 00	0 00	1	0 02	0 00	0 000♦	0 01	0 09	0 000♦	0 00	0 05	0 000♦
yellow perch	small	2007	0 00	0 00	1	0 10	0 00	0 944	0 17	0 01	0 944	0 04	0 08	1	0 00	0 02	0 908
yellow perch	large	2006	0 10	0 02	0 06	0 06	0 34	0 628	0 27	0 00	0 000♦	0 06	0 21	0 001♦	0 03	0 02	1
yellow perch	large	2007	0 00	0 00	1	0 10	0 21	1	0 35	0 00	0 000♦	0 20	0 38	0 002♦	0 03	0 02	0 161
white bass	small	2006	0 67	0 04	0 000♦	0 12	1 05	0 000♦	0 00	0 00	0 000♦	0 08	0 03	0 907	0 00	0 00	1
white bass	small	2007	N/A	0 60	N/A	N/A	0 20	N/A	N/A	0 00	N/A	N/A	0 00	N/A	N/A	0 00	N/A
white bass	large	2006	0 39	0 00	0 664	1 14	6 20	0 000♦	0 00	0 00	1	2 65	0 25	0 664	0 00	0 00	1
white bass	large	2007	0 00	0 11	0 853	4 16	1 42	0 020♦	0 00	0 00	1	0 03	0 30	0 524	0 00	0 00	1
walleye	all	2006	0 00	0 00	1	3 35	6 46	0 028♦	0 05	0 00	0 000♦	0 40	0 00	0 000♦	0 00	0 00	1
walleye	all	2007	0 00	0 00	1	1 34	5 06	0 187	0 00	0 00	1	0 00	0 00	1	0 00	0 00	1

Table 3.4 Statistics for intraspecific comparisons of individual taxa consumption (number of prey) between Maumee and Detroit River plume white perch, yellow perch, white bass, and walleye from western Lake Erie during 2006 and 2007. A two sample Kolmogorov-Smirnov test was calculated to make comparisons between fishes of the same size group (small, large) and year. Average consumption (#) for Maumee (M) and Detroit (D) plume fishes are listed to facilitate interpretation of results. Significant differences are highlighted (♦) and were assigned as $p < 0.05$.

Predator	Size	Year	Zooplankton			Fish			Dreissenid			Ephemeroptera			Chironomid & Trichoptera		
			M (#)	D (#)	p	M (#)	D (#)	p	M (#)	D (#)	p	M (#)	D (#)	p	M (#)	D (#)	p
white perch	small	2006	71 91	13 62	0 000♦	0 00	0 05	0 000♦	0 04	0 00	1	0 40	0 46	0 392	0 03	10 39	0 000♦
white perch	small	2007	14 72	21 851		0 07	0 03	1	0 53	0 00	0 003♦	2 71	2 36	0 489	2 03	20 01	0 126
white perch	large	2006	75 66	23 13	0 126	0 03	0 42	0 126	0 09	0 00	0 000♦	35 25	11 83	0 001♦	0 54	0 38	1
white perch	large	2007	28 20	65 73	0 213	0 22	0 10	1	0 42	0 04	0 009♦	0 36	3 49	0 076	0 22	1 73	0 537
yellow perch	small	2006	33 48	0 00	0 000♦	0 00	0 00	1	0 25	0 00	0 000♦	0 09	1 98	0 000♦	0 00	4 32	0 000♦
yellow perch	small	2007	0 00	0 00	1	0 33	0 00	0 944	1 44	0 07	0 944	1 33	1 38	1	0 00	1 88	0 863
yellow perch	large	2006	26 67	5 72	0 06	0 05	0 22	0 628	2 31	0 00	0 000♦	0 57	2 89	0 002♦	1 46	1 52	1
yellow perch	large	2007	0 00	0 00	1	0 09	0 07	1	2 69	0 02	0 000♦	2 12	7 35	0 000♦	1 43	1 33	0 161
white bass	small	2006	173 74	9 42	0 000♦	0 17	1 19	0 000♦	0 02	0 00	0 000♦	1 04	0 42	0 907	0 00	0 01	1
white bass	small	2007	N/A	154 53	N/A	N/A	0 34	N/A	N/A	0 00	N/A	N/A	0 00	N/A	N/A	0 00	N/A
white bass	large	2006	100 44	0 00	0 664	1 20	3 90	0 030♦	0 00	0 00	1	22 30	4 40	0 664	0 00	0 00	1
white bass	large	2007	0 00	28 80	0 853	3 54	1 54	0 023♦	0 00	0 00	1	0 19	6 81	0 333	0 00	0 00	1
walleye	all	2006	0 00	0 00	1	1 41	3 28	0 000♦	0 41	0 00	0 000♦	2 26	0 00	0 000♦	0 00	0 00	1
walleye	all	2007	0 00	0 00	1	1 50	2 58	0 906	0 00	0 00	1	0 00	0 00	1	0 00	0 00	1

