

The ecological consequences of hypoxia for yellow perch (*Perca flavescens*) in Lake Erie

By

James J. Roberts

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Natural Resources and Environment)
in The University of Michigan
2010

Doctoral committee:

Professor Donald Scavia, Co-Chair

Assistant Professor Tomas O. Höök, Purdue University, Co-Chair

Professor Earl E. Werner

Adjunct Assistant Professor Stuart A. Ludsin

Adjunct Assistant Research Scientist Edward S. Rutherford

To my loving wife and family

Acknowledgements

I first would like to thank my dissertation committee members Drs Don Scavia, Tomas O. Höök, Stuart A. Ludsin, Earl E. Werner, and Edarward S. Rutherford as they provided me with superior guidance and invaluable suggestions along my doctoral career. I would also like to thank all those that helped with laboratory work including, Kristi Sabo, Kara Lindeoff, Krista Latta, Megan Miner, Grace Milanowski, Alex Bajcz, Anna Belenneya, Dave Fanslow, Joann Cavaletto, Dan Rueberg and Ted Bambikidis. There was an equally important faction deserving thanks for their help with the field portion of this study including Greg Jacobs, Aaron Adamack, Margaret Lansing, Sean Sisler, Hal Gunder, Marco Constantini, Brad Utrup, and the captain and crews of the RV Laurentian and Lake Gaurdian all of whom's tireless work and dedication made this research possible. I would to particularly like to thank Brad Utrup for his tireless dedication to the yellow perch laboratory experiments including experimental design (i.e., the "utrump curve"), experimental implementation, and help in the field.

Drs. Jim Breck and Li Wang of the Michigan Department of Natural Resources Institute for Fisheries Research were extremely helpful in allowing me to use their Saline Fisheries Research Station facilities to conduct my experiments within. The help and hospitality of Drs. Paul Gre cay, Tim Targett, and the Targett Lab at the University of Delaware's college of marine sciences were more than helpful in performing experiments within their unique laboratory setup. I would also like to thank the Höök lab at Purdue

University particularly including Drs. Lori Ivan and Kristi Arend for their helpful comments on presentations and manuscripts. The Scavia lab at the University of Michigan was also extremely helpful, providing comments and insights on my research. I am also very grateful to all those at the National Oceanic and Atmospheric Administration's Great Lakes Environmental Research Laboratory who provided physical and intellectual space crucial to my growth as a doctoral student particularly Tom Nalepa, Henry Vanderpleog, and Doran Mason. I would also like to thank the Cooperative Institute for Limnology and Ecosystem research particularly Dr. Tom Johengen for support. For the intellectual and social stimulation provided by 'The Tank', including the aquatic and non-aquatic members, especially Solomon David and Damon Krueger, I am endlessly grateful.

I would especially like to thank my wonderful parents Mike and Linda Roberts for their unending encouragement and support (both financial and personal) during my life and doctoral career I know, I would have never made it to this point without you. Lastly, I want to thank the animals (Scout and Wally) and my lovely wife Christie Roberts for all their support and encouragement, which made this journey possible and unforgettable.

Table of Contents

Dedication.....	ii
Acknowledgements.....	iii
List of Tables.....	vi
List of Figures.....	viii
Abstract.....	xi
Chapter	
1. Introduction.....	1
2. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch (<i>Perca flavescens</i>).....	11
3. Spatial variation of yellow perch (<i>Perca flavescens</i>) diet and distribution in response to hypolimnetic hypoxia in Lake Erie's central basin.....	50
4. Growth and condition of yellow perch (<i>Perca flavescens</i>) in response to hypoxia.....	87
5. Sub-daily behavioral response and associated consequences of hypolimnetic hypoxia for yellow perch (<i>Perca flavescens</i>).....	131
6. Conclusion.....	164

List of Tables

Table

2.1 Physical characteristics of sample sites by month during 2005.....	34
2.2 Diets of yellow perch collected in Lake Erie's central basin during 2005.....	35
2.3 Yellow perch selectivity coefficients (W' :Vanderploeg and Scavia 1979) for prey taxa in Lake Erie's central basin from June through October 2005.....	36
3.1 Summary statistics for RNA:DNA measured yellow perch (Total length 100-180 mm) collected using trawling at different sites within Lake Erie's central basin during 2005 and 2007.....	72
3.2 Mean yellow perch summary statistics for fish size and specific diet patterns sampled during August and September 2007 from Lake Erie's central basin	73
3.3 Mean yellow perch summary statistics for fish size and specific diet patterns sampled during the summer of 2005 from Lake Erie's central basin	74
4.1 Mean abiotic habitat characteristics of sites sampled in Lake Erie's central basin during summers 2005 and 2007.....	111
4.2 Summary statistics of yellow perch, abiotic treatments, and results for ration and temperature experiment, which consisted of three acclimation days followed by five experimental days	112
4.3 Summary statistics of yellow perch and abiotic treatments averaged across three trials of dissolved oxygen and temperature experiments with each trial consisting of three acclimation days followed by five experimental days.....	113
4.4 Summary statistics for RNA:DNA measured yellow perch (Total length 100-180 mm) collected using trawling at different sites within Lake Erie's central basin during 2005 and 2007.....	114
5.1 Abiotic conditions observed at sample sites within the central basin of Lake Erie during 2007.....	149

5.2 Summary of yellow perch size and species compositions at sites sampled in Lake Erie's central basin during 2007, where BTR represents bottom trawl and MTR represent mid-water trawl150

List of Figures

Figures

2.1 Lake Erie with locations of central basin sampling sites (A, B, D, and H) and 10 meter bathymetry lines.....	37
2.2 Vertical profiles of temperature (black) and dissolved oxygen (dashed) at site B.....	38
2.3. Seasonal patterns of proportional zooplankton biomass density by taxa (bars) and total dry zooplankton biomass density ($\text{mg}\cdot\text{m}^{-3}$; in parentheses above columns).....	39
2.4 Seasonal patterns of proportional benthic macroinvertebrate biomass density by taxa (bars) and total dry macroinvertebrate biomass density ($\text{mg}\cdot\text{m}^{-3}$; in parentheses above columns).....	40
2.5 Mean (+SE) trawl catch per unit effort (natural logarithm of CPUE+1; number of fish per minute of trawling) of yellow perch in bottom (black) and mid-water (gray) trawls..	41
2.6 Yellow perch diets: a) proportional composition by number of prey items, and b) proportional composition by dry biomass of prey items.....	42
2.7 Canonical Correspondence Analysis (CCA) axes one and two are plotted in ordination space overlain with a biplot of environment variables.....	43
2.8 Yellow perch mean (+SE) condition (proportion of dry mass; black bars) and mean (+SE) total mass of stomach contents (dry mass of prey per dry mass of yellow perch; g g^{-1} ; gray bars).....	44
3.1 The location of Lake Erie within the Laurentian Great Lakes and our 2007 sites sampled during August and September.....	75
3.2 Trawl results shown as catch per unit effort (CPUE; yellow perch per minute of trawling \pm SE) for a. bottom trawls (BTR) and b. mid-water trawls (MTR).....	76
3.3 Benthic biomass results for sites used in our diet analyses. We show results for total benthic biomass (a.) and benthic biomass excluding dreissenid mussels (b.; +SE).....	77
3.4 Proportional composition by biomass of yellow perch diets from August (a.) and September (b) 2007.....	78

3.5 Biplot showing our Canonical Correspondance Analysis results depicting the relationship between yellow perch diet patterns and environmental conditions.....	79
3.6 Individual proportional similarity (IS) results for 2007 diet data.	80
3.7 Individual proportional similarity (IS) results for 2005 diet data.....	81
4.1 The location of Lake Erie within the Laurentian Great Lakes (and our 2005 and 2007 sample sites).....	115
4.2a-d Nucleic acid (RNA or DNA) concentrations ($\mu\text{g}\cdot\text{mg}^{-1}$ muscle tissue) and RNA:DNA ratios versus total length of yellow perch from <i>a.</i> ration and temperature experiment, <i>b.</i> dissolved oxygen and temperature experiment, <i>c.</i> 2005 field samples, and <i>d.</i> 2007 field samples.....	116
4.3a-c Results from ration and temperature experiment, corresponding 2-way ANOVA statistics and post-hoc Tukey comparison ($\alpha=0.05$).....	117
4.4a & b Scatter plot and corresponding regression statistics from ration and temperature effects experiment with observed growth (a) and consumption (b) as dependent variables.....	118
4.5a-c Results from dissolved oxygen and temperature experiment and corresponding 2-way ANOVA statistics and post-hoc Tukey comparison ($\alpha=0.05$).....	119
4.6a-c Contour plots depicting response surfaces generated from a quadratic multiple-regression analysis	120
4.7a-c Short-term somatic growth of yellow perch indexed by RNA:DNA ratios from white epaxial muscle tissue collected during summer 2005 from Lake Erie's central basin	121
4.8a & b Short-term somatic growth of yellow perch indexed by RNA:DNA ratios from white epaxial muscle tissue collected during summer 2007 from Lake Erie's central basin	122
5.1 The location of Lake Erie within the Laurentian Great Lakes and 2007 August and September sample sites. Lake Erie bathymetry is depicted with 10 meter depth contours.....	151
5.2 A hypothetical stratified water column and the potential movements of yellow perch as observed with our drifting hydroacoustic sampling method	152
5.3a-e Example of the oxygen concentrations from our five treatment regimes throughout one 24-hr day of our experimental trial	153

5.4a & b Vertical distribution of mean yellow perch biomass determined from transect hydroacoustic and trawl estimates collected in Lake Erie’s central basin during 2007, with data presented within epilimnetic and hypolimnetic vertical layers(+SE).....	154
5.5a & b Regression results relating relative vertical distribution of hydroacoustically estimated yellow perch biomass from both normoxic and hypoxic habitats versus dissolved oxygen concentration.....	155
5.6a & b Sample TS echograms displaying yellow perch fish tracks in Lake Erie’s central basin during 2007.....	156
5.7a-f Summary of mean fish track statistics (change in depth, change in temperature and change in dissolved oxygen concentration) and corresponding one-way ANOVA results (+SE).	157
5.8 Consumption results from our laboratory experiments where yellow perch were exposed to different fluctuation oxygen regimes.....	158

ABSTRACT

The ecological consequences of hypoxia for yellow perch (*Perca flavescens*) in Lake Erie

by

James J Roberts

Co-Chairs: Donald Scavia and Tomas O Höök

Hypoxia ($<2 \text{ mg O}_2 \cdot \text{L}^{-1}$) is a widespread phenomenon in marine and freshwater systems worldwide, yet the ecological consequences of hypoxia are generally unknown, especially for mobile species such as fish. Areas of hypoxic conditions or “dead zones”, due primarily to eutrophication (i.e. nutrient enrichment), are viewed as a major threat to aquatic ecosystem function worldwide. Areas of bottom water (hypolimnetic) hypoxia have long been documented and are increasing in the Lake Erie ecosystem, an economically and ecologically important water body within the Laurentian Great Lakes. Quantifying the ecological consequences of hypoxia for highly mobile organisms (e.g., yellow perch *Perca flavescens*) is a complex task. Such organisms are capable of avoiding direct lethal effects of hypolimnetic hypoxia, but may be indirectly affected as they are forced to occupy inferior habitats (i.e., novel prey, predators, competitors and physical conditions). I used field, and laboratory techniques to address the overall hypothesis that hypolimnetic hypoxia in Lake Erie negatively affects yellow perch.

Laboratory results suggest yellow perch growth and consumption are negatively affected by low oxygen conditions. However, my field results suggest yellow perch

attempt to mitigate these potential consequences by altering their distribution and foraging patterns in the presence of hypoxic conditions. My results also suggest a change in the sub-daily behaviors of yellow perch. This behavioral change involves short-term forays to forage within hypoxic habitats. The largest consequence of hypoxia for yellow perch in LECB is altered distribution patterns due to vertical or horizontal migrations in avoidance of low oxygen conditions. Overall, it appears hypoxia has the potential to negatively affect yellow perch however, behavioral modifications allow yellow perch to mitigate the extent of these consequences in Lake Erie. These results will have management implications for Lake Erie resource agencies and provide important conclusions concerning the ecological consequences of hypoxia for freshwater fishes.

Chapter 1

Introduction

Overview

Hypoxic conditions ($< 2 \text{ mg O}_2 \cdot \text{l}^{-1}$) develop in a wide range of aquatic systems and are believed to impair ecosystem functioning through multiple pathways (Diaz and Rosenberg 2008). Hypoxia-induced ecological alterations may cascade to negatively influence a wide range of biota (Breitburg et al. 1997), including economically important fishes. However, quantifying the ecological impacts of hypoxia is a complex issue. In fact, several studies of marine systems suggest that certain fisheries have experienced increased yields under hypoxic conditions (Breitburg 2002; Altieri 2008) and little empirical evidence currently exists linking hypoxia to reduced fishery production (Rose et al. 2009). In short, to more fully appreciate tradeoffs between hypoxia and fishery production thorough and effective assessments of potential ecological consequences of hypoxia are required (Breitburg et al. 2009; Rose et al. 2009).

Within aquatic systems, a suite of biological, chemical, and physical factors interactively structure spatially and temporally varying habitat conditions. Temperate freshwater lentic systems (lakes, ponds, and reservoirs) generally experience a dimictic cycle, whereby two periods of thermal stratification are bookended by mixing events at the end and beginning of summer and winter. These seasonal thermal conditions create

discrete masses of water, separated vertically by differences in density (i.e., epilimnion and hypolimnion). The combination of vertical stratification and high hypolimnetic oxygen demand can lead to the seasonal development of hypolimnetic hypoxia.

Much of a lentic system's primary production takes place in the warm epilimnion, leading to the deposition of organic material as dead phytoplankton or heterotrophic feces into the atmospherically isolated hypolimnion. Epilimnetic biological productivity can also be enhanced by increased organic material and nutrient enrichment via various anthropogenic activities (e.g., agricultural run-off and combined sewer overflow). In general, hypolimnetic biological processes (i.e., nitrification and decomposition of organic matter) consume oxygen, but do not produce a large amount of oxygen (low light levels inhibit photosynthesis). The vertical separation between the epi- and hypolimnion prohibits introduction of gasses via atmospheric mixing, resulting in lowered hypolimnetic dissolved oxygen concentrations. Therefore, the combination of large amounts of primary production in surface waters, vertical stratification of a water body, and low hypolimnetic volume can create hypolimnetic hypoxia.

Evidence exists at the local-scale to indicate that hypoxia can influence the distribution and foraging behavior of fishes in coastal marine (Craig and Crowder 2005; Prince and Goodyear 2006), estuarine (Petersen and Pihl 1995; Eby and Crowder 2002; Taylor et al. 2007; Brady et al. 2009; Ludsin et al. 2009; Stierhoff et al. 2009), and lentic freshwater (Aku et al. 1997; Aku and Tonn 1999; Baldwin et al. 2002; Vanderploeg et al. 2009) systems. A subset of these field studies also suggest that hypoxia negatively affects prey consumption and fish growth (Aku and Tonn 1997; Eby et al. 2005; Stierhoff et al. 2009), with laboratory studies reporting similar findings (Stewart et al. 1967;

Carlson et al. 1980; Chabot and Claireaux 2008; Brandt et al. 2009). Given that fish require oxygen for basic metabolic processes, these results are not surprising; however, understanding these types of site- and species-specific responses to hypoxia are paramount to assessing large-scale effects on aquatic ecosystems (Rose et al. 2009).

Lake Erie is the warmest and volumetrically most productive of the five Laurentian Great Lakes (Fuller et al. 1995). This system contains a diversity of fish species, which in turn support economically important commercial and sport fisheries. Seasonal hypoxia is a long-standing phenomenon within Lake Erie's central basin (LECB; Delorme 1982) and has recently expanded both in duration and severity (Bertram 1993; Burns et al. 2005). The occurrence of hypoxia in LECB is partially due to its physical characteristics. Specifically, the bathymetry of the central basin facilitates a stratified water column with a small hypolimnetic volume (Hartman 1972). This, coupled with the naturally elevated trophic state of Lake Erie, create conditions suitable for hypoxia (Rao et al. 2008). Hypoxia was recognized as an anthropogenically-induced phenomenon in LECB during the 20th century, and after aggressive nutrient abatement programs, this problem was assumed to be resolved (Makarewicz and Bertram 1991; Ludsins et al. 2001). However, recent findings have suggested a reemergence of this phenomenon possibly, driven by changes in loading patterns and invasive species (Edwards et al. 2005). Fishery resources are an important aspect of LECB and an ecosystem attribute that may respond to changing oxygen conditions (Ludsins et al. 2001).

Within LECB, yellow perch (*Perca flavescens*) are an economically and ecologically important member of the fish community (Ryan et al. 2003). In LECB, yellow perch are demersal and frequently consume benthic macroinvertebrates within the

cool hypolimnion (Hayward and Margraf 1987; Parrish and Margraf 1994). These ecological characteristics suggest that yellow perch in LECB are confronted with hypoxic conditions.

Previous studies have reported that juvenile yellow perch within a prairie marsh system will move horizontally to avoid hypoxic conditions (Suthers and Gee 1986). Laboratory studies suggest that yellow perch will also alter their ventilation rates when subjected to low oxygen conditions (Petrosky and Magnuson 1973). Yellow perch exposed to hypoxic conditions within the laboratory also experienced reduced growth rates (Carlson et al. 1980). Despite these negative effects of low oxygen on yellow perch, not all individuals completely avoid hypoxic conditions. In fact, a study by Hergenrader and Hasler (1966), investigating winter time distributions of yellow perch in Lake Mendota (Wisconsin, US), captured individuals within hypoxic regions of the water column.

This previous work suggests that yellow perch in LECB may either avoid hypoxic conditions by altering their distributions or continue to forage through altered behavioral patterns within cool hypolimnetic habitats. Of those yellow perch that completely avoid hypoxic habitats in LECB, I hypothesize that individuals would either 1) migrate vertically into warmer normoxic habitat and forage on pelagic prey items, or 2) migrate horizontally to warmer normoxic (and sometimes unstratified) nearshore areas where they might alter their foraging patterns in response to novel prey and fish assemblages. Given the range of possible yellow perch responses to hypoxic conditions, it is important to determine which specific response is occurring, because the consequences of each are different. These consequences for yellow perch could include reduced growth rates and

changes in food-web dynamics. Therefore, determining the response of yellow perch to hypoxic conditions will help determine if hypoxia influences their population dynamics in LECB.

Goals and methods

The overall goal of my dissertation research is to explore the effects of hypoxia on yellow perch biology and ecology. Toward this end, I have examined the ecological consequences of hypoxia for yellow perch within LECB using both field and laboratory approaches. My overall research hypothesis is that hypoxia within LECB negatively affects yellow perch. I addressed this hypothesis using four complimentary studies. I used field observations and sampling to examine how yellow perch foraging and distribution patterns varied over time (Chapter 2) and space (Chapter 3) in response to differing hypolimnetic oxygen conditions. I also used laboratory and field techniques to investigate how oxygen and temperature influence yellow perch growth and consumption interactively (Chapter 4).

To assess yellow perch growth, I used a molecular technique, which examined the ratio of RNA to DNA in yellow perch muscle tissue from areas of LECB with differing oxygen conditions. This sensitive measure reflects change in growth rates over short periods of time. I performed laboratory experiments to calibrate the relationship between growth and RNA:DNA ratios of yellow perch and compared RNA:DNA ratios of perch from hypoxic and normoxic sites. Lastly, I examined how hypoxia may influence fine-scale behavioral patterns of yellow perch (Chapter 5) with hydroacoustic observations of sub-daily distribution and movement patterns. To examine how movements into and out

of hypoxic waters may influence yellow perch, I also performed a set of laboratory experiments exposing fish to static and fluctuating oxygen conditions.

Literature cited

- Aku, P. M. K., L. G. Rudstam, and W. M. Tonn. 1997. Impact of hypolimnetic oxygenation on the vertical distribution of cisco (*Coregonus artedi*) in Amisk Lake, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2182-2195.
- Aku, P. M. K., and W. M. Tonn. 1997. Changes in population structure, growth, and biomass of cisco (*Coregonus artedi*) during hypolimnetic oxygenation of a deep, eutrophic lake, Amisk Lake, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2196-2206.
- Aku, P. M. K., and W. M. Tonn. 1999. Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. *Transactions of the American Fisheries Society* 128:17-30.
- Altieri, A. H. 2008. Dead zones enhance key fisheries species by providing predation refuge. *Ecology* 89:2808-2818.
- Baldwin, C. M., D. A. Beauchamp, and C. P. Gubala. 2002. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. *Transactions of the American Fisheries Society* 131:143-158.
- Bertram, P. E. 1993. Total phosphorus and dissolved oxygen trends in the central basin of Lake Erie, 1970-1991. *Journal of Great Lakes Research* 19:224-236.
- Brady, D. C., T. E. Targett, and D. M. Tuzzolino. 2009. Behavioral responses of juvenile weakfish (*Cynoscion regalis*) to diel-cycling hypoxia: swimming speed, angular correlation, expected displacement, and effects of hypoxia acclimation. *Canadian Journal of Fisheries and Aquatic Sciences* 66:415-424.
- Brandt, S. B., M. Gerkin, K. J. Hartman, and E. Demers. 2009. Effects of hypoxia on food consumption and growth of juvenile striped bass (*Morone saxatilis*). *Journal of Experimental Marine Biology and Ecology* 381:S143-S149.
- Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25:767-781.
- Breitburg, D. L., D. W. Hondorp, L. A. Davias, and R. J. Diaz. 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. *Annual Review of Marine Science* 1:329-349.
- Breitburg, D. L., T. Loher, C. A. Pacey, and A. Gerstein. 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecological Monographs* 67:489-507.
- Burns, N. M., D. C. Rockwell, P. E. Bertram, D. M. Dolan, and J. J. H. Ciborowski. 2005. Trends in temperature, secchi depth, and dissolved oxygen depletion rates

- in the central basin of Lake Erie, 1983-2002. *Journal of Great Lakes Research* 31:35-49.
- Carlson, A. R., J. Blocher, and L. J. Herman. 1980. Growth and survival of channel catfish and yellow perch exposed to lowered constant and diurnally fluctuating dissolved oxygen concentrations. *The progressive fish-culturist* 42:73-78.
- Chabot, D., and G. Claireaux. 2008. Environmental hypoxia as a metabolic constraint of fish: The case of Atlantic cod, *Gadus morhua*. *Marine Pollution Bulletin* 57:287-294.
- Craig, J. K., and L. B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series* 294:79-94.
- Delorme, L. D. 1982. Lake Erie oxygen; the prehistoric record. . *Canadian Journal of Fisheries and Aquatic Sciences* 39:1021-1029.
- Diaz, R. J., and R. Rosenberg. 2008. Spreading Dead Zones and Consequences for Marine Ecosystems. *Science* 321:926-929.
- Eby, L. A., and L. B. Crowder. 2002. Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Canadian Journal of Fisheries and Aquatic Sciences* 59:952-965.
- Eby, L. A., L. B. Crowder, C. M. McClellan, C. H. Peterson, and M. J. Powers. 2005. Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Marine Ecology-Progress Series* 291:249-261.
- Edwards, W. J., J. D. Conroy, and D. A. Culver. 2005. Hypolimnetic oxygen depletion dynamics in the central basin of Lake Erie. *Journal of Great Lakes Research* 31:262-271.
- Fuller, K. H., H. Shear, and J. Wittig. 1995. *The Great Lakes: an environmental atlas and resource book*. Environment Canada and U.S. Environmental Protections Agency, Chicago, Ill.
- Hartman, W. L. 1972. Lake Erie-effects of exploitation, environmental changes and new species on fishery resources. *Journal of the Fisheries Research Board of Canada* 29:899.
- Hayward, R. S., and E. J. Margraf. 1987. Eutrophication effects on prey size and food available to yellow perch in Lake Erie. *Transactions of the American Fisheries Society* 116:210-223.
- Hergenrader, G. L., and A. D. Hasler. 1966. Diel activity and vertical distribution of yellow perch (*Perca flavescens*) under the ice. *Journal of the Fisheries Research Board of Canada* 23:499-509.

- Ludsin, S. A., M. W. Kershner, K. A. Blocksom, R. L. Knight, and R. A. Stein. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecological Applications* 11:731-746.
- Ludsin, S. A., and coauthors. 2009. Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: implications for food web interactions and fish recruitment. *Journal of Experimental Marine Biology and Ecology* 381:S121-S131.
- Makarewicz, J. C., and P. Bertram. 1991. Evidence for the restoration of the Lake Erie ecosystem. *Bioscience* 41:216-223.
- Parrish, D. L., and F. J. Margraf. 1994. Spatial and temporal patterns of food use by white perch and yellow perch in Lake Erie. *Journal of Freshwater Ecology* 9:29-35.
- Petersen, J. K., and L. Pihl. 1995. Responses to hypoxia of plaice, *Pleuronectes platessa* and dab, *Limanda limanda*, in the south-east Kattegat: distribution and growth. *Environmental Biology of Fishes* 43:311-321.
- Petrosky, B. R., and J. J. Magnuson. 1973. Behavioral responses of northern pike, yellow perch and bluegill to oxygen concentrations under simulated winterkill conditions. *Copeia* 1:124-133.
- Prince, E. D., and C. P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography* 15:451-464.
- Rao, Y. R., N. Hawley, M. N. Charlton, and W. M. Schertzer. 2008. Physical processes and hypoxia in the central basin of Lake Erie. *Limnology and Oceanography* 53:2007-2020.
- Rose, K. A., and coauthors. 2009. Does hypoxia have population-level effects on coastal fish? Musing from the virtual world. *Journal of Experimental Marine Biology and Ecology*.
- Ryan, P. A., and coauthors. 2003. Fish-community goals and objectives for Lake Erie. *Great Lakes Fishery Commission Special Publication* 03-02:56.
- Stewart, N. E., D. L. Shumway, and P. Doudoroff. 1967. Influence of oxygen concentration on the growth of juvenile largemouth bass. *Journal of Fisheries Research Board of Canada* 24:475-494.
- Stierhoff, K. L., T. E. Targett, and J. H. Power. 2009. Hypoxia-induced growth limitation of juvenile fishes in an estuarine nursery: assessment of small-scale temporal dynamics using RNA:DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1033-1047.
- Suthers, L. M., and J. H. Gee. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1562-1570.

- Taylor, J. C., P. S. Rand, and J. Jenkins. 2007. Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. *Marine Biology* 152:939-957.
- Vanderploeg, H. A., and coauthors. 2009. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *Journal of Experimental Marine Biology and Ecology* 381:S92-S107.

Chapter 2

Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch (*Perca flavescens*)

Abstract

Bottom hypoxia ($<2 \text{ mg O}_2 \text{ l}^{-1}$) is a widespread phenomenon in marine and freshwater systems, yet the ecological consequences of hypoxia are generally unknown, especially for mobile organisms such as fish. Herein, we explore how a large area of hypolimnetic (i.e., sub-thermocline) hypoxia that develops seasonally in Lake Erie's central basin influences yellow perch (*Perca flavescens*), a demersal species of both ecological and economic importance. We hypothesized that hypolimnetic hypoxia would negatively affect yellow perch by limiting access to benthic prey and preferred (cool) temperatures. To explore how hypoxia influences yellow perch foraging and migration patterns in central Lake Erie, we collected a suite of biological (i.e., fish with bottom and mid-water trawls, benthic macroinvertebrates using Ponar grabs, and zooplankton via depth-specific pumping) and physical (i.e., temperature and dissolved oxygen) data monthly during June through October 2005. Our results indicate that yellow perch avoid hypoxic bottom waters by either moving horizontally (away from the hypoxic zone) or migrating above the oxycline. We also found evidence to suggest that individuals that moved above the hypoxic hypolimnetic layer continue to "dive" into the hypoxic layer to feed on benthic invertebrates. Even so, during the height of hypoxia, both the amount and proportion of benthic macroinvertebrates consumed decreased, whereas consumption of zooplankton

increased. While hypoxia-induced changes in yellow perch distributions and foraging likely affect individual condition and growth in the short term, the long-term effects on population production remain equivocal.

1. Introduction

Large areas of hypoxia ($<2 \text{ mg O}_2 \cdot \text{L}^{-1}$) occur in both marine and freshwater aquatic systems worldwide, and have been shown to influence dynamics of both marine and freshwater organisms across trophic levels, including zooplankton (Marcus 2001), benthic macroinvertebrates (Diaz and Rosenberg 1995; Wetzel et al. 2001), and fishes (Aku and Tonn 1999; Breitburg et al. 2001). Through their influence on ecological interactions, large areas of hypoxia may disrupt entire aquatic food webs (Breitburg et al. 1997; Turner 2001) and may critically impair ecosystem function (Diaz 2001; Rabalais and Turner 2001).

Although relatively understudied as compared to sessile benthic invertebrates, the effects of hypoxia on large, highly mobile organisms such as fish are of particular interest due to their ecological and economic importance (Breitburg 2002). Since oxygen is a requirement for basic physiological processes of all metazoans, low concentrations of dissolved oxygen will likely have negative effects for fishes (Kramer 1987; Pollock et al. 2007), through both direct and indirect pathways. Not surprisingly, extremely low dissolved oxygen concentrations have been shown to be lethal for fishes in the laboratory (Petrosky and Magnuson 1973; Petersen and Pihl 1995). However, it is less clear how hypoxia can influence fish populations in natural systems, given their behavioral ability to avoid low oxygen conditions. Such avoidance behavior has been reported in response to hypoxia in freshwater (Aku et al. 1997; Baldwin et al. 2002) and marine (Craig and Crowder 2005; Prince and Goodyear 2006) systems. While avoidance of low oxygen conditions may overcome direct hypoxia-related mortality, such a behavioral response may nonetheless lead to various indirect consequences. For instance, fish that avoid low

oxygen waters may in turn occupy different thermal and optic habitats and be exposed to novel sets of predators and prey. Thereby, hypoxia-induced behavioral effects can lead to a shift in diets (Pihl 1994; Aku and Tonn 1999), occupation of inferior thermal habitats that may result in decreased growth and condition (Eby and Crowder 2002; Prince and Goodyear 2006) and increased predation mortality (Breitburg et al. 1994; Breitburg et al. 1999).

Lake Erie, the 11th largest freshwater lake by volume in the world, is an example of a large freshwater system that experiences hypolimnetic (i.e., sub-thermocline) hypoxia. Within Lake Erie's central basin (LECB), which represents two-thirds of the lake in terms of both area and volume (Fuller et al. 1995), a large hypolimnetic region consistently becomes hypoxic during late summer (Boyce et al. 1987; Bertram 1993; Hawley et al. 2006). The physical properties of LECB (i.e., intermediate depth resulting in summer stratification with a thin hypolimnetic layer) render it susceptible to hypoxia development (Boyce et al. 1987), but hypoxia is also likely exacerbated by cultural eutrophication (Boyce et al. 1987; Bertram 1993; Burns et al. 2005). Regardless of the underlying primary causes of hypoxia, a better understanding of the ecological consequences of hypolimnetic hypoxia is needed in LECB, given that it supports numerous ecologically and economically important fisheries, including yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), and lake whitefish (*Coregonus clupeaformis*). While historical trends in catches of fish species in Lake Erie are suggestive that hypoxic conditions may have affected fish community composition (Hartman 1972; Ludsin et al. 2001), the actual direct and indirect ecological effects of hypoxia in LECB remain largely unknown.

As part of the International Field Years on Lake Erie (IFYLE) program (Hawley et al, 2006), we evaluated the ecological consequences of hypoxia for Lake Erie yellow perch, an important component of the Lake Erie ecosystem, which supports economically important recreational and commercial fisheries (Ryan et al. 2003). Specifically, we conducted a comprehensive field investigation during June through October 2005 to quantify how hypoxia influences yellow perch foraging and habitat-use patterns in LECB. Given that low oxygen concentrations can be lethal for yellow perch (Petrosky and Magnuson, 1973), and due to the demersal behavior of this primarily benthivorous species (Keast 1977; Knight et al. 1984; Tyson and Knight 2001), yellow perch likely are directly confronted with hypolimnetic hypoxia in LECB. As such, we hypothesized that hypolimnetic hypoxia would alter yellow perch spatial distributions (e.g., force yellow perch to move horizontally and/or vertically to avoid hypoxia), which in turn, might negatively affect foraging ability (e.g., lead to reduced consumption and altered prey selection). We discuss the likely consequences of our findings for fisheries management in this system.

2. Methods

We sampled four sites (A, B, D, and H) in LECB (Figure 1.1) to characterize a suite of biological and physical variables on a monthly basis during June through October 2005, excluding July. Owing to weather and ship availability, the particular sites sampled varied by month with only site B sampled during every monthly cruise (Table 2.1). Each site consisted of a 5-km longitudinal transect, which was sampled at the endpoints and midpoint every 4 h over a 24 h period. Sampling occurred while aboard one of two research vessels (R/V *Laurentian* or R/V *Lake Guardian*) in coordination with the IFYLE program (Hawley et al., 2006).

2.1 Physical variables and potential prey

To quantify abiotic conditions (e.g., temperature and dissolved oxygen) of the entire water column, we used vertical casts of a Sea-Bird 911⁺ CTD (conductivity, temperature and depth) profiler equipped with a Sea-Bird Electronics 13 dissolved oxygen sensor (Sea-Bird Electronics, Bellevue WA). Casts were conducted at the east, west, and midpoint of each site transect at least once per 24 h sampling period. Measurements were made at ~0.03 m depth intervals, but subsequently grouped into 1-m depth bins for analysis.

We quantified densities of potential invertebrate prey, including both zooplankton and benthic macroinvertebrates. Zooplankton were collected every 4 h at each site by pumping water with a diaphragm pump (Sandpiper, Warren Rupp) from discrete vertical zones of the water column (hypo-, meta-, and epilimnion) as determined from CTD profiles. Water was pumped from each zone at 1 m intervals into a 64 μm mesh net at a rate of 2.0 L s⁻¹ using a 4 cm diameter hose. Each vertical zone was sampled for a specified period resulting in 1 m³ of water being pumped from each zone. Upon collection, zooplankton samples from each depth zone were concentrated and preserved separately in carbonated, sugar-buffered formalin (2%).

In the laboratory, samples were sub-sampled and at least 600 individual organisms per sample were identified to species level and enumerated. Abundances of large invertebrate species (*Leptodora kindti*, *Cercopagis pengoi*, and *Bythotrephes longimanus*) were determined by screening the entire sample through 550 μm mesh, and the biomass of these taxa were determined using length and dry-mass relationships (e.g., Culver et al., 1985). For each vertical zone, the biomass of smaller zooplankton species

constituting 8% or more of the sample was determined from the measurement of total length (nearest 0.1 μm) for 25 immature and 10 adults using established length and dry-mass relationships (e.g., Culver et al., 1985). Dry biomass of small-bodied species constituting less than 8% of organisms from a vertical zone was determined using published mean dry mass (e.g., Culver et al., 1985). To expand these biomass measurements to the entire water column, taxa-specific measures of zooplankton number and biomass (per m^{-3}) were interpolated within each vertical zone. These measures were then summed across all zones sampled and finally divided by the entire depth of the water column resulting in a measure of zooplankton number or biomass for the entire water column for each 4 h period.

Benthic macroinvertebrates were collected once during each 24 h sampling period at each site using a Ponar grab sampler (250 μm mesh; 0.047 m^2). Samples were collected in triplicate at the east, west, and midpoint of each site transect (i.e., $n=9$ per site). Upon collection, ponar samples were concentrated in 5% formalin with rose-bengal dye (to facilitate subsequent laboratory analysis).

In the laboratory, samples were placed in a white enamel pan and organisms were located and removed from sediments under a 1.5x magnifying lens. We identified and enumerated organisms by coarse taxonomic groups (i.e., Chironomidae larva and pupae, Oligochaetes, Spherids, *Dreissena* spp., and others). For each sample, total lengths (nearest 0.1 μm) of up to 30 individuals per taxonomic group were measured under dissecting microscopes equipped with computer imaging software (Image-Pro® plus 5.1). Then, using taxa-specific length-mass relationships (e.g., Benke et al. 1999), individual dry masses were estimated from measured total lengths, and the mean

individual dry mass was multiplied by density counts to estimate taxa-specific biomass density.

2.2 Fish samples and diet analysis

Yellow perch were collected using bottom (7.6 m semi-balloon: 13mm stretched-mesh cod-liner) and mid-water trawls (9.1 x 9.1m: 6.4mm stretched-mesh cod-liner), which targeted benthic (hypolimnion) and pelagic (meta- and epilimnion) habitats, respectively. During the 24 h sampling period at a site, we deployed each trawl at least once every 4 h. Tows generally lasted 10 min, although tow durations were lengthened in some instances to ensure collection of sufficient numbers of fish. Upon collection, yellow perch were enumerated and frozen at -20°C.

In the laboratory, fish were thawed, their total length (nearest 1 mm) and wet mass (nearest 0.1 mg) were measured, and stomach contents were removed and inspected under a dissecting microscope. We identified stomach contents to the lowest possible taxonomic level (Table 2.2). Using dissecting microscopes equipped with Image-Pro® plus 5.1 software, whole organisms were measured for total length (nearest 1 µm), which then was used to calculate individual dry masses using taxa-specific length-mass relationships (Rosen 1981; Culver et al. 1985; Benke et al. 1999). Counts of diet items and estimated mean taxa-specific dry mass were used to estimate the proportional composition of each individuals' diet by biomass. After all diet items were identified, enumerated, and measured, stomach contents and the entire fish were placed in separate containers and allowed to dry (70°C) for 3-4 days, after which dry masses were measured (nearest 0.1 mg). To minimize the effect of individual size on consumption patterns, we only present diet information for yellow perch from 100-200 mm total length. Yellow

perch within this length range comprised 91% of all yellow perch collected, and likely included age 1, 2 and 3 individuals (Belore et al. 2007).

2.3 Data analysis

Data were grouped into one of three categories depending on time of collection: day, night, and crepuscular. All samples taken within ± 2 h of civil twilight were considered crepuscular, and other samples were grouped as either day or night. We focused our analysis of trawl data separately by day and night given the clear distinction between these two time periods. When analyzing the zooplankton data, we only included the four time periods not considered crepuscular in our analyses. However, to examine diet and benthic macroinvertebrate patterns, we include data from all time periods. We used mean values of yellow perch diet composition by number and biomass for our final analyses. The frequency of occurrence of each diet item was calculated as the proportion of yellow perch stomachs in which a given diet item was present. Trawl catches were converted to catch per unit of effort (number of fish per minute of trawling; CPUE).

To relate yellow perch diet composition to available prey, we performed a selectivity analysis using the W' index (Vanderploeg and Scavia 1979), which has previously been used to relate the density of both pelagic and benthic prey to foraging patterns of alewife (*Alosa pseudoharengus*) in Lake Michigan (Pothoven and Vanderploeg 2004). This index also has been useful in linking foraging strategy to food selection for vertebrate (Pothoven et al. 2007) and invertebrate (Vanderploeg et al. 1984) organisms. To relate observed yellow perch diet patterns to measures of both benthic and pelagic available prey at each site during each month, we used biomass ($\text{g}\cdot\text{m}^{-2}$) for both prey types. We excluded Chironomidae pupae from this selectivity analysis because our

sampling methodologies likely inadequately characterized densities of this prey type. In fact, yellow perch consumed Chironomidae pupae even when this prey type was not collected in the environment, suggesting strong selection.

We used Canonical Correspondence Analysis (CCA) to help identify important environmental variables that could help explain foraging patterns of yellow perch (ter Braak, 1995; Jaworski and Ragnarsson 2006). For this analysis, an ordination on the diet data (biomass for all prey types) matrix was conducted, which was compared to a separate environmental matrix. We also used Monte Carlo simulations (n=100 runs) to test the significance ($\alpha=0.05$) of CCA axis eigenvalues, wherein the resulting p-value was the proportion of runs with an eigenvalue greater than or equal to the observed value. We tested the null hypothesis that no linear relationship exists between the diet and environmental matrix with these p-values. The variables used in our environmental matrix included mean epilimnetic temperature ($^{\circ}\text{C}$), mean hypolimnetic dissolved oxygen concentration ($\text{mg O}_2\cdot\text{L}^{-1}$), and mean hypolimnetic thickness (m). We selected these three variables for the environmental matrix because they are the least correlated subset of the abiotic variables we collected. The diet matrix described the mean diet at a site during each sampling occasion. The environmental matrix was comprised of the three variables mentioned above for each site and sampling period. To interpret the results of this analysis, we graphed yellow perch diet composition for each month and site within the environmental space described by two axes. A biplot of the environmental variable scores was then overlaid on this graph to give more interpretive power to the analysis. All CCA analyses were performed using PC-ORD version 4.14.

We used one-way ANOVA with *post hoc* Tukey comparison to compare mean yellow perch condition (proportional dry mass; $\text{g dry fish} \cdot \text{g}^{-1}$ wet fish) and stomach content mass ($\text{g dry food} (\text{g dry fish})^{-1}$). Comparisons were across months, using only 1) data from site B and 2) data combined across all sites. We also used one-way ANOVAs to compare mean total benthic prey biomass (samples from the middle, east, and west used as replicates; $n=3$ per site) and mean total pelagic prey biomass (samples from 4 h diel periods used as replicates) across 1) sites within each month and 2) months for each site. Statistical comparisons were performed with SYSTAT® 11 (Chicago, IL), and significant differences were noted at the $\alpha=0.05$ level of significance.

3. Results

3.1 Physical variables and potential prey

During 2005, LECB hypolimnetic oxygen concentrations decreased at a rate of about $3 \text{ mg O}_2 \cdot \text{L}^{-1} \text{ month}^{-1}$ at all sites during June through September (Table 2.1). Following autumn turnover, which occurred during early October, the whole water column became isothermal and well oxygenated (Table 2.1). Hypolimnetic oxygen concentrations were low at site H during August ($2.5 \text{ mg} \cdot \text{l}^{-1}$) and hypoxic at sites A, B, and H during September (1.2 , 1.6 , and $0.9 \text{ mg} \cdot \text{l}^{-1}$, respectively; Table 2.1). However, the thickness of the hypolimnion varied among sites, and during September, the distance from the bottom of the thermocline to the substrate was much greater at deeper sites A and B (5.8 and 6.1 m , respectively) than at shallower site H (2.0 m). Seasonal changes in depth-specific temperature and oxygen concentration were particularly evident at site B, the only site sampled during all months (Figure 2.2). While sites A, B, and D were located across similar depths, site H ranged from a depth of 17 m at the east end to 11 m

at the west end with a mean depth of 14.2 m (Table 2.1; Figure 2.1). During September, shallower portions of site H were not stratified (i.e., normoxic bottom waters), whereas deeper portions were stratified with a hypoxic hypolimnion.

To elucidate how variable prey availability influences yellow perch foraging, we examined spatio-temporal variation in prey (zooplankton and benthic macroinvertebrate) densities at a coarse taxonomic level. Detailed descriptions of the spatial and temporal patterns of zooplankton in response to hypolimnetic hypoxia in LECB are presented elsewhere (Vanderploeg et al. 2009b). In short, whole water column zooplankton biomass densities varied both spatially and temporally; however, the degree of temporal variation was modest. For instance, zooplankton biomass at site D was consistently low relative to site B. At site B, zooplankton biomass during June differed from August and October, but not September (ANOVA: $F_{3, 12}=6.728$; $P=0.006$). Results from site A show similar patterns as site B, except that zooplankton biomass was greater during June than September at site A (Figure 2.3; ANOVA: $F_{1, 6}=10.191$; $P=0.019$). Shallow site H was only sampled for zooplankton during August, and showed similar taxonomic composition to the other three sites (Figure 2.3). Total zooplankton biomass did not differ across sites during September (ANOVA: $F_{1, 6}=3.366$; $P=0.116$). However, during June biomass at site D was less than A and B (ANOVA: $F_{2, 9}=13.539$; $P=0.002$) and in August biomass at site H was greater than B and D (ANOVA: $F_{2, 9}=14.243$; $P=0.002$). The seasonal emergence of certain large pelagic invertebrates (*B. longimanus* in August and Chironomidae pupae in October) also was noteworthy.

Benthic macroinvertebrate biomass densities varied dramatically across sites, but within-site temporal variation was less pronounced (Figure 2.4). Total benthic

macroinvertebrate biomass was higher at site D than A and B during June (ANOVA: $F_{2,6}=65.607; P<0.001$), but differences between sites were not significant during August (ANOVA: $F_{3,8}=0.854; P=0.508$) or September (ANOVA: $F_{2,6}=1.779; P=0.261$). Much of the spatial variation in benthic macroinvertebrate biomass was attributable to Dreissenid mussels (primarily quagga mussels *Dreissena bugensis*), which were particularly abundant at sites D and H, and largely absent at sites A and B. The temporal variation represented by total macroinvertebrate biomass at site B was not significant (ANOVA: $F_{3,8}=1.199; P=0.370$). Chironomidae larvae (an important prey item for yellow perch) were present at every site.