3.4 Discussion

Analysis of 1,490 stomachs of fishes from two tributary plumes in the western basin of Lake Erie revealed significant differences in diet composition of predators from each plume. Differences in nutrient and sediment concentrations between plumes (Table 3.5) coupled with their expected effects on prey availability and visual acuity provide plausible mechanisms for the differences. My results demonstrate the importance of watershed-scale influences on fish population dynamics in large lakes and are unique because I evaluated the effects of two distinct river plumes on feeding behaviours of fishes in a single freshwater lake (i.e., previous studies have focused on marine river plumes and variation in diets between different lakes; e.g., Dauvin and Dodson 1990; Hayes and Rutledge 1991).

Table 3.5 Summary statistics for average physio-chemical properties of the Maumee and Detroit River plumes of western Lake Erie collected during spring-summer of 2006 and 2007. Total suspended materials (TSM), total phosphorous (TP), total dissolved phosphorous (TDP), and chlorophyll (CHL) values were derived from analyses of water samples (T. H. Johengen, University of Michigan, unpublished data).

Measurement	Year: 2006		Year: 2007	
	Maumee	Detroit	Maumee	Detroit
TSM (mg/L)	16.7	5.3	53.0	6.8
TP (ug/L)	69.7	13.8	148.1	14.6
TDP (ug/L)	33.1	3.7	106.2	13.6
CHL (ug/L)	11.0	2.3	7.1	1.4

Understanding variation in feeding behaviours between fishes can be difficult, because foraging behaviours are influenced by many intrinsic (e.g., gape, swimming capacity, visual acuity) and extrinsic (e.g., turbidity, temperature, presence of

macrophytes) factors, including resource availability and habitat. Foraging behaviour and prey consumption also vary spatially, temporally, and by species. Of the fishes I examined, walleye and white bass are typically deemed piscivorous, while yellow perch and white perch are more omnivorous (Scott and Crossman 1973). Each of these species undergo ontogenetic diet shifts; as juveniles they are limited by gape to smaller prey (i.e., phytoplankton and zooplankton) and they make a progression to larger prey (i.e., invertebrates and fish) as they grow (Heath and Roff 1996).

In Western Lake Erie, diet differences between Maumee and Detroit River plume fishes are likely being driven by prey availability and abundance. Zooplankton density was over 6 times greater, and individual zooplankton were over 2 times larger, in the Maumee plume compared to the Detroit plume in 2006 (Table 6) and almost all Maumee plume predators consumed more zooplankton (ration and proportion). Between years, zooplankton densities decreased in the Maumee plume but increased in the Detroit plume, resulting in similar densities between plumes in 2007 (Table 3.6). Likewise, consumption of zooplankton by Maumee plume fishes decreased in 2007 whereas consumption of zooplankton by Detroit plume fishes increased slightly (ration and proportion). Abundance of preferred soft-rayed forage fishes (i.e., shiners, rainbow smelt, trout-perch, round goby) was greater in the Detroit plume compared to the Maumee plume in 2006 and 2007 (Table 3.6) and predators consumed more fish (ration and proportion) in the Detroit plume. Density of *Dreissena bugensis* were estimated to be at least one order of magnitude greater in the Maumee plume compared to the Detroit plume in 2004 (Table 3.6). Consistent with these estimates, dreissenids were important (proportion and frequency of occurrence) prey of yellow perch and white perch in the

Maumee plume, while almost no dreissenids were consumed in the Detroit plume. Fishes in the Maumee and Detroit plumes appear to be choosing prey that are abundant, a result that is consistent with optimal foraging (Ricklefs 2007).