3.2 Fish samples and diet analysis

Catches of yellow perch were relatively high at normoxic sites and low at hypoxic sites (Figure 2.5). During normoxic conditions, the majority (proportionally) of yellow perch were caught in the bottom trawl during both day and night. However, during hypoxic conditions, the majority of yellow perch collected at night were caught in the mid-water trawl. In total, yellow perch constituted 18% of fish captured with bottom and midwater trawls. Rainbow smelt (*Osmerus mordax*) and emerald shiners (*Notropis atherinoides*) were the other numerically dominant species, accounting for 57% and 22% of the total trawl catch (by number), respectively (i.e., these three species collectively accounted for 97% of fish captured; Vanderploeg et al. 2009a).

Analyses of diets show that during normoxic conditions yellow perch fed largely on benthic macroinvertebrates, primarily Chironomidae larvae and pupae (Figure 2.6a, b; Table 2.2). This pattern of feeding on benthic macroinvertebrates was consistent across sites and analyses, regardless of whether diet items were quantified by number, biomass

(Figure 2.6a, b), or frequency of occurrence (Table 2.2). With the exception of *B. longimanus*, a large predatory cladoceran that can be a preferred prey of yellow perch (Bur and Klarer 1991), pelagic zooplankton were rarely selected at sites with a normoxic hypolimnion. Instead, pelagic zooplankton were primarily consumed when hypolimnetic oxygen concentrations were low (e.g. Site H during August and all sites during September; Figures 2.6a, b; Table 2.2). This shift away from benthic prey during hypoxic conditions was most prevalent at site B, the only site sampled every month and the site with the thickest hypolimnion during the hypoxic period (Table 2.1).

Spatio-temporal variation in prey selection by yellow perch was evident at our study sites. Most importantly, yellow perch selected Chironomidae larvae during normoxic conditions, whereas during hypoxic conditions, selection for zooplankton increased and selection for Chironomidae decreased (Table 2.3). In fact, with exception of the large, non-native predatory cladoceran *B. longimanus*, zooplankton were only highly selected for at low oxygen sites (e.g., H during August and B during September; Table 2.3). Nonetheless, it should be noted that, despite a hypoxic hypolimnion, yellow perch continued to positively select Chironomidae larvae at site A in September.

Our CCA analyses support our selectivity analyses, which indicate that yellow perch feed on Chironomids during normoxic conditions and zooplankton during hypoxic conditions. CCA analyses and Monte Carlo simulations identified only one important axis ($p=0.03$), which explained 35 % of the total variation of diet data (Figure 2.7). Axis 2, although presented in Figure 2.7 for graphical purposes only, was not significant ($p=0.24$) and only explained 11% of the variation in diet data. Axis 1 was highly, negatively correlated to hypolimnetic DO and positively correlated to epilimnetic

temperature ($r=-0.88$ and 0.78 , respectively), indicating that a large amount of the variation in yellow perch diet patterns can be explained along an environmental gradient dominated by hypolimnetic dissolved oxygen concentration and epilimnetic temperature.

In addition to seasonal and spatial changes in the type of food consumed by yellow perch, the amount of food in yellow perch stomachs ($\text{g dry food}(\text{g dry fish})^{-1}$) declined seasonally. Stomach content mass was significantly less during September and October than during June, and significantly less in August than during October (all sites ANOVA; $F_{3,461}=15.16$; $P<0.001$; Figure 2.8). At site B, mean stomach content mass did not differ between September and October; however, stomach biomass during June and August were significantly greater than during October (ANOVA: $F_{3,165}=13.88$; $P<0.001$; Figure 2.8). In addition, the percentage of empty stomachs at site B was greatest during the height of hypoxia in September (Table 2.2). Finally, yellow perch condition ($\text{g dry}(\text{g wet})^{-1}$) did not differ among August, September and October, but was significantly lower in June than during later months (ANOVA; across all sites, $F_{3,643}=151.32$; $P<0.001$; site B, $F_{3,229}=63.88$; $P<0.001$).

4. Discussion

Similar to research conducted in other freshwater and coastal marine systems (Pihl, 1994; Aku and Tonn, 1999; Eby and Crowder, 2002; Craig and Crowder, 2005; Prince and Goodyear, 2006), our findings support the hypothesis that hypolimnetic hypoxia can influence the spatial distributions of demersal fish, and in turn, foraging patterns. Below, we discuss our findings and underscore some management implications.

Movement effects. Mid-water and bottom trawl catches suggest that yellow perch actively move both horizontally and vertically to avoid hypoxia. In support of the notion

that fish move horizontally to escape hypolimnetic hypoxia, we found that a reduction in CPUE at offshore sites from August into September (e.g., B) was accompanied by an increase in trawl catches at site H, the shallowest site which was on the edge of the hypoxic zone (Table 2.1; Figure 2.5). Acoustics data collected in conjunction with our trawling also support this hypothesis (Vanderploeg et al. 2009a). Further, yellow perch that remained in the hypoxic region appeared to alter their vertical distributions, occupying zones higher in the water column during hypoxic periods. In support of this notion, we found relatively greater nighttime mid-water trawl catches (relative to bottom trawl catches) across all sites in September, excluding shallow site H. Fish acoustics data collected during 2005 along transects spanning our sites also demonstrate that most of the fish biomass (including yellow perch) aggregates at the edges of the hypoxic zone, with those fish residing in the hypoxic zone found at or above the oxycline (Vanderploeg et al. 2009a; Ludsin unpublished data).

Changes in horizontal and vertical distributions in response to low oxygen conditions have been observed for a number of teleost fish populations in freshwater (e.g., Suthers and Gee, 1986; Aku and Tonn, 1999; Baldwin et al., 2002), estuarine (e.g., Eby and Crowder 2002; Ludsin et al. 2009) and marine (e.g., Craig and Crowder, 2005; Stanley and Wilson, 2004; Prince and Goodyear, 2006) systems. For instance, Baldwin et al. (2002) found that within a Utah reservoir, adult Bear Lake cutthroat trout (*Oncorhynchus clarkii utah*) moved higher in the water column when the hypolimnion became hypoxic during late summer. Similarly, Stanley and Wilson (2004) found that hypoxic bottom waters in the northern Gulf of Mexico led many fishes, including demersal species like red snapper (*Lutjanus campechanus*), to occupy depth strata above

the hypoxic zone. In a study highly relevant to the research presented herein, Suthers and Gee (1986) used both laboratory experiments and observations within a prairie marsh to evaluate distributions of yellow perch in response to hypoxia. Their results suggest that yellow perch will readily move into and out of habitats in response to diurnally fluctuating oxygen concentrations and avoid waters with oxygen concentrations $<1.5 - 3.0 \text{ mg O}_2 \cdot \text{L}^{-1}$. Thus, while we cannot rule out that reduced catches at our study sites were due to hypoxia-induced mortality, we feel that direct mortality is unlikely given that many teleost fishes (including yellow perch) can sense hypoxia and have shown ability to avoid it.

Foraging effects. During normoxic conditions, yellow perch selected for benthic macroinvertebrates, primarily Chironomidae larvae and pupae. However, when *B. longimanus* was at its highest abundance (e.g., August at site B) but still representing a small portion of the total zooplankton biomass (2%), yellow perch also targeted this prey. Preferential selection of this large, invasive zooplankton by yellow perch has been previously observed in Lake Erie (Bur and Klarer 1991). Most of the *B. longimanus* population was found in the hypolimnion during the day (Vanderploeg et al. 2009b), and was thus accessible to yellow perch. Further, when Chironomidae pupae emerged (e.g., October at site B), yellow perch also targeted this large pelagic prey. These normoxic dietary patterns are consistent with previous studies on yellow perch in the western and central basins of Lake Erie (Hayward and Margraf 1987; Bur and Klarer 1991; Tyson and Knight 2001). These previous studies primarily evaluated yellow perch diets in inshore areas that were unlikely to be directly affected by seasonal hypolimnetic hypoxia.

During hypoxic conditions, however, yellow perch selected small pelagic zooplankton prey (i.e., pelagic prey other than *B. longimanus* and Chironomidae pupae). Our analyses suggest that these changes in foraging were likely attributable to the development of hypolimnetic hypoxia, given that we found no dramatic changes in available benthic or small zooplankton prey within any of our sites (with the exception that *B. longimanus* was not found at our study sites during September). While there were significant differences among sites within months these were primarily due to the presence of dreissenid mussels which have been shown to increase the total abundance of other benthic macroinvertebrates while also increasing the cost of foraging success for fishes (Cobb and Watzin 2002; Beekey et al. 2004). Changes in selectivity are very strong indicators of impacts to foraging in that selectivity, unlike diet, is not sensitive to changes in prey abundance (e.g. Vanderploeg and Scavia, 1979). Similarly, Aku and Tonn (1999), who quantified the feeding behavior of cisco (*Coregonus artedii*) in response to hypolimnetic hypoxia, found that ciscoes consumed deepwater zooplankton species and benthic taxa (e.g., Chironomidae larvae) in areas with an oxygenated hypolimnion. In areas with a hypoxic hypolimnion, cisco instead consumed pelagic zooplankton because they were avoiding the hypoxic bottom layer.

Along with this similar shift in yellow perch diet, we also observed a reduction in the amount of food consumed by yellow perch during hypoxic and post-hypoxic conditions. One might expect relatively low stomach content biomass during hypoxic conditions, when yellow perch feed on small zooplankton prey and move higher in the water column (i.e., experience relatively warm temperatures, whereby food should pass quickly through the gut; Persson 1981). However, low stomach content biomass in

October following turnover are enigmatic. Given that our October sampling occurred less than a week after fall turnover, perhaps the low abundance of prey in yellow perch stomachs is a delayed effect due to these individuals experiencing continuous hypoxic conditions for nearly 30 days. Further, given the strong effect of temperature on digestion time (Persson 1981), it is unclear if seasonal differences in mass of stomach contents necessarily imply seasonal differences in daily ration.

While yellow perch shift foraging patterns to consume more pelagic prey when the hypolimnion is hypoxic, some yellow perch were caught in bottom trawls at hypoxic sites (A and H). Although these individuals could have been captured as nets were lowered or retrieved, the fact that we found some yellow perch with benthic prey items (e.g., Chironomidae larvae) in their stomachs at these sites, suggests that some yellow perch undertake foraging forays into the hypoxic hypolimnion in order to continue to consume benthic prey. This phenomenon was particularly apparent at site A in September and site H in August. These sites were characterized by relatively thin hypolimnia or high densities of Chironomidae. Previous field observations document yellow perch swimming into hypoxic habitat during the winter in Lake Mendota, WI (Hasler 1945). However, gillnets used by Hasler (1945) precluded the author from performing a detailed diet analysis of the yellow perch caught in hypoxic habitats. Similar behavior was linked to foraging patterns of central mudminnow (*Umbra limi*) in a northern Wisconsin lake (Rahel and Nutzman 1994). Both field observations and laboratory experiments demonstrate that central mudminnow will undertake foraging excursions into hypoxic waters in order to consume preferred prey (Rahel and Nutzman 1994). Similarly, using stationary acoustics, Taylor et al. (2007) found that bay anchovy

(*Anchoa mitchilli*) undergo feeding forays into severely hypoxic sub-pycnocline waters of the Neuse River Estuary in order to capture zooplankton prey.

Given shifts in vertical distributions and diets in response to hypoxia, one might expect a negative impact on yellow perch growth and condition. Yellow perch metabolic demands increase with temperature (Kitchell et al. 1977) and thus maintenance ration is higher at warmer temperatures (e.g., 21.7°C, the mean epilimnetic temperature at site B in September) than at cooler temperatures (e.g., 11.3°C, the mean hypolimnetic temperature at site B in September). Further, feeding on zooplankton may require more active foraging (i.e., greater energy expenditure) than foraging on benthic macroinvertebrates, and Chironomidae larvae likely have higher energy density than most zooplankton taxa (3,138 J g⁻¹ and 2,510 J g⁻¹, respectively; Schaeffer et al., 1999). Additionally, hypoxia itself may cause individuals to swim at relatively fast speeds, as has been demonstrated for bay anchovy in the Neuse River Estuary (Taylor et al. 2007).

While it is highly feasible that hypoxia negatively impacts yellow perch growth and condition in LECB, our study does not demonstrate this unequivocally. In fact, relatively few field-based studies have demonstrated negative growth consequences related to hypoxic conditions (Eby and Crowder 2002; Prince and Goodyear 2006). Despite a reduction in stomach content biomass, our results demonstrate that yellow perch condition (g dry(g wet)⁻¹), a proxy of energy density (Hartman and Brandt 1995), in offshore LECB did not decrease during August through October, but instead remained unchanged. We do, however, find it noteworthy that yellow perch condition did not increase from August into October, which would be expected as yellow perch tend to acquire energy stores (i.e., lipids) as winter and the reproductive season approach. For

example, studies in western Lake Erie (Henderson et al. 2000) and Saginaw Bay (Diana and Salz 1990; Schaeffer et al. 1999), where seasonal hypoxia is not an issue, suggest a seasonal peak in yellow perch energy density should occur during September. Thus, the conspicuous absence of an increase in somatic condition of yellow perch that remain in offshore waters of LECB is suggestive that hypolimnetic hypoxia may negatively affect condition of a fraction of the Lake Erie yellow perch population.

In addition, consider that increases in system productivity can mirror the magnitude of hypoxia, and possibly compensate for potential negative impacts of hypoxia-induced habitat loss (Diaz, 2001). We have no knowledge as to whether Lake Erie productivity is higher during hypoxic years to compensate for brief habitat loss.

5. Summary and conclusions

Our results suggest that yellow perch alter their foraging and distribution patterns in response to hypolimnetic hypoxia within LECB. Yellow perch move either horizontally or vertically to avoid hypoxic conditions. Individuals remaining in an area with a hypoxic hypolimnion appear to increase their consumption of pelagic diet items, but interestingly even in the presence of a hypoxic hypolimnion, some yellow perch continued to consume benthic prey. Finally, hypoxia-driven changes in yellow perch diet and distribution may have growth and condition consequences for individuals.

As to whether these short-term changes in distribution and foraging at the individual level ultimately have meaningful population-level impacts remains an open issue. For example, we do not know whether the period of reduced growth and condition during late summer and early fall can be offset by rapid growth between fall turnover and the onset of winter. Likewise, we are uncertain as to how horizontal movement of yellow

perch into shallow, normoxic waters might influence growth (e.g., perhaps intra- or inter-specific competition for prey occurs; Eby and Crowder, 2002). Further, hypoxia-induced concentration of yellow perch may affect vulnerability to commercial fishers and may influence agency-based population assessments. Given the expanse and duration of hypoxia in LECB, we urge continued research to elucidate the system-wide, population-level impacts and consequences of these impacts for fisheries management and assessment.

Acknowledgments

This work was supported by the NOAA Great Lakes Environmental Research Laboratory and the NOAA National Sea Grant Program, as part of the International Field Years on Lake Erie (IFYLE) program. Additional ship support was provided by the US EPA, Great Lakes National Program Office. I would like to thank my co-authors Tomas O. Höök, Stuart A. Ludsin, Steven A. Pothoven, Henry A. Vanderploeg, and Stephen B. Brandt who helped prepare this manuscript for publication in the *Journal of Experimental Marine Biology and Ecology*. We would like to thank the captains and crew of the R/V *Laurentian* and R/V *Lake Guardian* for their dedication and field assistance along with Marco Constantini, Hal Gunder, Darryl Hondorp, and Sean Sisler. We also thank Joann Calvaletto, Theodore Bambakidis, Anna Belyeava, Grace Milanowski, Megan Miner, and

Chris Rae for laboratory assistance. This paper is NOAA-GLERL contribution # 1511 and ECOFORE publication # 09-002.

Table 2.1 Physical characteristics of sample sites by month during 2005. Epilimnion (Epi-) defined as isothermal waters above thermocline. Thermocline depth determined as distance (m) from surface to beginning of thermocline. Hypolimnion (Hypo-) defined as isothermal waters below thermocline. A "--" denotes period when site was not sampled or not stratified.

Month (dates)	Site	Depth (m)	Epi- temp (°C)	Epi- DO (mg O₂ l⁻¹)	Thermocline depth (m)	Hypo- temperature (°C)	Hypo- DO (mg O₂ l⁻¹)	Hypo- thickness (m)
June (17-21)	A	20.7	18.2	8.9	9.8	9.6	9.0	8.8
	B	23.2	17.9	8.8	10.8	8.7	10.5	9.8
	D	20.5	18.3	8.9	12.0	10.2	11.2	7.5
	H	14.2	--	--	--	--	--	--
August (15-18)	A	20.7	--	--	--	--	--	--
	B	23.2	25.0	7.1	12.8	10.3	4.6	9.2
	D	20.5	25.2	7.1	17.9	13.0	4.8	3.1
	H	14.2	23.3	6.6	8.0	11.7	2.7	4.1
September (17-19)	A	20.7	21.6	6.3	14.7	11.6	1.1	5.8
	B	23.2	21.7	6.4	16.8	11.3	1.5	6.1
	D	20.5	--	--	--	--	--	--
	H	14.2	21.9	6.8	14.5	15.4	0.9	2.0
October (13-14)	A	20.7	--	--	--	--	--	--
	B	23.2	18.8	7.5	--	--	--	--
	D	20.5	--	--	--	--	--	--
	H	14.2	--	--	--	--	--	--

Table 2.2 Diets of yellow perch collected in Lake Erie's central basin during 2005. The number of yellow perch analyzed, the size range of fish analyzed, proportion of empty stomachs, frequency of occurrence of prey taxa in stomachs, and taxonomic diet category (B-Benthic invertebrates, Z-Zooplankton and O-Other) are presented.

Month	June			August			September			October
Site	A	B	D	B	D	H	A	B	H	B
Number of yellow perch	92	57	57	54	103	19	72	17	72	103
Mean length of yellow perch (mm) (range)	130.8 (100-194)	133.1 (100-194)	143.6 (100-191)	154.7 (101-196)	136.5 (102-197)	147.4 (121-196)	152.3 (115-194)	142.1 (110-176)	155.5 (113-196)	153.7 (110-192)
Proportion of stomachs empty	0.20	0.32	0.40	0.11	0.32	0.73	0.29	0.53	0.32	0.29
Prey taxa frequency of occurrence (taxonomic diet category)										
Amphipoda (B)	0.03	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00
Chironomidae (larvae)	0.16	0.39	0.81	0.52	0.51	0.16	0.63	0.06	0.60	0.55
<i>Dreissena</i> spp. (B)	0.00	0.02	0.16	0.00	0.01	0.00	0.00	0.00	0.01	0.01
Gastropoda (B)	0.01	0.00	0.00	0.02	0.00	0.00	0.01	0.00	0.00	0.00
Hirudinea (B)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.03	0.00
Ostracoda (B)	0.04	0.02	0.00	0.02	0.04	0.00	0.04	0.00	0.04	0.04
Spheridae (B)	0.01	0.00	0.00	0.00	0.01	0.00	0.14	0.06	0.08	0.07
Oligochaeta (B)	0.06	0.02	0.00	0.11	0.02	0.16	0.06	0.00	0.06	0.17
Chironomidae (pupae)	0.41	0.61	0.88	0.50	0.25	0.16	0.36	0.06	0.01	0.65
Fish (O)	0.00	0.00	0.00	0.00	0.01	0.05	0.00	0.00	0.00	0.00
Unknown (O)	0.01	0.02	0.04	0.02	0.00	0.00	0.04	0.00	0.06	0.03
<i>Bosmina</i> spp. (Z)	0.00	0.00	0.00	0.00	0.00	0.05	0.01	0.06	0.00	0.00
<i>Bythotrephes longimanus</i>	0.17	0.00	0.00	0.30	0.01	0.00	0.00	0.00	0.00	0.00
Calanoida (Z)	0.02	0.00	0.00	0.04	0.00	0.00	0.04	0.06	0.00	0.01
Cyclopoida (Z)	0.01	0.04	0.00	0.00	0.01	0.00	0.04	0.12	0.03	
Chydoridae (Z)	0.21	0.04	0.02	0.04	0.24	0.00	0.00	0.18	0.00	0.00
<i>Daphnia</i> spp. (Z)	0.02	0.00	0.00	0.02	0.02	0.05	0.08	0.18	0.01	0.01
<i>Diaphanosoma</i> spp. (Z)	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.06	0.00	0.00
<i>Eubosmina</i> spp. (Z)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00
Harpacticoida (Z)	0.02	0.00	0.00	0.00	0.02	0.00	0.03	0.00	0.00	0.00
<i>Leptodora kinditi</i> (Z)	0.05	0.00	0.00	0.07	0.01	0.00	0.15	0.06	0.01	0.00
<i>Moina</i> spp. (Z)	0.01	0.00	0.00	0.02	0.00	0.00	0.03	0.06	0.00	0.01
Nauplii (Z)	0.01	0.02	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Other Cladocera (Z)	0.05	0.00	0.00	0.04	0.05	0.05	0.00	0.12	0.00	0.00

Table 2.3 Yellow perch selectivity coefficients (W':Vanderploeg and Scavia 1979) for prey taxa in Lake Erie's central basin from June through October 2005. W' values vary from 0-1: 1 represents the most preferred prey item (bolded). We used "--" to represent instances where a prey item is neither represented in our prey sampling or yellow perch diets. Selectivity coefficients for Chironomidae pupae were unavailable due to incomplete sampling for this prey category in the environment. However, a "Y" indicates some consumption of Chironomidae pupae at a site. Zooplankton was not sampled at site H during September; therefore, *B. longimanus* and zooplankton were not included for the September site H selectivity analysis. See Table 2.2 for description of taxa comprising different prey categories.