Table 3.6 Summary statistics for abundance of forage fish (i.e., shiners, rainbow smelt, trout-perch, and round goby) (M. Bur, United States Geological Survey, unpublished data; E. Weimer, Ohio Department of Natural Resources, unpublished data), large bodied zooplankton (i.e., adult cladocera and copepoda) (T.B. Johnson, Ontario Ministry of Natural Resources, unpublished data), and *Dreissena bugensis* (J. H. Ciborowski, University of Windsor, personal communication) within the Maumee and Detroit River plumes of western Lake Erie.

Prey Taxon & Unit of Measurement	**Year: 2006**		**Year: 2007**	
	Maumee	**Detroit**	**Maumee**	**Detroit**
Forage fish biomass (kg/ha)	0.0254	0.2826	0.0013	0.6066
Zooplankton density (#/m^3)	519	84	256	248
Individual zooplankton size (ug)	3.6	1.45	3.36	5.63
Zooplankton biomass (g/m^3)	1868	122	861	1393
Prey taxon & unit of measurement	**Year: 2004**			
	Maumee		**Detroit**	
Dreissena bugensis density (#/m^2)	1,000 – 10,000		100 – 1,000	

Although prey availability provides the simplest and likely best explanation for variation in diet between Maumee and Detroit plume fishes, differences in turbidity between plumes (Table 3.5) may also be influencing prey consumption. Turbidity impedes a fish's ability to see objects that are far away more then objects that are nearby (Duntley 1962). Turbidity should therefore reduce encounter rates with large prey which are usually detected at greater distances than small prey which are visible at short distances in clear water (Robertis et al. 2003). Since zooplankton and dreissenids were consumed more in the turbid Maumee plume, while fish were more important in the relatively clear Detroit plume, turbidity may be contributing to predator's choice in the

Maumee plume to consume smaller and more sedentary prey, rather than energetically superior forage fish which may be harder to detect.

My results show consistent spatial variability in prey consumption patterns across the western basin of Lake Erie. I suggest that these differences are being driven by inputs of nutrients and sediments from tributary river plumes. My findings support the need for watershed-scale management practices by demonstrating that biological and physico-chemical attributes can simultaneously produce distinct patterns in productivity and feeding behaviours. Knowing that fundamental differences in predator-prey interactions are being driven by watershed-scale effects is an important step towards developing watershed-based approaches to fisheries management in large lakes.

3.5 References

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4.0 General Conclusion

My research addressed several ecological questions pertinent to understanding larger concepts involving predator-prey interactions in aquatic systems. I used laboratory experiments to quantify the digestion of larval fishes and a field study to explore the effects of river discharge on prey consumption. Collectively, my results exemplify the difficulties associated with quantifying larval fish predation mortality and the importance of watershed-scale interactions on foraging behaviours.

4.1 Thesis Summary

Predator-prey interactions play a major role in structuring fish populations, largely by influencing survival and growth. For example, predation mortality occurring when fishes are young (i.e., larval stages) are thought to greatly influence recruitment (Hjort 1914, 1926; Anderson 1988; Govoni 2005). Rates of predation mortality are likely high for larval fishes, due to their small size and undeveloped sensory and motor skills, yet most diets studies (including mine; Chapter 1) have been unable to identify larval prey in stomach contents of predatory fishes. As a result, estimates of larval predation mortality based on quantitative, empirical evidence are generally lacking. Rapid digestion of small, soft bodied larval prey is a possible reason for this shortcoming. I evaluated the digestion of larval fishes (Chapter 2) and confirmed that indeed, larval fishes digest rapidly, quickly loose morphological characters (i.e., fins, head), and the probability of identifying a larval fish during stomach content analyses is low, even after short periods of digestion time.