Month	Site	Chironomidae (larvae)	Benthos	<i>B. longimanus</i>	Chironomidae (pupae)	Zooplankton
June	A	1.00	0.00	0.00	Y	0.04
September	A	1.00	0.00	--	Y	0.10
June	B	1.00	0.01	0.00	Y	0.00
August	B	0.06	<0.01	1.00	Y	0.00
September	B	0.50	0.31	--	--	1.00
October	B	1.00	0.02	0.00	Y	0.00
June	D	1.00	<0.01	0.00	Y	0.00
August	D	0.04	<0.01	1.00	Y	0.02
August	H	0.02	0.00	0.00	Y	1.00
September	H	1.00	0.03	n/a	--	n/a

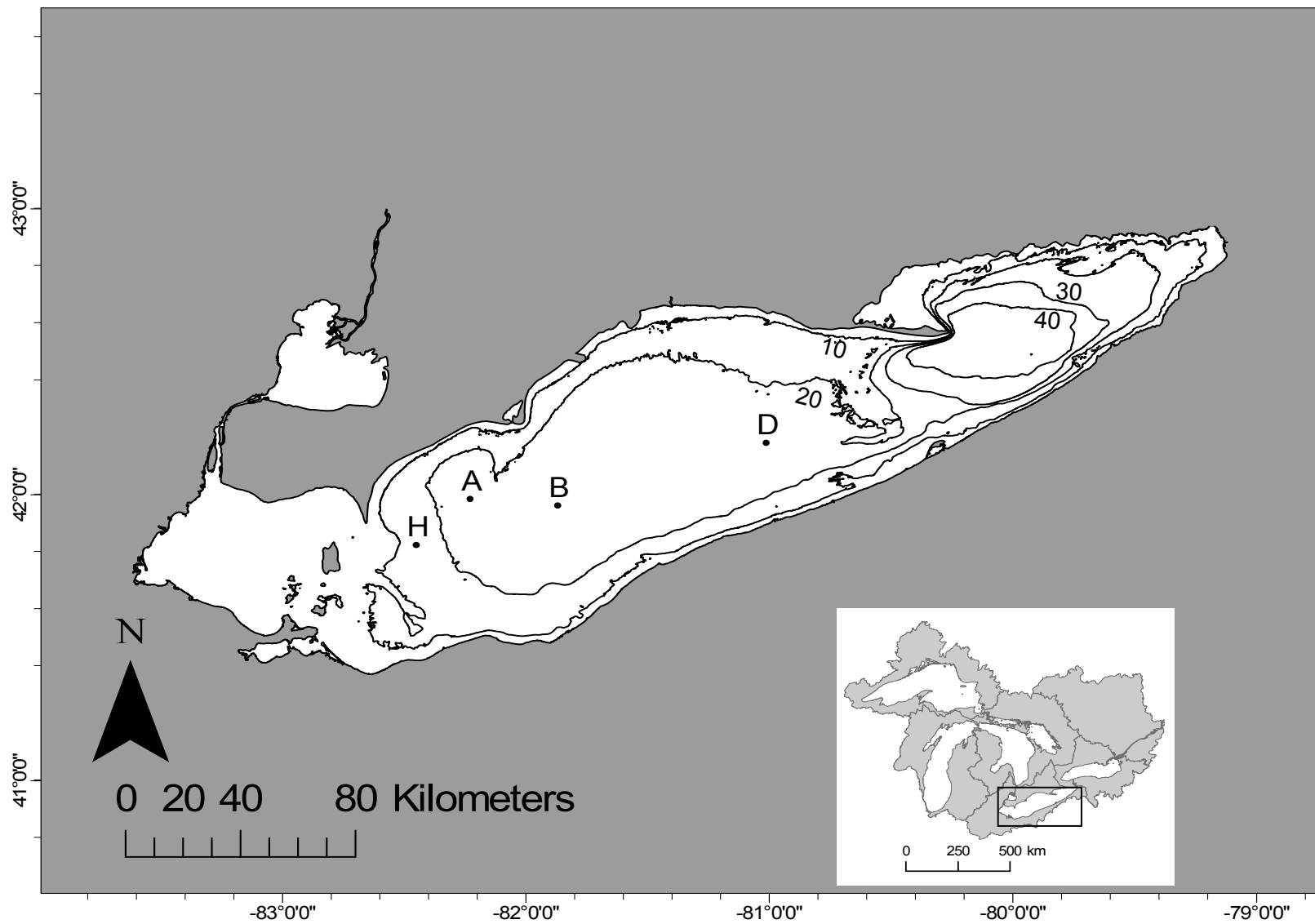


Figure 2.1. Lake Erie with locations of central basin sampling sites (A, B, D, and H) and 10 meter bathymetry lines.

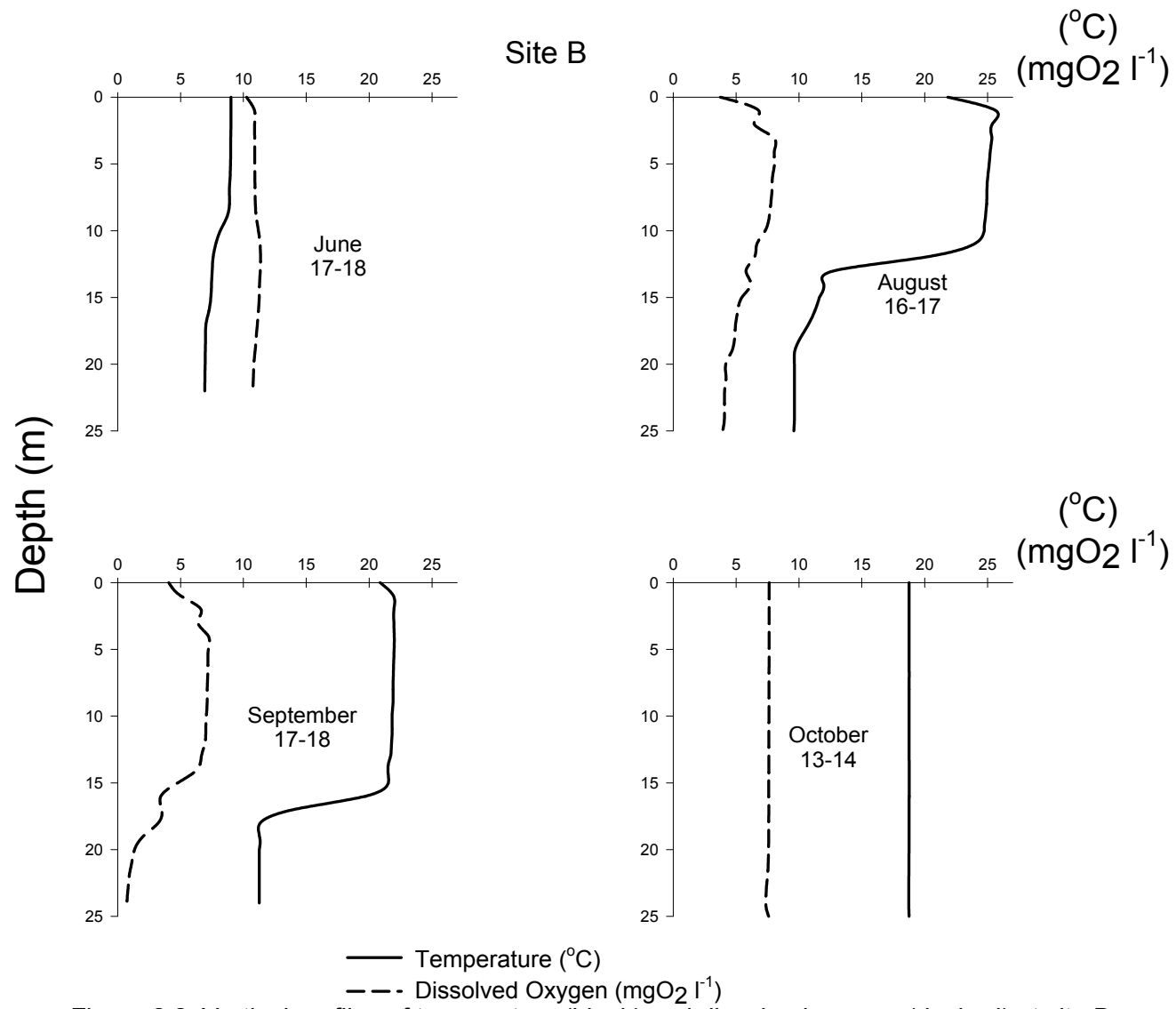


Figure 2.2 Vertical profiles of temperature (black) and dissolved oxygen (dashed) at site B.

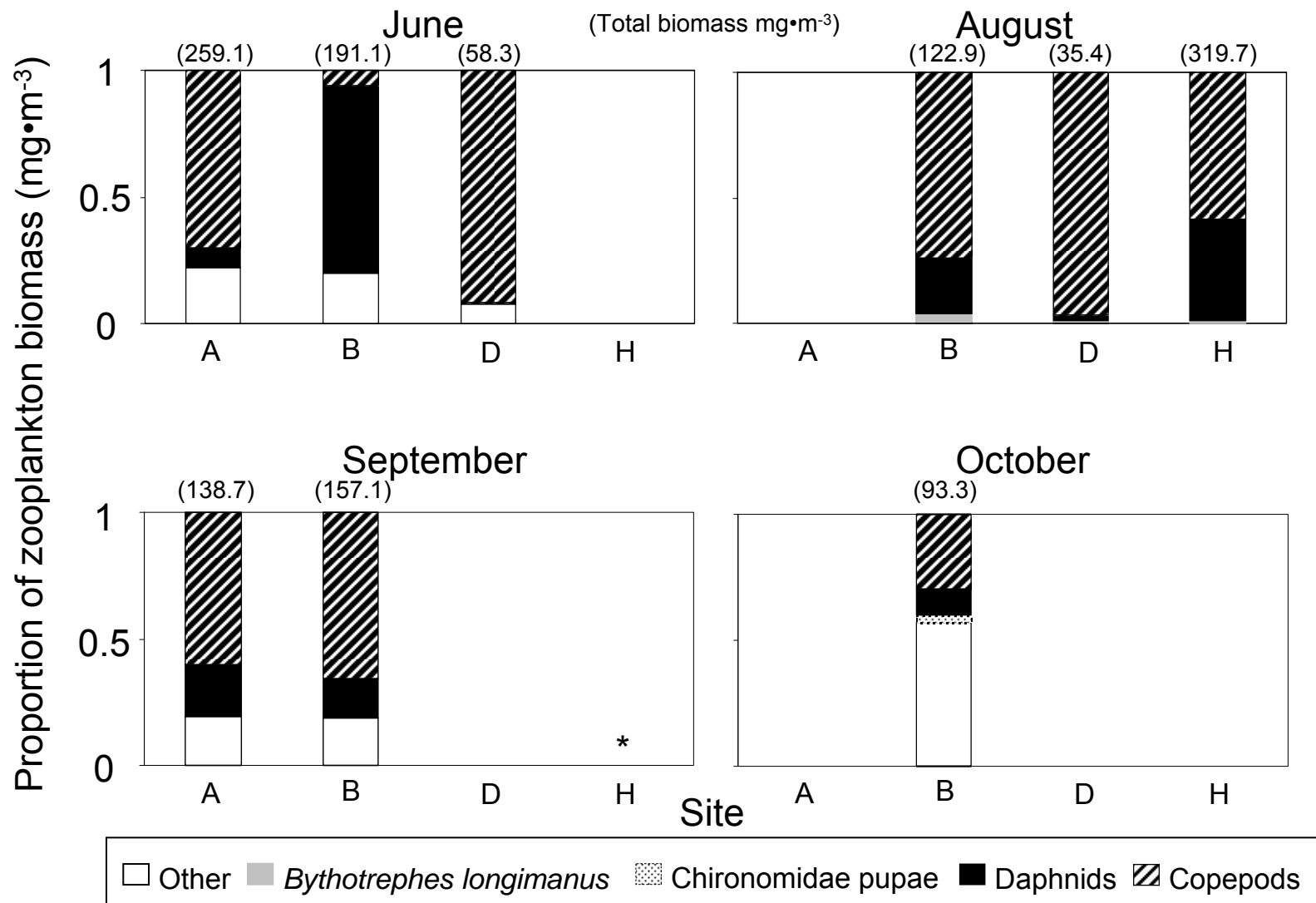


Figure 2.3 Seasonal patterns of proportional zooplankton biomass density by taxa (bars) and total dry zooplankton biomass density ($\text{mg}\cdot\text{m}^{-3}$; in parentheses above columns). Data are combined day and night and presented by site.

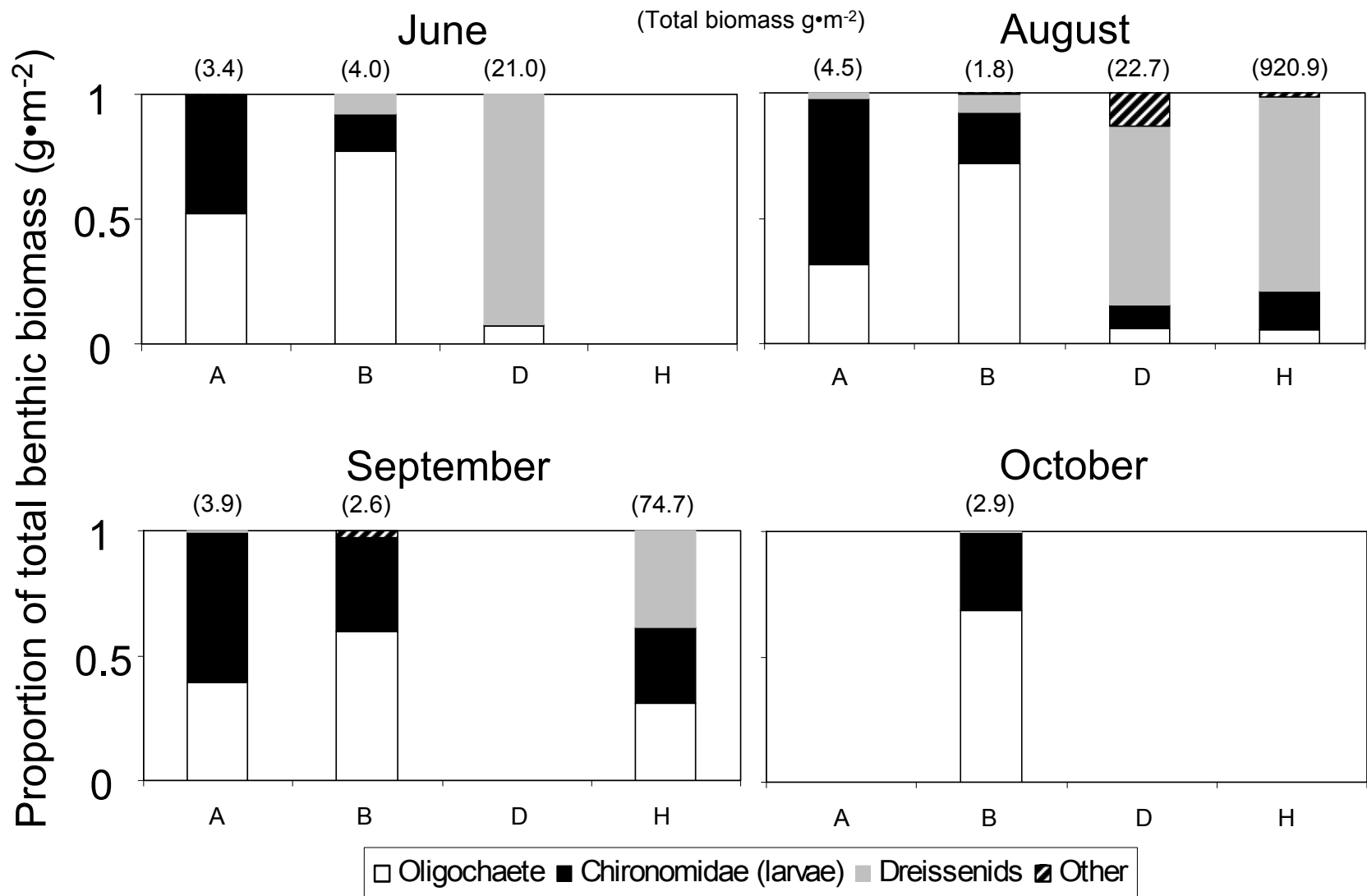


Figure 2.4 Seasonal patterns of proportional benthic macroinvertebrate biomass density by taxa (bars) and total dry macroinvertebrate biomass density ($\text{mg}\cdot\text{m}^{-3}$; in parentheses above columns).

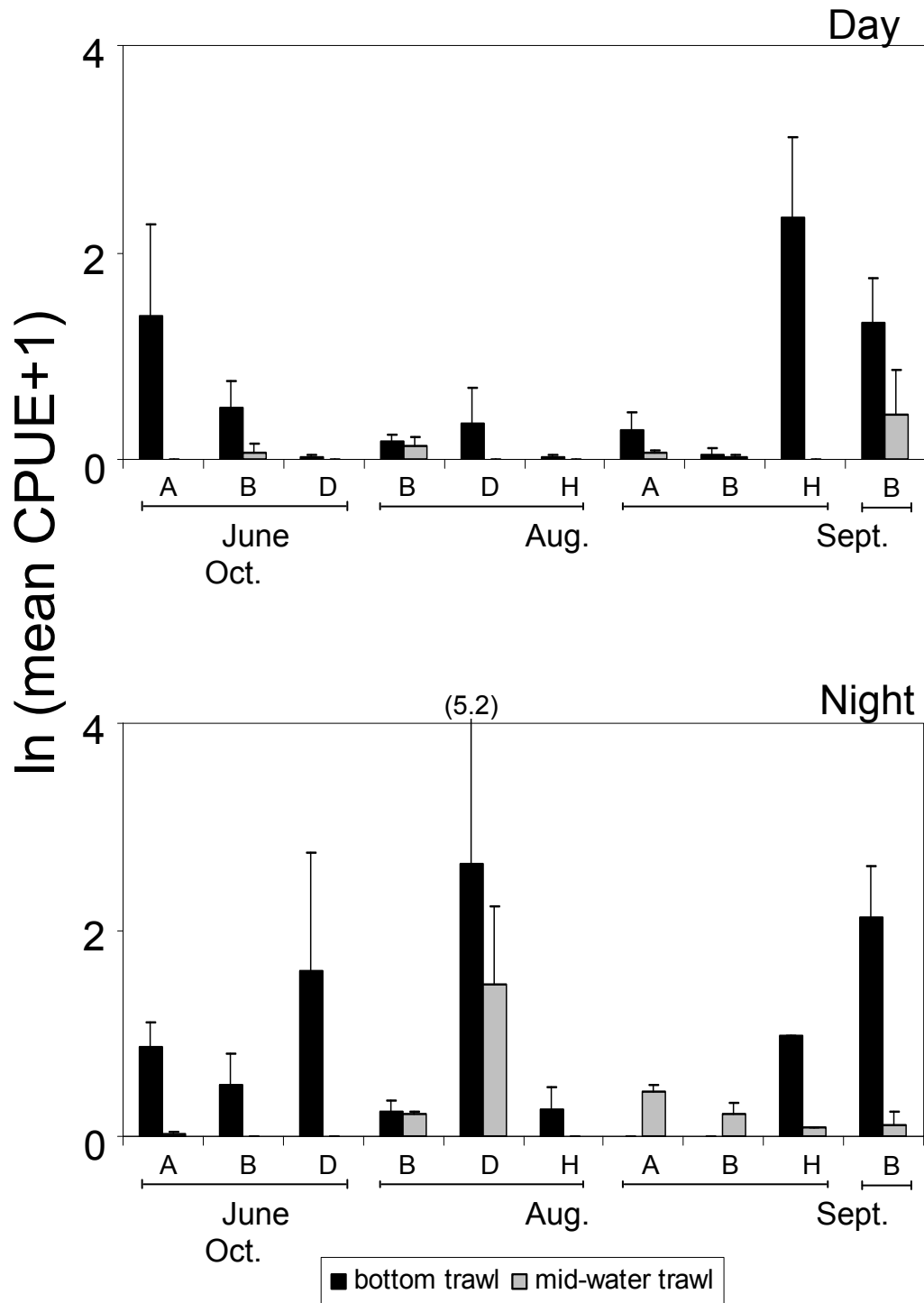


Figure 2.5 Mean (+SE) trawl catch per unit effort (natural logarithm of CPUE+1; number of fish per minute of trawling) of yellow perch in bottom (black) and mid-water (gray) trawls. Data are presented by site, month and time of collection (day or night).

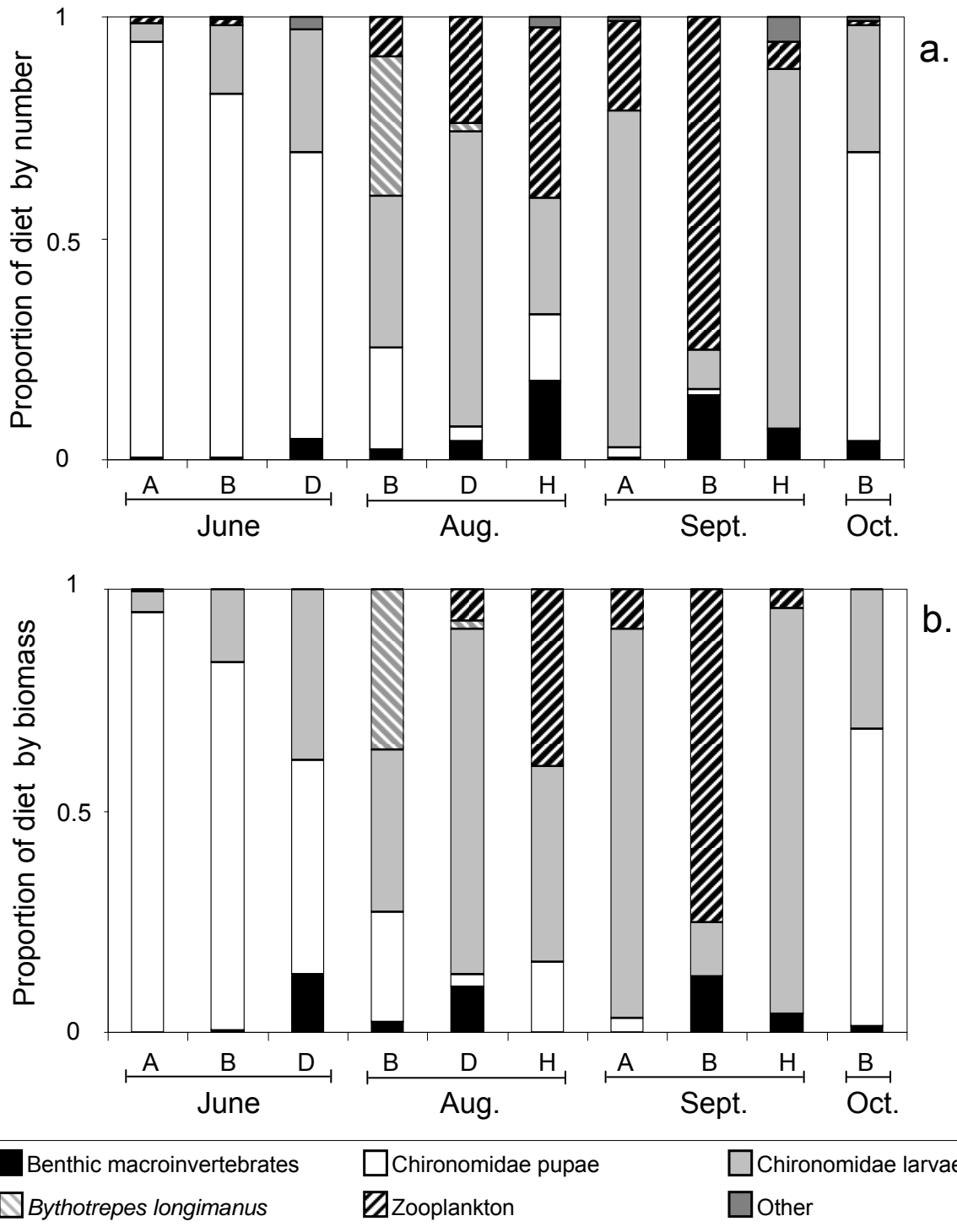


Figure 2.6 Yellow perch diets: a) proportional composition by number of prey items, and b) proportional composition by dry biomass of prey items. Data are presented by site, and month across all collection periods. See Table 2 for description of taxa comprising different prey categories.

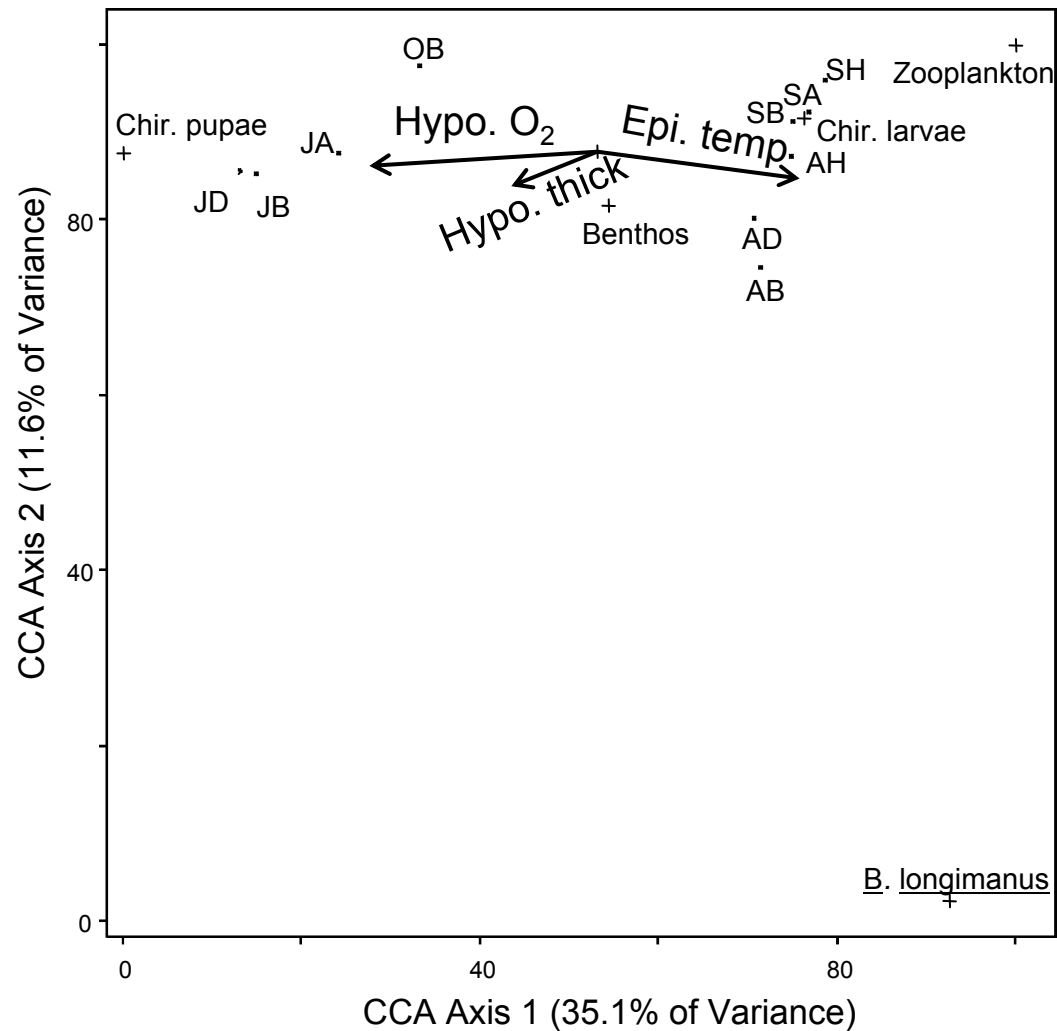


Figure 2.7 Canonical Correspondence Analysis axes one and two are plotted in ordination space overlain with a biplot of environment variables. Sites are represented by two letter codes: first letter depicts sample month (J=June; A=August; S=September; and O=October) and second letter depicts sample site. Centroids of diet categories are represented by '+'s.

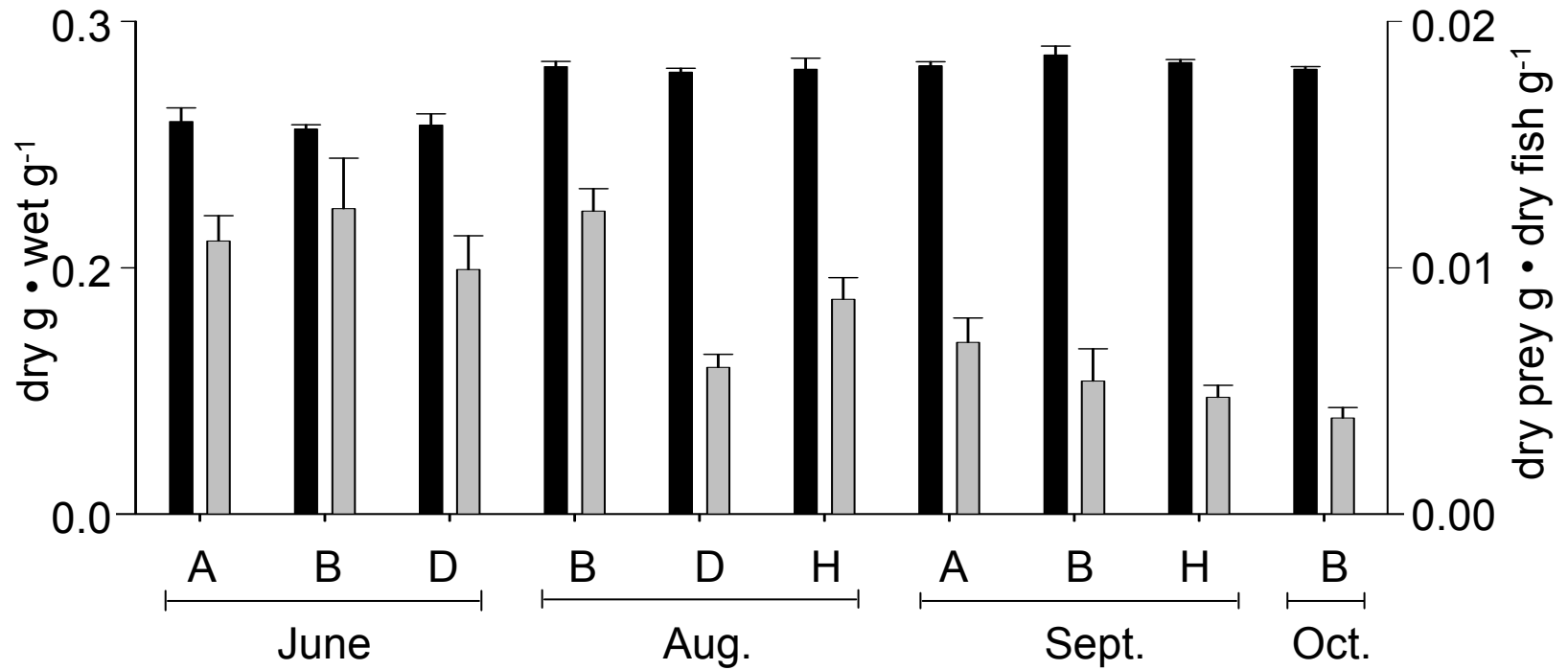


Figure 2.8 Yellow perch mean (+SE) condition (proportion of dry mass; black bars) and mean (+SE) total mass of stomach contents (dry mass of prey per dry mass of yellow perch; g g⁻¹; gray bars). Data are presented by site, and month across all collection periods.

Literature cited

- Aku PMK, Rudstam LG, Tonn WM (1997) Impact of hypolimnetic oxygenation on the vertical distribution of cisco (*Coregonus artedii*) in Amisk Lake, Alberta. *Can J Fish Aquat Sci* 54: 2182-2195
- Aku PMK, Tonn WM (1999) Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. *Trans Am Fish Soc* 128: 17-30
- Baldwin CM, Beauchamp DA, Gubala CP (2002) Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. *Trans Am Fish Soc* 131: 143-158
- Beekey MA, McCabe DJ, Marsden JE (2004) Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. *Oecologia (Berl)* 141: 164-170
- Belore M, Cook A, Einhouse D, Hartman T, Kayle K, Kenyon R, Knight C, MacDougall T, Thomas M (2007) Report of the Lake Erie yellow perch task group. Great Lakes Fishery Commission
- Benke AC, Huryn AD, Smock LA, Wallace JB (1999) Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J North Am Benthol Soc* 18: 308-343
- Bertram PE (1993) Total phosphorus and dissolved oxygen trends in the central basin of Lake Erie, 1970-1991. *J Gt Lakes Res* 19: 224-236
- Boyce FM, Charlton MN, Rathke D, Mortimer CH (1987) Lake Erie research: Recent results, remaining gaps. *J Gt Lakes Res* 13: 826-840
- Breitburg D (2002) Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25: 767-781
- Breitburg DL, Loher T, Pacey CA, Gerstein A (1997) Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. *Ecol Monogr* 67: 489-507
- Breitburg DL, Pihl L, Kolesar SE (2001) Effects of low dissolved oxygen on the behavior, ecology and harvest of fishes: a comparison of the Chesapeake Bay and Baltic-Kattegat systems. In: Rabalais NN, Turner RE (eds) *Coastal hypoxia: consequences for living resources and ecosystems*. American Geophysical Union, Washington DC, pp 241-268
- Breitburg DL, Rose KA, Jr JHC (1999) Linking water quality to larval survival: predation mortality of fish larvae in a oxygen-stratified water column. *Mar Ecol Prog Ser* 178: 39-54

- Breitburg DL, Steinberg N, DuBeau S, Cooksey C, Houde ED (1994) Effects of low dissolved oxygen on predation on estuarine fish larvae. *Mar Ecol Prog Ser* 104: 235-246
- Bur MT, Klarer DM (1991) Prey selection for the exotic cladoceran *Bythotrephes cederstroemi* by selected Lake Erie fishes. *J Gt Lakes Res* 17: 85-93
- Burns NM, Rockwell DC, Bertram PE, Dolan DM, Ciborowski JJH (2005) Trends in temperature, secchi depth, and dissolved oxygen depletion rates in the central basin of Lake Erie, 1983-2002. *J Gt Lakes Res* 31: 35-49
- Cobb SE, Watzin MC (2002) Zebra mussel colonies and yellow perch foraging: spatial complexity, refuges, and resource enhancement. *J Gt Lakes Res* 28: 256-263
- Craig JK, Crowder LB (2005) Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Mar Ecol Prog Ser* 294: 79-94
- Culver DA, Boucherle MM, Bean DJ, Fletcher JW (1985) Biomass of freshwater crustacean zooplankton from length-weight regressions. *Can J Fish Aquat Sci* 42: 1380-1390
- Diana JS, Salz R (1990) Energy storage, growth, and maturation of yellow perch from different location in Saginaw Bay, Michigan. *Trans Am Fish Soc* 119: 976-984
- Diaz RJ (2001) Overview of hypoxia around the world. *J Environ Qual* 30: 275-281
- Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology Annual Review* 33: 245-303
- Eby LA, Crowder LB (2002) Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Can J Fish Aquat Sci* 59: 952-965
- Fuller KH, Shear H, Wittig J (1995) *The Great Lakes: an environmental atlas and resource book*. Environment Canada and U.S. Environmental Protections Agency, Chicago, Ill
- Hartman KJ, Brandt SB (1995) Estimating energy density of fish. *Trans Am Fish Soc* 124: 347-355
- Hartman WL (1972) Lake Erie-effects of exploitation, environmental changes and new species on fishery resources. *J Fish Res Board Can* 29: 899
- Hasler AD (1945) Observations of the winter perch population of Lake Mendota. *Ecology* 26: 90-94

- Hawley N, Johengen TH, Rao YR, Ruberg SA, Beletsky D, Ludsin SA, Eadie BJ, Schwab DJ, Croley TE, Brandt SB (2006) Lake Erie hypoxia prompts Canada-U.S. study. *Eos Trans Amer Geophys Union* 87: 313-315
- Hayward RS, Margraf EJ (1987) Eutrophication effects on prey size and food available to yellow perch in Lake Erie. *Trans Am Fish Soc* 116: 210-223
- Henderson BA, Trivedi T, Collins N (2000) Annual cycle of energy allocation to growth and reproduction of yellow perch. *J Fish Biol* 57: 122-133
- Jaworski A, Ragnarsson SA (2006) Feeding habits of demersal fish in Icelandic waters: a multivariate approach. *ICES J Mar Sci* 63: 1682-1694
- Keast A (1977) Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). *Environ Biol Fishes* 2: 53-70
- Kitchell JF, Stewart DJ, Weininger D (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *J Fish Res Board Can* 34: 1922-1935
- Knight RL, Margraf FJ, Carline RF (1984) Piscivory by walleyes and yellow perch in western Lake Erie. *Trans Am Fish Soc* 113: 677-693
- Kramer DL (1987) Dissolved oxygen and fish behavior. *Environ Biol Fishes* 18: 81-92
- Ludsin SA (unpublished data)
- Ludsin SA, Kershner MW, Blocksom KA, Knight RL, Stein RA (2001) Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecol Appl* 11: 731-746
- Ludsin SA, Mason DM, Zhang X, Brandt SB, Roman MR, Boicourt W, Constantini M (2009) Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: implications for food web interactions and fish recruitment. *J Exp Mar Biol Ecol* 381: S121-S131
- Marcus NH (2001) Zooplankton: responses to and consequences of hypoxia. In: Rabalais NN, Turner RE (eds) *Coastal hypoxia: consequences for living resources ecosystems*. American Geophysical Union, Washington DC, pp 49-60
- Persson L (1981) The effects of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) feed on fish larvae. *Freshw Biol* 11: 131-138
- Petersen JK, Pihl L (1995) Responses to hypoxia of plaice, *Pleuronectes platessa* and dab, *Limanda limanda*, in the south-east Kattegat: distribution and growth. *Environ Biol Fishes* 43: 311-321

- Petrosky BR, Magnuson JJ (1973) Behavioral responses of northern pike, yellow perch and bluegill to oxygen concentrations under simulated winterkill conditions. *Copeia* 1: 124-133
- Pihl L (1994) Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. *Can J Fish Aquat Sci* 51: 321-336
- Pollock MS, Clarke LMJ, Dube MG (2007) The effects of hypoxia on fishes: from ecological relevance to physiological effects. *Environ Rev* 15: 1-14
- Pothoven SA, Vanderploeg HA (2004) Diet and prey selection of alewives in Lake Michigan: seasonal depth, and interannual patterns. *Trans Am Fish Soc* 133: 1068-1077
- Pothoven SA, Vanderploeg HA, Cavaletto JF, Krueger DM, Mason DM, Brandt SB (2007) Alewife planktivory controls the abundance of two invasive predatory cladocerans in Lake Michigan. *Freshw Biol* 52: 561-573
- Prince ED, Goodyear CP (2006) Hypoxia-based habitat compression of tropical pelagic fishes. *Fish Oceanogr* 15: 451-464
- Rabalais NN, Turner RE (2001) Hypoxia in the northern Gulf of Mexico: description causes and change. In: Rabalais NN, Turner RE (eds) *Coastal hypoxia consequences for living resources and ecosystems*, pp 1-36
- Rahel FJ, Nutzman JW (1994) Foraging in a lethal environment: fish predation in hypoxic water of a stratified lake. *Ecology* 75: 1246-1253
- Rosen R (1981) Length-dry weight relationships of some freshwater zooplankton. *J Freshw Ecol* 1: 225-229
- Ryan PA, Knight R, MacGregor R, Towns G, Hoopes R, Culligan W (2003) Fish-community goals and objectives for Lake Erie. *Great Lakes Fishery Commission Special Publication 03-02*: 56
- Schaeffer JS, Haas RC, Diana JS, Breck JE (1999) Field test of two energetic models for yellow perch. *Trans Am Fish Soc* 128: 414-435
- Stanley DR, Wilson CA (2004) Effect of hypoxia on the distribution of fishes associated with a petroleum platform off coastal Louisiana. *N Am J Fish Manag* 24: 662-671
- Suthers IM, Gee JH (1986) Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. *Can J Fish Aquat Sci* 43: 1562-1570
- Taylor JC, Rand PS, Jenkins J (2007) Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. *Marine Biology* 152: 939-957

- ter-Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57: 255-289
- Turner RE (2001) Some effects of eutrophication on pelagic and demersal marine food webs. In: Rabalais NN, Turner RE (eds) *Coastal hypoxia: consequences for living resources and ecosystems*. American Geophysical Union, Washington DC, pp 371-398
- Tyson JT, Knight RL (2001) Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. *Trans Am Fish Soc* 130: 766-782
- Vanderploeg HA, Ludsin SA, Cavaletto JF, Höök TO, Pothoven SA, Brandt SB, Liebig JR, Lang GA (2009a) Hypoxic zones as habitat for zooplankton in Lake Erie: refuges from predation or exclusions zones? *J Exp Mar Biol Ecol* 381: S108-S120
- Vanderploeg HA, Ludsin SA, Ruberg SA, Höök TO, Pothoven SA, Brandt SB, Lang GA, Liebig JR, Cavaletto JF (2009b) Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *J Exp Mar Biol Ecol* 381: S92-S107
- Vanderploeg HA, Scavia D (1979) Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecol Model* 7: 135-149
- Vanderploeg HA, Scavia D, Liebig JR (1984) Feeding rate of *Diaptomus-Sicilis* and its relation to selectivity and effective food concentration in algal mixtures and Lake Michigan. *J Plankton Res* 6: 919-941
- Wetzel MA, Fleeger JW, Powers SP (2001) Effects of hypoxia and anoxia on meiofauna: a review with new data from the Gulf of Mexico. In: Rabalais NN, Turner RE (eds) *Coastal hypoxia: consequences for living resources and ecosystems*. American Geophysical Union, Washington DC, pp 165-185

Chapter 3

Spatial variation of yellow perch (*Perca flavescens*) diet and distribution in response to hypolimnetic hypoxia in Lake Erie's central basin

Abstract

Large areas of hypolimnetic hypoxia ($< 2 \text{ mg O}_2 \cdot \text{l}^{-1}$) recur seasonally in Lake Erie's central basin. This limnological phenomenon may negatively influence the biota of Lake Erie, which include economically important fishes. However, the ecological consequences of such hypoxic areas remain largely unknown. Yellow perch (*Perca flavescens*), a demersal benthivore, may be negatively influenced by seasonal hypoxia as such phenomena can limit access to benthic prey or preferred temperatures. To assess the ecological consequences of hypoxia for yellow perch in central Lake Erie, we collected a suite of biological (i.e., fish with bottom and mid-water trawls, benthic macroinvertebrates using Ponar grabs) and physical (depth, temperature, and dissolved oxygen concentration) data during August and September 2007. We assessed spatial patterns of yellow perch distribution and feeding behavior in response to hypoxia in Lake Erie by sampling within and outside hypoxic areas. We also compared patterns in individual diet specialization among discrete groups of yellow perch. Bottom trawl catches reveal increasing yellow perch catch per unit effort (CPUE) with increasing dissolved oxygen concentrations, while we only captured yellow perch with our mid-water trawls at hypoxic sites. Surprisingly we found no consistent spatial trends in

yellow perch diet composition, and noted that benthic foraging at hypoxic sites was not uncommon. Patterns of yellow perch intrapopulation diet variation suggest some areas exhibit individual specialization in their diet, but these patterns are inconsistent and difficult to interpret. Together, these results suggest that yellow perch avoid hypoxic conditions by moving horizontally or vertically; however, resulting foraging patterns vary spatially.

Introduction

Large areas of hypoxia ($<2 \text{ mgO}_2 \cdot \text{l}^{-1}$) have the potential to critically impair functioning of aquatic systems (Diaz 2001; Diaz and Rosenberg 2008). However, mechanistic understanding of hypoxia-induced ecological consequences is lacking. Evaluating the spatial patterns of responses to hypoxia is a potentially useful approach for understanding how aquatic organisms respond to this environmental stressor.

Environmental stressors can affect mobile aquatic organisms such as fish in a variety of ways, from short-term, subtle behavioral effects to longer-term, population- and ecosystem-level impacts (Rose 2000). A broad range of studies demonstrate that hypoxia can directly and indirectly influence the behavior, growth, and condition of fishes in freshwater (Aku and Tonn 1997; Aku and Tonn 1999; Roberts et al. 2009), estuarine (Eby and Crowder 2002; Stierhoff et al. 2009), and coastal marine (Craig and Crowder 2005) environments. Specifically, hypoxia has potential to alter the distribution of fishes through avoidance behavior (Suthers and Gee 1986; Aku et al. 1997; Eby and Crowder 2002). Eby and Crowder (2002) suggest species-specific thresholds may govern such avoidance behaviors within an estuarine environment and Aku et al. (1997) suggest the complete isolation of cisco (*Coregonus artedii*) from the preferred cool hypolimnetic waters within a hypoxic temperate lake. Avoidance behaviors also have been suggested to compress fishes into smaller areas where inter- and intra-specific density dependent processes may impact individuals (Eby and Crowder 2002; Eby et al. 2005).

Limited evidence exists, however, to indicate that hypoxia-induced consequences translate into population responses (Rose et al. 2009). Elucidation of spatial variation in foraging, distribution, and growth of fishes in response to hypoxia is an important step

towards ultimately evaluating the population- and community-level consequences of this phenomenon (Rose et al. 2009). However, field studies exploring individual-level responses to hypoxia may be confounded by a high degree of inherent variability across space (e.g., different habitats) and time (e.g., seasonal effects). While such confounding effects are difficult to account for in natural systems, we suggest that evaluation of patterns across multiple scales, both spatial and temporal, may overcome some biases related to single dimensional approaches.