Energy-pathways are also an important component of predator-prey interactions. The type and amount of prey consumed by fishes (i.e., energy intake) largely determines survival and growth and can be influenced by many natural and anthropogenic factors (e.g., prey availability, prey size and predator gape limitation, , prey handling time, competition, eutrophication, pollution, etc.). I evaluated prey consumption by fishes in western Lake Erie (Chapter 3) and found significant differences in diets colleted from the Maumee and Detroit River plumes. An analysis of prey assemblages in each river plume revealed differences in abundance that were consistent with predator diets. Differences in nutrient and sediment concentrations of the Maumee and Detroit River plumes, created by watershed influences, provide some explanation for these differences.

4.2 Research Considerations & Suggestions

My digestion rate experiments and diet study were simplifications of natural conditions necessary to facilitate testing of specific hypotheses. My digestion rate experiments were conducted by feeding a single fish larva to a fasted predator. In nature, prey consumption is much more complex. Many fishes are opportunistic feeders, and thus eat a variety of prey types and multiple meals throughout a day. A mixed diet consisting of easily digestible, soft bodied prey (e.g., larval fishes, worms), hard bodied prey that resist digestion (e.g., insects with exoskeletons, forage fishes with scales, mussels with shells), and multiple meals, consumed at varying time intervals, will certainly digest differently then a single prey, single meal diet. Additionally, I calculated degree of digestion using wet weights, which likely introduced error since experimental prey were very small. For my field study, I compared stomach contents of fishes

collected during two weeks in both 2006 and 2007 This sampling design enabled me to make comparisons using only a very narrow timeframe when larval fish are present but may not reflect feeding behaviours at other times of the year when relative prey availability and predator behaviour may be different.

To build on my results, future studies evaluating the digestion of larval fishes could use mixed prey, multiple meal experiments to evaluate the effects of diet type and ration size on rate of digestion. Studies evaluating diets of western Lake Erie fishes should be conducted on both spatial and temporal scales, to see how seasonal changes in plume dynamics and prey availability influence prey consumption. Research that addresses these suggestions will likely be challenging, largely because laboratory feeding studies and field diet studies are both expensive and labour intensive.

4.3 Ongoing Research

Ongoing analyses related to the larger project objectives are using both molecular genetic techniques and bioenergetics modeling to further analyse the stomach content samples collected for this thesis. Molecular genetic techniques will be used to identify prey items that I deemed 'unidentifiable' using morphological techniques (L. Carreon, University of Windsor, personal communication). Additionally, archived stomach contents from digestion rate experiments will be used as 'known samples' to test molecular identification techniques and evaluate how long genetic markers remain viable during digestion. Bioenergetics will be used to evaluate the effects of diet and water temperature on growth rates of Maumee and Detroit River plume fishes and to calculate estimates for larval yellow perch mortality rates due to predation.

4.4 Importance

My research efforts are both important and novel. My laboratory feeding experiments help explain why most diet studies have been unable to quantify predation mortality of larval fishes and is the first study to describe the morphological breakdown of larval fishes during digestion. My field diet study demonstrates the importance of watershed-scale interactions on fish population dynamics and is unique because it evaluated river plumes in a freshwater system (as opposed to marine systems; e.g., Dauvin and Dodson 1990; Grimes and Finucane 1991; Sirois and Dodson 2000; North and Houde 2001; Roman et al. 2001) and showed diet variability on a spatial scale within a single basin, of a single lake (opposed to different lakes; e.g., Hayes and Rutledge 1991).

4.5 Management Implications

The call for ecosystem-scale fisheries management has been strong in recent years (GLFC 2008). Traditional fishery management approaches based on single species assessments are inadequate, simply because they fail to recognize trophic and watershed-scale interactions that simultaneously influence population dynamics. In Lake Erie, yellow perch, walleye, white bass, and white perch are dominant fishes in a complex food web and they each support important recreational and commercial fisheries (Hushak et al. 1988; YPTG 2007; OMNR 2008). My research will allow Lake Erie managers to better understand predator-prey interactions of these species, and the effects of watersheds, through tributary inputs, on prey consumption. This will enable managers to better

anticipate how watershed-scale changes (e.g., restricted fertilizer use, implementation of agricultural practices that minimize erosion, dredging of shipping channels, precipitation events, etc.) might influence food-web interactions and ultimately fishery production.

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