Hypoxia occurs seasonally in Lake Erie's central basin (LECB). The severity and duration of hypoxia in LECB is thought to be partially driven by anthropogenically induced nutrient enrichment (Makarewicz and Bertram 1991; Edwards et al. 2005). This phenomenon generally occurs in the late summer and early fall and lasts until fall turnover (Rao et al. 2008). A previous study of hypoxia's influence on the spatial distribution of fish, zooplankton, and phytoplankton suggests an overall shift in fish biomass from benthic habitats during periods of normoxia ($>2 \text{ mgO}_2 \cdot \text{l}^{-1}$) to pelagic habitats during hypoxic conditions (Vanderploeg et al. 2009). A detailed foraging pattern study of important prey fishes (emerald shiner; *Notropis atherinoides* and rainbow smelt; *Osmerus mordax*) in LECB documents shifts in rainbow smelt diet patterns as hypoxia restricts smelt access to preferred cool hypolimnetic habitats, and foraging shifts from benthic to pelagic prey items (Pothoven et al. 2009). We are interested in how yellow perch (*Perca flavescens*), a species at a slightly higher trophic level than rainbow smelt and emerald shiner, and an ecologically important member of the LECB fish assemblage (Ryan et al. 2003), may respond to hypoxic conditions.

Yellow perch in LECB are primarily demersal and benthivorous (Keast 1977; Knight et al. 1984; Tyson and Knight 2001) and thereby may be impacted by hypolimnetic hypoxic conditions. Through a previous study, we examined how hypoxia in LECB affects the ecology of yellow perch by examining temporal variation in their foraging and distribution (Roberts et al. 2009). Based on differences in these temporal patterns, Roberts et al. (2009) suggested that yellow perch either a) avoid areas where any portion of the water column is hypoxic or b) remain in hypoxic zones and occupy upper regions of the water column and consumed a greater amount of pelagic prey than prior to hypoxia. However, ecological interactions of yellow perch outside of low oxygen zones during the presence of hypoxic conditions are unknown. Moreover, the degree of intra-population variation between the two previously described yellow perch responses (a. and b.) remains unquantified. The extent of intra-population ecological variation could have important implications for overall population dynamics (Bolnick et al. 2003). For example, intra-population variation could influence the overall spatial structure of LECB populations and therefore potentially influence their genetic structure and ultimately influence their overall ecological characteristics (Svanback and Eklov 2003; Svanback and Persson 2004; Martin and Pfennig 2009).

Herein, we build on our previous study examining temporal variation of yellow perch ecology, to explore how hypoxia influences spatial distributions (both horizontal and vertical), and diets (amount consumed, composition, and intra-population variation) of yellow perch in LECB. During 2007, we sampled on two occasions during the height of hypoxia (late August and mid September) in areas with an unstratified water column and in stratified areas containing either a hypoxic or normoxic hypolimnia (Figure 3.1).

We evaluated the hypothesis that hypoxia forces yellow perch into normoxic habitats, thereby altering their foraging patterns. In contrast to Roberts et al. (2009), we explored variation in space rather than in time by sampling only while hypoxia was present in LECB. This sample design enabled us to evaluate and compare areas with hypoxic and normoxic hypolimnia, independent of non-hypoxia related seasonal differences.

Methods

During 2007, we sampled LECB twice during hypoxic conditions, 27-30 August and 17-20 September, and collected a suite of biotic and abiotic data. Sampling sites consisted of 5 km long transects and data were collected during day and night periods over the course of 24 hours. We did not collect samples during crepuscular periods (i.e. ± 2 hours of civil twilight), thereby we coarsely captured diel variation of physical and biological variables (Table 3.1; Figure 3.1). We selected sampling sites based on data from pilot trips that mapped the severity and extent of hypoxia in LECB. This sampling design ensured that we would include sites with and without hypoxic conditions. During August, three hypoxic (B, Y, and S) and three normoxic (U, T* and X*; * night only) sites were sampled, whereas during September two hypoxic (B and SN), one normoxic (SS), and two unstratified (D2 and D3) sites were sampled (Table 3.1; Figure 3.1).

Physical variables and potential prey: Field collection

To quantify abiotic environmental conditions of the entire water column, we deployed vertically a sensor package consisting of conductivity, temperature and depth profiler (CTD), fluorometer, and dissolved oxygen sensors (Sea-Bird 911⁺ CTD with Sea-Bird electronic-13 dissolved oxygen sensor; Sea-Bird Electronics, Bellevue WA). Physical and chemical variables were measured once per 24-hour sampling period at

~0.03-m depth intervals at the east, west, and middle of each station transect (i.e., n=3 per transect). When analyzing these data, we grouped measurements into 1-m depth bins.

We collected benthic macroinvertebrates once during each 24-hour sampling period at each site using a Ponar grab sampler (250- μm mesh; 0.047-m²), to determine densities of potential benthic prey items. Samples were collected in triplicate at the east, west, and midpoint of each site transect (i.e., n=9 per site) and concentrated in 5% formalin with rose-bengal dye to facilitate subsequent laboratory analysis.

In the laboratory, benthic samples were placed in a white enamel pan and organisms were located and removed from sediments under a 1.5x-magnifying lens. We identified and enumerated organisms by coarse taxonomic groups (i.e., Chironomidae larva and pupae, oligochaetes, spherids, *Dreissena* spp., and other). For each sample, total lengths (nearest 0.1 μm) of up to 30 individuals per taxonomic group were measured under dissecting microscopes equipped with computer imaging software (Image-Pro® plus 5.1). Then, using taxa-specific length-mass relationships (e.g., Benke et al. 1999), individual dry masses were estimated from measured total lengths, and the mean individual dry mass was multiplied by density counts to estimate taxa-specific biomass density. To quantify oligochaete biomass, we measured dry mass of sub-sampled individuals in each sample.

Fish collection: Trawl methods

Yellow perch were collected using bottom (7.6 m semi-balloon: 13 mm stretched-mesh cod-liner) and mid-water trawls (9.1 x 9.1 m: 13 mm stretched-mesh cod-liner) aboard the R/V *Laurentian*. During a 24-hour sampling period, each type of trawl was deployed at least twice during daylight hours and twice during nighttime conditions. In

general, trawls were towed for 10 min, but the tow duration was adjusted to maximize collection of fish. Upon collection, yellow perch were rapidly enumerated, measured for total length (TL; nearest 1-mm) and mass (nearest 1-g), and frozen (-20 °C).

Foraging patterns: Laboratory techniques

In the laboratory, fish were thawed, their TL (nearest 1-mm) and wet mass (nearest 0.1-mg) were measured, and stomach contents were removed. We identified stomach contents to the lowest possible taxonomic level and grouped these organisms into the same coarse groups for analysis as Roberts et al. (2009). Using dissecting microscopes equipped with Image-Pro® plus 5.1 software, whole organisms TL were measured (nearest 1- μ m) and used to calculate individual dry masses using taxa-specific length-mass relationships (Rosen 1981; Culver et al. 1985; Benke et al. 1999). Estimated mean taxa-specific dry mass were used to estimate the proportional composition of each fish's diet. After all diet items were identified, enumerated, and measured, stomach contents and the entire fish were placed in separate containers and allowed to dry (70°C) for 3-4 days, after which dry mass was measured (nearest 0.1-mg). To minimize the effect of individual size on foraging patterns, we only present diet information for yellow perch between 100-300 mm in total length corresponding to ages 1-3, the most common size class within LECB (Belore et al. 2007).

Data analysis

Potential prey

We used a one-way analysis of variance (ANOVA) with a post-hoc Tukey comparison to compare mean total benthic prey biomass (mean values from the middle, east, and west were used as replicates; n=3 per site) across sites within each month.

Statistical comparisons were performed with SYSTAT® 12 (Chicago, IL), and significant differences were noted at $\alpha=0.05$.

Fish collection

We examined spatial variation of yellow perch relative abundance as catch per unit effort (CPUE, with effort defined as minutes of trawling). Given the differential catchability of bottom and mid-water trawls, we only compared yellow perch CPUE within the same sampling gear. Mean CPUE for a site was calculated by initially determining a mean CPUE for a specific time (day or night), and mean overall site CPUE was calculated as the average of day and night CPUE. We used regression analysis to explore relationships between yellow perch relative abundance and hypolimnetic dissolved oxygen concentration. We conducted separate analyses for daytime, nighttime, and overall CPUE. However, inspection of mid-water trawl CPUE suggested non-linear relationships with hypolimnetic oxygen concentration, and we used a one-way ANOVA to test for variation in mid-water trawl catch between hypoxic ($<2 \text{ mg O}_2 \cdot \text{l}^{-1}$) and normoxic sites ($\geq 2 \text{ mg O}_2 \cdot \text{l}^{-1}$).

Foraging patterns

We used the mean proportional diet composition for each site to summarize overall patterns in diet compositions. We grouped prey into seven coarse groups for our diet analysis: 1) Chironomidae larvae, 2) Chironomidae pupae, 3) other benthos, 4) *Bythotrephes longimanus*, 5) zooplankton, 6) fish and 7) other (i.e., eggs, and unidentifiable organisms). To examine the effects of environmental conditions and prey availability on yellow perch diet patterns, we analyzed proportional diet composition by

biomass across sites, and used Canonical Correspondence Analysis (CCA; ter-Braak and Verdonschot 1995).

For our CCA analysis, an ordination matrix of the diet data (biomass for all prey types) was generated, which was then compared to a separate environmental matrix. We also used Monte Carlo simulations (n=100 runs) to evaluate the significance ($\alpha=0.05$) of CCA axis eigenvalues, wherein the resulting p-value was the proportion of runs with an eigenvalue greater than or equal to the observed value. We tested the null hypothesis that no linear relationship exists between the diet and environmental matrix with these p-values. The variables used in our environmental matrix included mean epilimnetic temperature ($^{\circ}\text{C}$), mean hypolimnetic dissolved oxygen concentration ($\text{mg O}_2 \text{ l}^{-1}$), depth (m), and mean benthic biomass (minus *Dreissena* spp. biomass). We selected these four variables for the environmental matrix because they are an uncorrelated subset of the environmental variables we collected that capture important aspects of the habitat. The environmental matrix was composed of the four variables mentioned above for each site. To interpret the results of this analysis, we graphed yellow perch diet composition for each month and site within the environmental space described by two axes. A biplot of the environmental variable scores was then overlaid on this graph to give more interpretive power to the analysis. All CCA analyses were performed using PC-ORD version 5.0 using a $\alpha=0.05$ level of significance.

To evaluate individual diet specialization of yellow perch and the impact of hypolimnetic oxygen concentrations on diet specialization, we used the individual proportional similarity index (IS) to quantify individual diet specialization (Bolnick et al. 2002). This index is based on Schoener's proportional similarity (PS) index (Schoener

1968) but modified for individual-level analysis (Equation 1). To index the level of individual specialization within a group of yellow perch, we computed the mean of all the individual PS values (Bolnick 2002; Equation 2).

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| \quad (\text{Equation 1})$$

$$IS = \frac{1}{N} \sum_i PS_i \quad (\text{Equation 2})$$

Where p_{ij} is the proportion of diet category j in individual i 's diet, q_j is the proportion of category j in the entire population of diets. We used the same diet categories for this analysis that were used for the proportional composition analysis. This measure of specialization varies from 0-1 and relates observed individual diet patterns to that of the entire population. Values close to zero indicate strong individual specialization while values close to one indicate a population of individuals proportionally foraging on similar prey items (Bolnick et al. 2002). We also used Monte Carlo bootstrapping techniques ($n=100$) to address the likelihood that IS values are significantly different from one (i.e., no individual specialization; Bolnick et al. 2002). All diet specialization values were calculated using the program IndSpec 1.0 (Bolnick et al. 2002). We used these measures to evaluate specialization of yellow perch both across and within sites. When determining the across site measures of specialization (IS_{all}) we used all the yellow perch sampled during a month regardless of the sample site to determine the overall proportion of each diet category (q_j). We then calculated the mean of individual PS values at each site to compare site IS values (IS_{mth}). We used a similar analysis to evaluate within-site IS values (IS_{site}) but used only yellow perch from each site as our population to determine the overall proportion of each diet category (q_j). To compare IS_{mth} values among sites we

used one-way ANOVA with a post-hoc Tukey comparisons ($\alpha=0.05$) using site as our factor.

Results

Trawl catch

We found a significant positive relationship between hypolimnetic dissolved oxygen concentration and bottom trawl yellow perch CPUE based on overall catches and nighttime catches (Figure 3.2a and c). We analyzed our mid-water trawl results using a one-way ANOVA with oxygen conditions as a factor ($>$ or $<$ $2 \text{ mg O}_s \cdot \text{l}^{-1}$) and found no statistical difference between overall hypoxic and normoxic mid-water yellow perch CPUE; however, note that yellow perch only were captured within the mid-water trawl at hypoxic sites (Figure 3.2b, d, and f).

Available prey

Benthic macroinvertebrate collections indicated that dreissenid mussels contributed the greatest proportion of benthic macroinvertebrate biomass at every site sampled (Figure 3.3a and b). ANOVA analyses demonstrate that total benthic biomass (g dry mass/m^2) did not differ among sites in August or September (Figure 3.3a). However, when we removed dreissenids and tested for differences in remaining biomass, ANOVA analyses revealed differences among sites during both August and September (Figure 3.3b). Among our August sites, only B and U were not significantly different (Tukey post-hoc comparison), with site Y having the highest mean benthic biomass (excluding dreissenids) and sites B and U having the lowest mean benthic biomass (Figure 3.3b). In September, mean benthic biomass at D2 was greater than SN and SS (Figure 3.3b).

Foraging patterns

We excluded site T and X from our diet analysis due to high proportions (>0.90) of yellow perch with empty stomachs. Site B was only included in our August diet analysis because no yellow perch were captured at this site during September (Table 3.2). Diet results from August suggest that, at moderately low oxygen levels (B and S), yellow perch consume primarily Chironomidae (72% and 83% by mass respectively), while at a severe hypoxic site (Y), yellow perch only consumed pelagic items (Figure 3.4). At site U (the only normoxic site in August), yellow perch consumed mostly *B. longimanus* (52% by mass), a highly preferred, large-bodied zooplankton species (Bur and Klarer 1991; Figure 3.4).

During September, yellow perch at a hypoxic site (SN) primarily consumed Chironomidae larvae (97% by mass), whereas fish from a stratified normoxic site (SS) targeted *B. longimanus* (71% by mass). At a relatively deep, unstratified site (D2) yellow perch consumed a large proportion of Chironomidae larvae (87% by mass), whereas yellow perch at a shallower, unstratified site (D3) foraged roughly equally upon zooplankton (32% by mass), fish (25% by mass), and Chironomidae larvae (27% by mass; Figure 3.4).

A CCA analysis suggests that during August-September 2007 a site's benthic macroinvertebrate density ($\text{g}\cdot\text{m}^{-2}$; excluding dreissenids), hypolimnetic dissolved oxygen concentration, and depth all explain some of the variation in yellow perch diet patterns. The first axis explained the most variation (38%) and was heavily weighted by benthic macroinvertebrate density and hypolimnetic dissolved oxygen, while the second axis was weighted primarily by depth (Figure 3.5). However, a Monte Carlo simulation to test the

significance in the relationship between our observed diet patterns and environmental conditions suggests these results are not statistically significant ($p= 0.29$).

The IS analysis of diet data is suggestive of individual diet specialization among LECB yellow perch. During August and September, a significant amount of diet specialization (IS_{all}) exists across all habitat types (Figure 3.6a). No difference in IS_{mth} exists among sites in August, when all sites seemed to exhibit individual diet specialization (Figure 3.6a). However, during September, the deeper sites (SN-hypoxic and D2-unstratified) had less IS_{mth} than the shallower sites SS (normoxic) and D3 (unstratified; Figure 3.6a). Within sites during August only, yellow perch within normoxic habitats appear to exhibit individual diet specialization (IS_{site} ; Figure 3.6b). However, during September yellow perch at D3 (shallow and unstratified) and SS (normoxic) exhibit IS_{site} in their diet patterns (Figure 3.6b). These results indicate a pattern of decreasing within-month, site-specific IS_{mth} values from August to September. However, within sites (i.e., IS_{site}), it appears hypoxic sites are less specialized than non-hypoxic sites (normoxic and unstratified). Overall, yellow perch diets exhibit individual specialization (IS_{all} and IS_{mth}) and some site-specific specialization (IS_{site}), but these patterns are inconsistent and not clearly explained by environmental variables.

To examine the specific taxonomic composition underlying specialization among yellow perch, we used the frequency of occurrence for each diet category and the average number of diet items in fish at each site (Table 3.2). During August at our hypoxic sites (S and Y), yellow perch either consumed benthic items (S) or pelagic zooplankton (Y) exclusively, except for *B. longimanus* foraging at site S (Table 3.2). At normoxic site B in August, the majority of yellow perch foraged upon benthic items exclusively.

However, at normoxic site U, foraging patterns included mostly pelagic zooplankton while a smaller proportion of these perch consumed benthic prey items as well (Table 3.2). During September, at our hypoxic site (SN) all yellow perch consumed Chironomidae larvae, at our normoxic site (SS) almost all the yellow perch consumed *B. longimanus* and benthic consumption was low (Table 3.2). At unstratified sites (D2 and D3) in September, we found that yellow perch at the deeper D2 site had more generalist foraging behavior, whereas at the shallower D3, our data suggest individual yellow perch consumed either benthic items or pelagic zooplankton (Table 3.2). We also note that these diet results should be interpreted with caution, given the small amount of yellow perch we were able to collect at hypoxic sites for diet analyses.

Discussion

Our results suggest yellow perch within LECB appear to avoid hypoxic conditions by either migrating vertically in the water column or horizontally to habitats with higher dissolved oxygen levels. However, given this somewhat drastic change in distribution, overall diet composition patterns appear independent of hypolimnetic oxygen conditions with some perch continuing to make foraging forays into hypoxic areas to forage upon benthic items. Interestingly, distinct groups appear to display varying degrees of individual specialization in foraging patterns. During normoxic conditions, yellow perch exhibit a range of foraging patterns within specific habitats. However, when hypoxic conditions arise, yellow perch seem to exhibit similar foraging patterns within a site or specific spatial location, therefore exhibiting less site-specific individual diet specialization (IS_{site}). However, our site-specific diet results (proportional

and individual specialization) should be interpreted with caution, given the small sample size of yellow perch captured at sites with hypoxic conditions.

The avoidance of hypoxic habitat is a potential manner by which fish could dampen or mitigate the potential negative effects of hypoxia (Kramer 1987). Avoidance as a behavioral response to hypoxia has been reported for freshwater (Suthers and Gee 1986; Aku et al. 1997; Baldwin et al. 2002), estuarine (Eby and Crowder 2002; Ludsin et al. 2009), and marine (Craig and Crowder 2005; Prince and Goodyear 2006) ecosystems. Eby et al. (2005) suggest that, within the Neuse River Estuary, the different abiotic and biotic conditions encountered by fishes when avoiding hypoxia can include crowding of individuals in small areas of normoxic habitat, eliciting density-dependent reductions in growth rates. Within LECB, previous studies have suggested that yellow perch and other fishes avoid hypoxic areas (Roberts et al. 2009; Vanderploeg et al. 2009) and the data presented herein further demonstrate that yellow perch do avoid low oxygen habitats. Moreover, our results suggest individual yellow perch confronted with hypoxic conditions may respond differently. That is, yellow perch avoidance behavior is manifested by either migrating vertically (higher in the water column) or horizontally (to shallower habitats).

The lack of consistent trends in our diet results suggests that yellow perch moving to avoid hypoxia may consequently be forced into fundamentally different habitats (i.e., prey items, fish community, and thermal conditions; Table 3.1; Figure 3.3). This change in habitat may result in different foraging opportunities, thus clouding the influence of oxygen conditions on yellow perch dietary patterns. These diet results are somewhat different from the 2005 study investigating temporal trends in diet and distribution that

suggested a consistent shift from benthic prey items to pelagic items during periods of hypoxia (Roberts et al. 2009). Our data presented herein suggest that yellow perch at hypoxic sites proportionally consume more benthic items than reported previously by Roberts et al. (2009). However, hypoxic conditions were more severe in 2007 than 2005 (Table 3.1; Roberts et al. 2009), and the severity of low oxygen conditions may influence benthic macroinvertebrate behavior, also helping to shape foraging patterns of yellow perch. For example, increased severity of hypoxic conditions may influence the behavior of Chironomidae larvae through an increase in their exposure (Kon and Hidaka 1983; Stief et al. 2005) and movement (Leuchs 1986) in an attempt to extract dissolved oxygen from an environment with depauperate oxygen conditions. These types of prey behaviors could influence the ability of yellow perch to successfully detect and consume these benthic organisms.

The presence of benthic organisms in diets of yellow perch collected at hypoxic sites is particularly noteworthy. However, examination of individual diets suggests that there may be intrapopulation level variation in diet patterns. To further explore individual specialization of yellow perch foraging patterns and how hypoxia may influence these patterns we performed a similar IS analysis on yellow perch from 2005. These 2005 data were collected using identical methods to those described herein, and previously used to examine temporal patterns in diet and distribution responses to hypoxia (Roberts et al. 2009). With the 2005 data we determined IS values 1) within one site (IS_{all}) across four months (June, August, September, and October; IS_{mth}) and 2) among sites (IS_{site}). At site B, across four months (including hypoxia during September) the amount of IS_{mth} is greatest during September (Figure 3.7a). Results from yellow

perch collected in 2005 suggest that there is a significant amount of IS_{site} during every month except September (Figure 3.7b). However, the IS_{site} values suggest these trends are not consistent among all sites (Figure 3.7b).

We also used these data to examine the taxonomic specific characteristics of these specializations by calculating the mean number of diet items, and frequency of occurrence for each diet category (Table 3.3). During normoxic conditions (June, August, and October), yellow perch consume Chironomidae larvae and pupae except at site D in August where some individuals forage on pelagic zooplankton. Conversely, during hypoxic conditions (September) at site B yellow perch consume either benthic or pelagic organisms (Table 3.3).

A significant amount of individual diet specialization exists for yellow perch diets from both 2005 and 2007, within normoxic habitats. Conversely, among the yellow perch remaining in hypoxic areas, individuals exhibit relatively uniform diet patterns, which are site-specific. However, these patterns are not consistent across all non-hypoxic sites (stratified-normoxic and unstratified) as evidenced by yellow perch from SS and D2 exhibiting IS_{site} values similar to hypoxic sites (S, Y, and SN). Overall, our results suggest there may be intra-specific groups of yellow perch displaying unique habitat use and foraging patterns within LECB, and therefore, our data suggest that within the LECB yellow perch population, individual diet specialization may be taking place.

These patterns could be characterized as phenotypic plasticity, a trait previously reported for Eurasian perch (*Perca fluviatilis*; Hjelm et al. 2000; Svanback and Eklov 2003; Olsson et al. 2007; Quevedo et al. 2009) and yellow perch within Lake Michigan (Parker et al. 2009). Variation of ecological characteristics at the intra-population level

has been hypothesized to have implications for population stability (Bolnick et al. 2003) and food-web interactions (Quevedo et al. 2009).

Individual diet specialization within fish populations has been reported for multiple species of temperate freshwater fish species. A long-term study of Arctic charr (*Salvelinus alpinus*) demonstrated that within a single population similar amounts of individual diet specialization were consistently present and could be a cause of speciation (Knudsen et al. 2010). The presence of individual specialization for this population was demonstrated to be maintained by genetic mechanisms through a laboratory experiment (Klemetsen et al. 2006). A study across multiple boreal lakes of northern pike (*Esox lucius*) reports intrapopulation individual diet specialization characterized by two foraging types, invertivores and piscivores (Beaudoin et al. 1999). Diet analysis and stable isotopes were used to demonstrate that the proportion of these two foraging types is dependent on the forage fish community of individual lakes (Beaudoin et al. 1999). Multiple studies of threespine stickleback (*Gasterosteus aculeatus*) have reported individual specialization of populations, which is driving speciation through intraspecific competition and disruptive selection (Bolnick et al. 2002; Bolnick 2004; Araujo et al. 2008). However, all of these studies provide little evidence to what common population characteristic(s) may be causing individual diet specialization among species.

A review of population characteristics and the degree of individual specialization demonstrated that populations of ecological generalists can actually be composed of heterogeneous groups of specialized individuals (Bolnick et al. 2007). Bolnick et al. (2007) found this trend to exist among a diverse set of organisms: Two fishes (threespine stickle back-*Gasterosteus aculeatus* and Eurasian perch), one reptile (anolis lizards-

Anolis sagrei, three amphibians (Brazilian savannah frogs-*Adenomera* sp., *Eleutherodactylus* sp., *Leptodactylus fuscus*), and one mollusk (Whelk-*Nucella* sp.). Within each of these five groups, the amount of individual diet specialization increased with increasing niche-width. However, the mechanisms for this diet specialization and increase in niche-width varied across groups, but included behavior, morphology, and interactions between these traits, both of which are heritable and plastic (Bolnick et al. 2007).

Yellow perch are an ecological generalist (Keast 1977; Knight et al. 1984; Jansen and Mackay 1992; Parrish and Margraf 1994; Tyson and Knight 2001; Roberts et al. 2009) with demonstrated phenotypic plasticity within the Great Lakes (Parker et al. 2009). Therefore, the likelihood that groups of individuals with specialized foraging patterns exist within Lake Erie is high. The diet specializations we observed are likely driven by either morphological or behavioral mechanisms (Bolnick et al. 2007). Consequently, a limnological event like hypoxia could potentially influence these groups differently. Future research of individual specialization in LECB yellow perch will help determine if assessments of intrapopulation groups are important to the population and community dynamics of economically and ecologically important fishes within Lake Erie.

Overall, our data suggest that during hypoxic conditions in LECB yellow perch display behavioral modifications (i.e., dispersal and diet). Therefore, we can speculate that these behaviors may be an attempt to mitigate the potential negative impacts of hypoxia. However, exactly how yellow perch move to avoid hypoxia and the proportional occurrence of horizontal versus vertical avoidance within LECB yellow

perch remains equivocal. These types of movement patterns are poorly understood for many Great Lakes fishes, but remain an important part of their ecology. Understanding the patterns of how and when fishes or any mobile organism move within an ecosystem has been suggested to have potential linkages to processes regulating populations and food web structure (Nathan 2008). Therefore, elucidating fine-scale habitat use and preference patterns should be essential for informing management decisions affecting harvest policies, habitat improvement, and habitat alteration.

Our results demonstrate that spatial patterns in the ecological response of yellow perch to hypoxia in LECB may have direct and indirect influences at multiple scales (i.e., individual- and population-level). The avoidance behavior of yellow perch suggested by our data also may influence their diet patterns. However, these diet patterns remain enigmatic. Nonetheless, our results suggest yellow perch can somewhat mitigate the direct negative affects of hypolimnetic hypoxia through behavioral modifications in the form of avoidance behavior. Hypolimnetic hypoxia within LECB undoubtedly influences individual yellow perch. Therefore, to examine the population-level consequences for fish of such a limnological phenomenon effectively, an ecosystem level approach that recognizes processes at multiple scales is warranted.

Acknowledgements

This work was supported by the NOAA Great Lakes Environmental Research Laboratory and the NOAA National Sea Grant Program, as part of the International Field Years on Lake Erie (IFYLE) program. This work was also supported by NOAA's Center for Sponsored Coastal Ocean Research, through the Ecological Forecasting: Hypoxia

Assessment in Lake Erie grant NA07OAR432000. I would like to thank my co-authors Tomas O. Höök, Stuart A. Ludsin, Steve Pothoven, and Henry A. Vanderploeg who help perform this research and produce this manuscript I would also like to thank all those who helped with field portions of this study including, Greg Jacobs, Brad Utrup, Dave Fanslow, Joann Cavaletto and Aaron Adamack. I would also like to thank those who help with the laboratory portion of this study including Krista Latta, and Kara Lindelof. Lastly, I would like to extend a special thanks to the captains and crew of the R/V Laurentian who were a tremendous help.

Table 3.1 Mean abiotic habitat characteristics of sites sampled in Lake Erie’s central basin during summer 2007. Sites are categorized as: Hypoxic (H), Normoxic (N), and Unstratified (U). Groupings based on the presence (H or N) or absence (U) of a thermocline, and (if thermocline is present) hypolimnetic dissolved oxygen concentration ($>2 \text{ mg O}_2 \cdot \text{l}^{-1} = \text{N}$, $\leq 2 \text{ mg O}_2 \cdot \text{l}^{-1} = \text{H}$). The absence of any vertical thermal structure at unstratified sites (U) is denoted by (--)’s within specific cells.

Month (dates)	Site	Depth (m)	Epilimnion Temp. (°C)	Epilimnion DO (mg O ₂ ·l ⁻¹)	Thermocline depth (m)	Hypolimnion temp. (°C)	Hypolimnion DO (mgO ₂ ·l ⁻¹)	Category
August (27-30)	B	24.0	23.1	7.5	15	11.8	2.1	H
	S	20.0	23.9	7.2	16	12.8	1.4	H
	U	13.5	23.4	7.5	11	20.5	4.1	N
	T	13.0	23.9	6.6	--	--	--	U
	Y	19.0	23.6	7.1	14	11.8	0.6	H
September (17-20)	B	23.5	19.4	6.9	19	12.1	1.0	H
	D2	21.0	20.8	6.7	--	--	--	U
	D3	17.5	20.9	6.8	--	--	--	U
	SN	22.5	19.9	7.2	20	12.7	1.4	H
	SS	18.0	21.0	6.8	18	18.6	4.5	N

Table 3.2 Mean yellow perch summary statistics for fish size and specific diet patterns sampled during August and September 2007 from Lake Erie's central basin. Frequency of occurrence for each diet category and the mean number or diet items per individual shown for each site and month.

Year	Month	Site	Total length (mm)	Number of yellow perch (% empty)	Average # of diet items	Frequency of occurrence					
						Chir. larvae	Chir. Pupae	<i>Bythotrephes longimanus</i>	Fish	Benthos	Zoop.
2007	August	B	132	38 (65%)	1.15	0.77	0.23	0.00	0.00	0.15	0.00
	August	S	194	8 (50%)	2.25	1.00	0.50	0.25	0.00	0.50	0.00
	August	U	203	36 (55%)	1.81	0.06	0.06	0.75	0.00	0.19	0.75
	August	Y	213	5 (20%)	1.75	0.00	0.00	0.75	0.00	0.00	1.00
	September	D2	153	67 (23%)	2.46	0.98	0.26	0.30	0.48	0.26	0.18
	September	D3	137	42 (64%)	1.38	0.46	0.31	0.15	0.00	0.15	0.31
	September	SN	243	5 (40%)	1.67	1.00	0.00	0.67	0.00	0.00	0.00
	September	SS	177	55 (53)	1.24	0.10	0.10	0.90	0.00	0.05	0.10

Table 3.3 Mean yellow perch summary statistics for fish size and specific diet patterns sampled during the summer of 2005 from Lake Erie's central basin. Frequency of occurrence for each diet category and the mean number or diet items per individual shown for each site and month.

Year	Month	Site	Total length (mm)	Average # of diet items	Frequency of occurrence					
					Chir. larvae	Chir. Pupae	<i>Bythotrephes longimanus</i>	Fish	Benthos	Zoop.
2005	June	A	130	1.23	0.21	0.99	0.00	0.00	0.01	0.01
	September	A	152	1.70	0.95	0.43	0.00	0.00	0.23	0.09
	June	B	139	1.53	0.50	0.90	0.00	0.00	0.03	0.10
	August	B	155	1.67	0.67	0.54	0.31	0.00	0.00	0.15
	September	B	134	1.14	0.14	0.00	0.00	0.00	0.14	0.86
	October	B	155	1.96	0.88	0.95	0.00	0.00	0.13	0.02
	June	D	150	1.96	0.88	0.96	0.00	0.00	0.13	0.00
	August	D	141	1.48	0.92	0.27	0.02	0.00	0.10	0.17
	August	H	135	1.75	0.75	0.75	0.00	0.00	0.00	0.25
	September	H	156	1.18	1.00	0.00	0.00	0.00	0.15	0.03

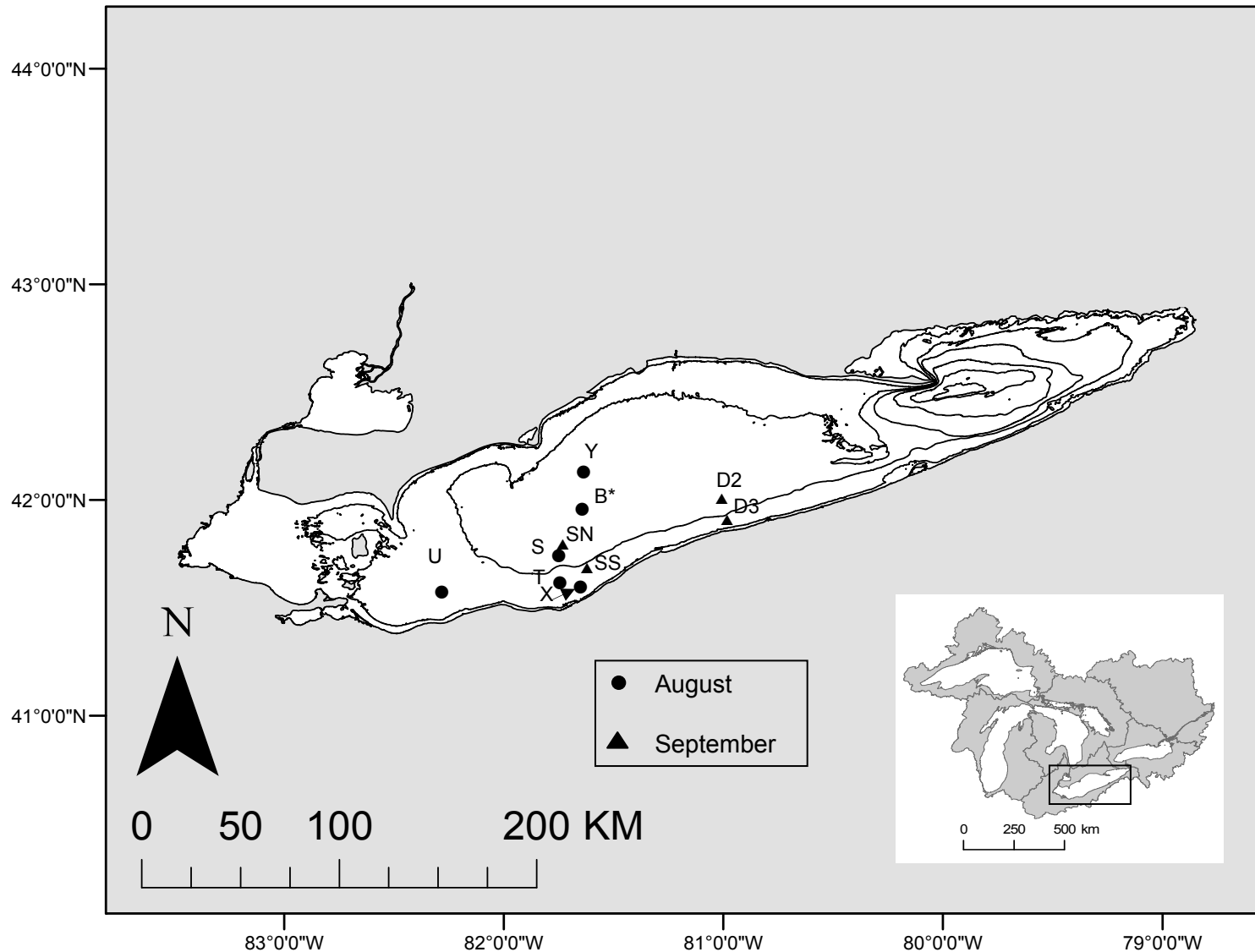


Figure 3.1 The location of Lake Erie within the Laurentian Great Lakes and our 2007 sites sampled during August and September. Lake Erie bathymetry is depicted with 10-meter depth contours. *Site B was sampled during both August and September.

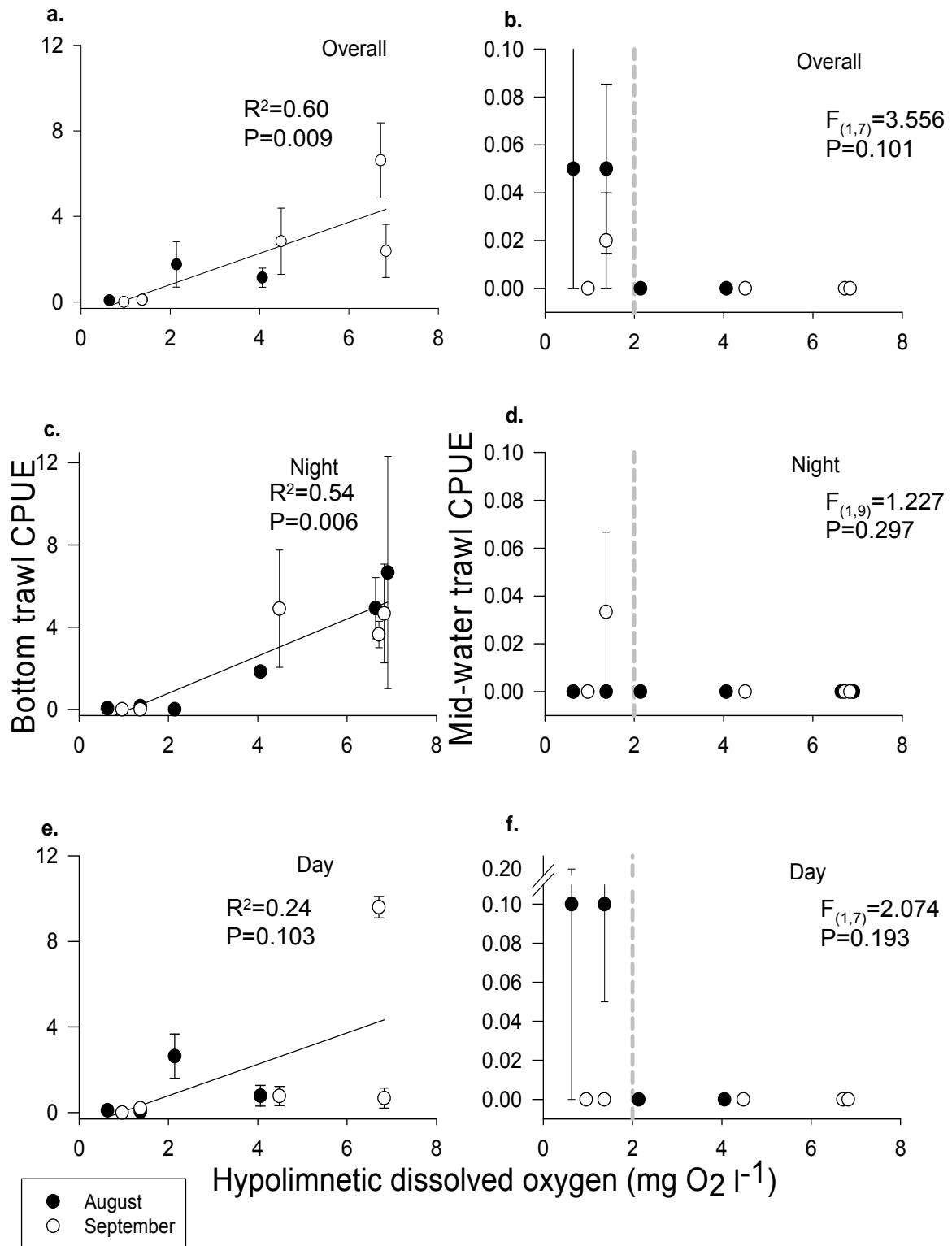


Figure 3.2 Trawl results shown as catch per unit effort (CPUE; yellow perch per minute of trawling \pm SE) for a. bottom trawls (BTR) and b. mid-water trawls (MTR). Trawl catches are shown as mean CPUE across all time periods (a and b), night (c and d), and day (e and f). Trawl results are plotted against hypolimnetic dissolved oxygen concentration ($\text{mg O}_2 \cdot \text{l}^{-1}$). BTR panels a, c, and e show regression analysis results while MTR panels b, d, and f depict our one-way ANOVA results. Grey dotted line at $2 \text{ mg O}_2 \cdot \text{l}^{-1}$ on panels b, d and f represents cutoff value for our two ANOVA factors ($< 2 \text{ mg O}_2 \cdot \text{l}^{-1}$ -Hypoxic, $\geq 2 \text{ mg O}_2 \cdot \text{l}^{-1}$ -Normoxic).

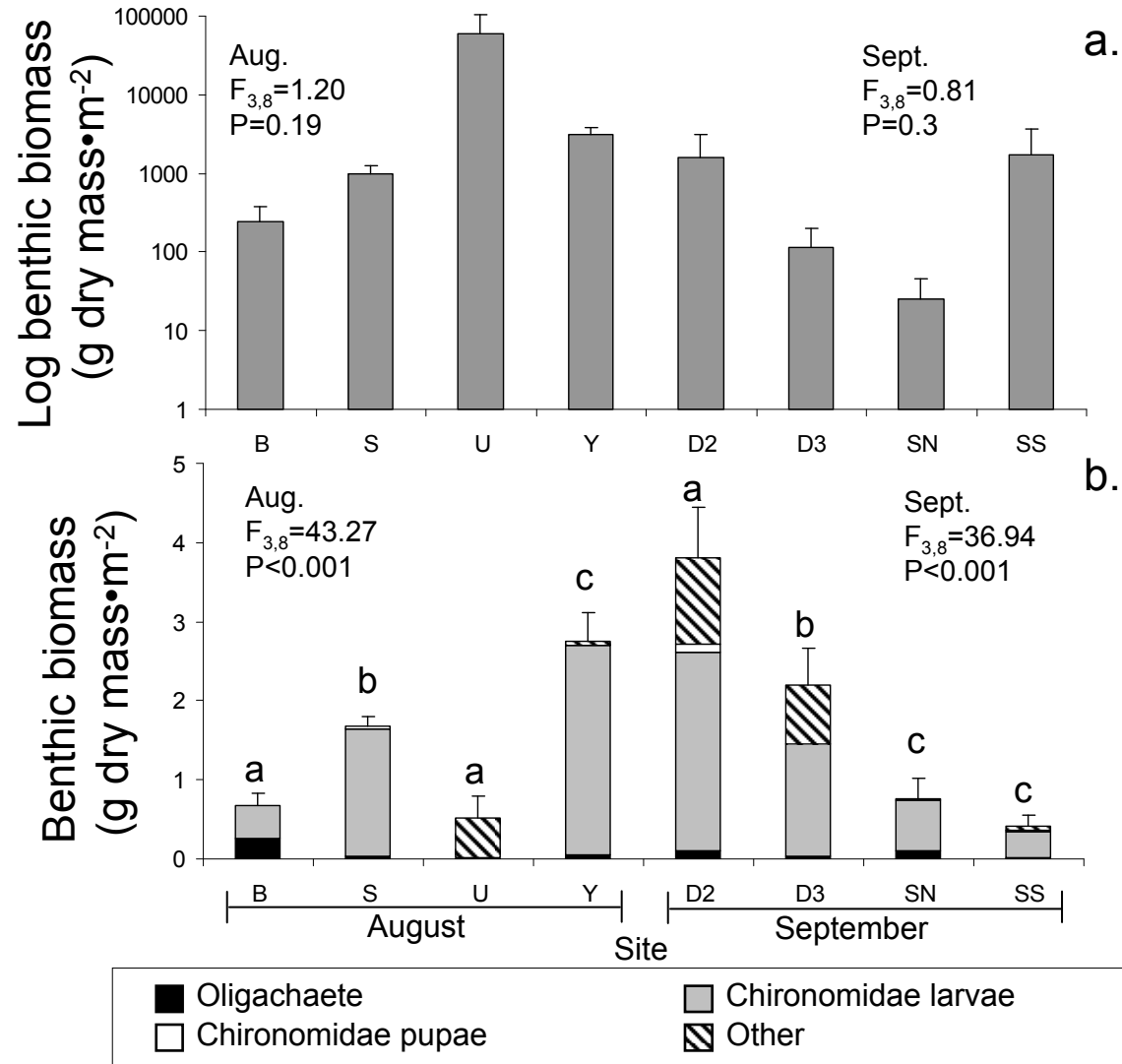


Figure 3.3 Benthic biomass results for sites used in our diet analyses. We show results for total benthic-biomass (a.) and benthic biomass excluding dreissenid mussels (b.; +SE). ANOVA results are shown for each month specific analysis and unique letters denote statistically significant results from a *post-hoc* Tukey analysis ($\alpha=0.05$).

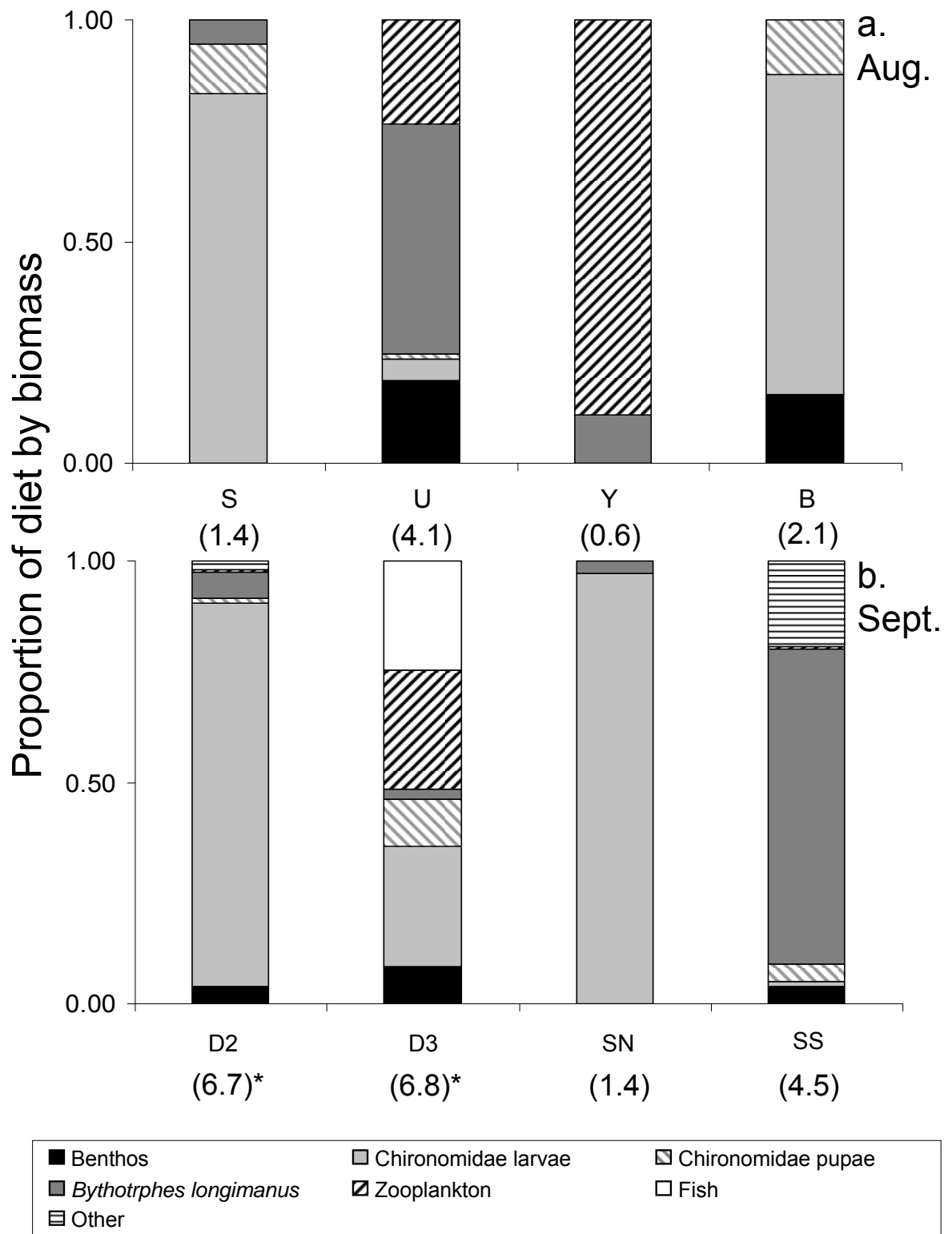


Figure 3.4 Proportional composition by biomass of yellow perch diets from August (a.) and September (b) 2007. Hypolimnetic dissolved oxygen concentration (mg O₂·l⁻¹) shown below site name. *Site D2 and D3 are unstratified.

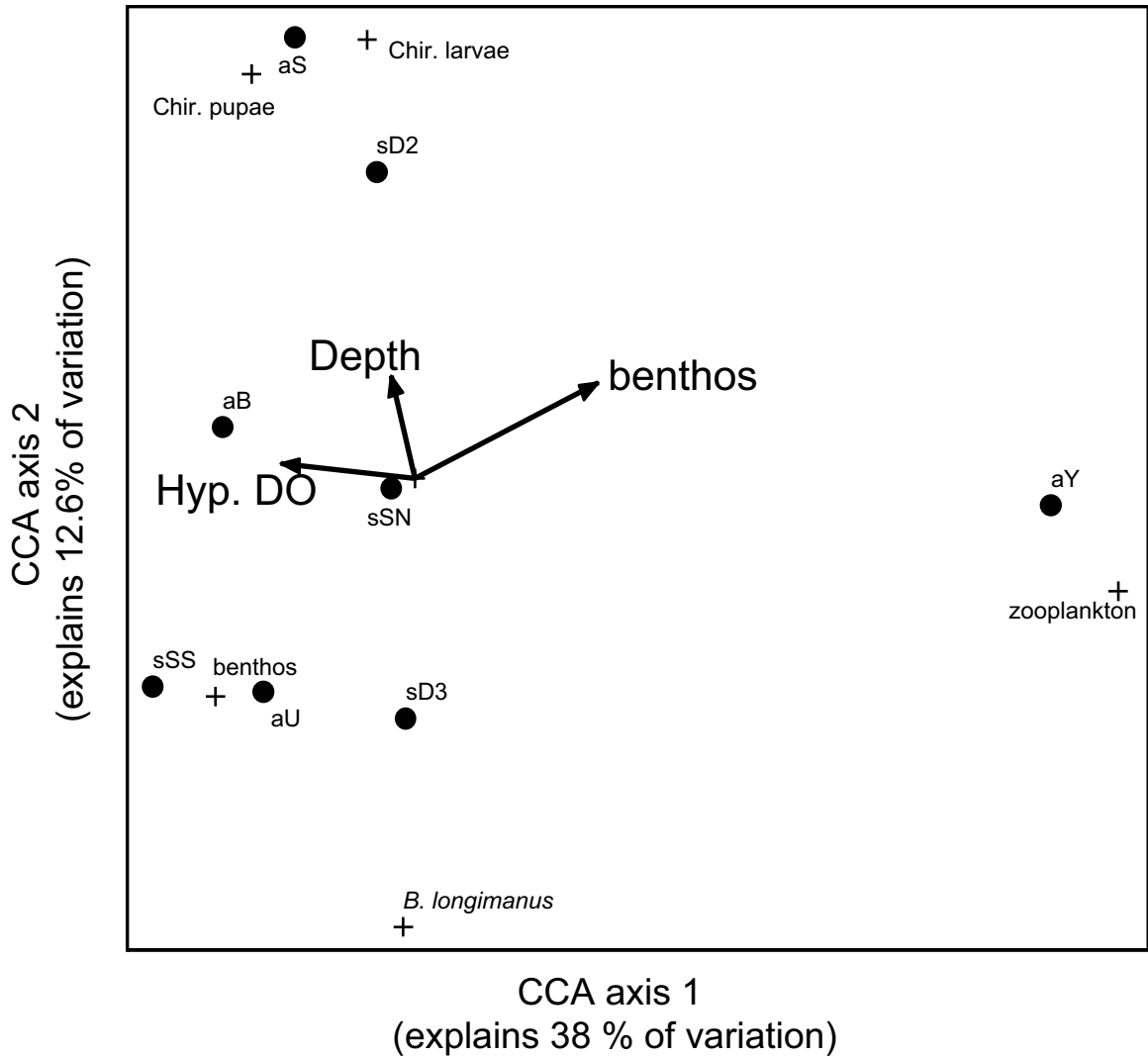


Figure 3.5 Biplot showing our Canonical Correspondence Analysis results depicting the relationship between yellow perch diet patterns and environmental conditions. August sites have an 'a' prefix while September sites have a 's' prefix and are represented by '•'. Diet item centroids are shown by '+' and axis loadings are represented by biplot arrows direction and length.

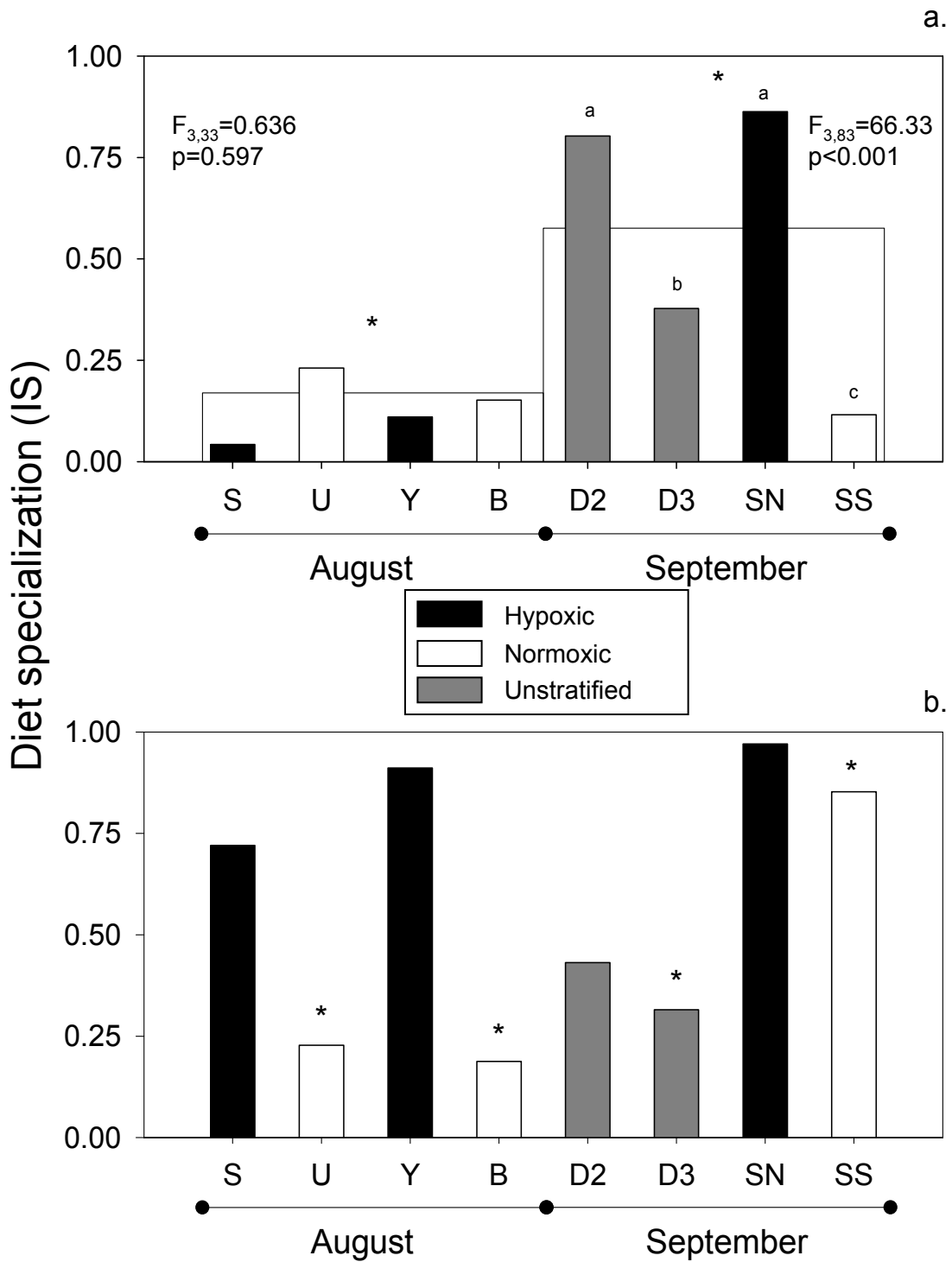


Figure 3.6 Individual proportional similarity (IS) results for 2007 diet data. IS values (0-1; where 1 indicates identical proportional diet composition among individual and 0 indicates high amounts of individual specialization among individuals) are shown pooled by month (IS_{all}) along with among sites (IS_{mth}; a) and site (IS_{site}; b), “*”s denote a statistically significantly result. Panel a. indicates how each site’s IS values compare to the yellow perch population across all sites during each month, while panel b. indicates how IS values vary within a site. ANOVA results are shown among sites and unique letters denote a statistically significant result, determined by a post-hoc Tukey analysis ($\alpha=0.05$).

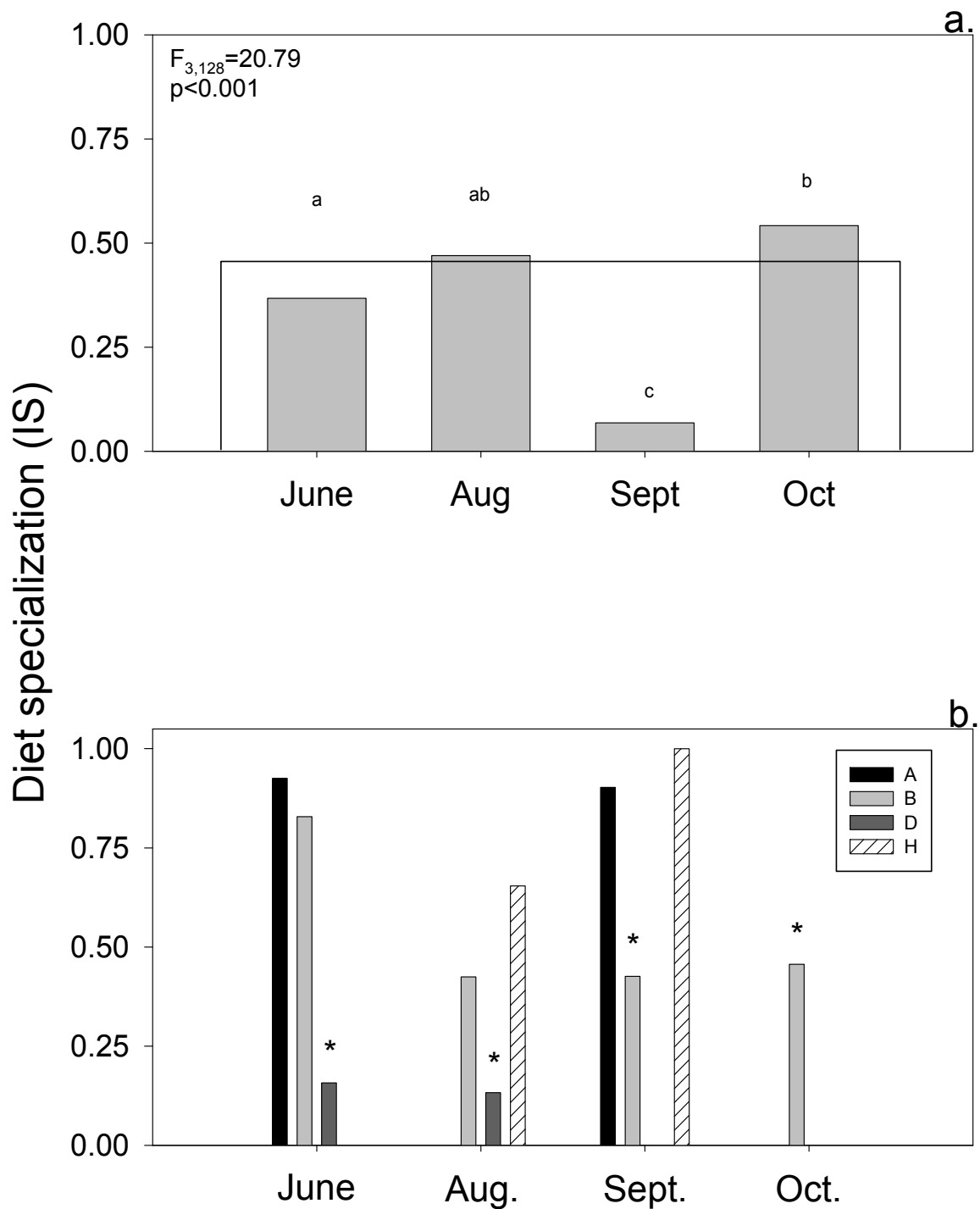


Figure 3.7 Individual proportional similarity (IS) results for 2005 diet data. IS values (0-1; where 1 indicates identical proportional diet composition among individual and 0 indicates high amounts of individual specialization among individuals) are shown pooled by month (IS_{all}) as well as among sites (IS_{mth} ; a) and site (IS_{site} ; b), '*'s denote an IS value significantly different from 1. Panel a. indicates how each site's IS values compare to the yellow perch population across all sites during each month, while panel b. indicates how IS values vary within a site. ANOVA results are shown among months within site B and unique letters denote statistically significant results from a post-hoc Tukey analysis ($\alpha=0.05$).

Literature Cited

- Aku, P. M. K., L. G. Rudstam, and W. M. Tonn. 1997. Impact of hypolimnetic oxygenation on the vertical distribution of cisco (*Coregonus artedi*) in Amisk Lake, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2182-2195.
- Aku, P. M. K., and W. M. Tonn. 1997. Changes in population structure, growth, and biomass of cisco (*Coregonus artedi*) during hypolimnetic oxygenation of a deep, eutrophic lake, Amisk Lake, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2196-2206.
- Aku, P. M. K., and W. M. Tonn. 1999. Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. *Transactions of the American Fisheries Society* 128:17-30.
- Araujo, M. S., and coauthors. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology* 89:1981-1993.
- Baldwin, C. M., D. A. Beauchamp, and C. P. Gubala. 2002. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. *Transactions of the American Fisheries Society* 131:143-158.
- Beaudoin, C. P., W. M. Tonn, E. E. Prepas, and L. I. Wassenaar. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia* 120:386-396.
- Belore, M., and coauthors. 2007. Report of the Lake Erie yellow perch task group. Great Lakes Fishery Commission.
- Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308-343.
- Bolnick, D. I. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* 58:608-618.
- Bolnick, D. I., and coauthors. 2003. The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist* 161:1-28.
- Bolnick, D. I., L. H. Yang, J. A. Fordyce, J. M. Davis, and R. Svanback. 2002. Measuring individual-level resource specialization. *Ecology* 83:2936-2941.
- Bolnick, e. I., R. Svanback, M. S. Araujo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more

heterogeneous. Proceedings of the National Academy of Sciences
104:1007510079.

- Bur, M. T., and D. M. Klarer. 1991. Prey selection for the exotic cladoceran *Bythotrephes cederstroemi* by selected Lake Erie fishes. *Journal of Great Lakes Research* 17:85-93.
- Craig, J. K., and L. B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series* 294:79-94.
- Culver, D. A., M. M. Boucherle, D. J. Bean, and J. W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1380-1390.
- Diaz, R. J. 2001. Overview of hypoxia around the world. *Journal of Environmental Quality* 30:275-281.
- Diaz, R. J., and R. Rosenberg. 2008. Spreading Dead Zones and Consequences for Marine Ecosystems. *Science* 321:926-929.
- Eby, L. A., and L. B. Crowder. 2002. Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Canadian Journal of Fisheries and Aquatic Sciences* 59:952-965.
- Eby, L. A., L. B. Crowder, C. M. McClellan, C. H. Peterson, and M. J. Powers. 2005. Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Marine Ecology-Progress Series* 291:249-261.
- Edwards, W. J., J. D. Conroy, and D. A. Culver. 2005. Hypolimnetic oxygen depletion dynamics in the central basin of Lake Erie. *Journal of Great Lakes Research* 31:262-271.
- Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. *Oecologia* 122:190-199.
- Jansen, W. A., and W. C. Mackay. 1992. Foraging in yellow perch, *Perca flavescens*: biological and physical factors affecting diel periodicity in feeding, consumption, and movement. *Environmental Biology of Fishes* 34:287-303.
- Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca Flavescens*). *Environmental Biology of Fishes* 2:53-70.
- Klemetsen, A., R. Knudsen, R. Primicerio, and P. A. Amundsen. 2006. Divergent, genetically based feeding behaviour of two sympatric Arctic charr, *Salvelinus alpinus* (L.), morphs. *Ecology of Freshwater Fish* 15:350-355.

- Knight, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society* 113:677-693.
- Knudsen, R., R. Primicerio, P. A. Amundsen, and A. Klemetsen. 2010. Temporal stability of individual feeding specialization may promote speciation. *Journal of Animal Ecology* 79:161-168.
- Kon, M., and T. Hidaka. 1983. Chimney projecting behaviour of chironomid larvae (*Chironomus yoshimatsui*: Diptera, Chironomidae). *Journal of Ethology* 1:111-113.
- Kramer, D. L. 1987. Dissolved oxygen and fish behavior. *Environmental Biology of Fishes* 18:81-92.
- Leuchs, H. 1986. The ventilation activity of chironomus larvae (diptera) from shallow and deep lakes and the resulting water circulation in correlation to temperature and oxygen conditions. *Archiv für Hydrobiologie* 108:281-299.
- Ludsin, S. A., and coauthors. 2009. Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: implications for food web interactions and fish recruitment. *Journal of Experimental Marine Biology and Ecology* 381:S121-S131.
- Makarewicz, J. C., and P. Bertram. 1991. Evidence for the restoration of the Lake Erie ecosystem. *Bioscience* 41:216-223.
- Martin, R. A., and D. W. Pfennig. 2009. Disruptive Selection in Natural Populations: The Roles of Ecological Specialization and Resource Competition. *American Naturalist* 174:268-281.
- Nathan, R. 2008. An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America* 105:19050-19051.
- Olsson, J., R. Svanback, and P. Eklov. 2007. Effects of resource level and habitat type on behavioral and morphological plasticity in Eurasian perch. *Oecologia* 152:48-56.
- Parker, A. D., C. A. Stepien, O. J. Sepulveda-Villet, C. B. Ruehl, and D. G. Uzarski. 2009. The interplay of morphology, habitat, resource use, and genetic relationships in young yellow perch. *Transactions of the American Fisheries Society* 138:899-914.
- Parrish, D. L., and F. J. Margraf. 1994. Spatial and temporal patterns of food use by white perch and yellow perch in Lake Erie. *Journal of Freshwater Ecology* 9:29-35.
- Pothoven, S. A., H. A. Vanderploeg, S. A. Ludsin, T. O. Höök, and S. B. Brandt. 2009. Feeding ecology of emerald shiners and rainbow smelt in central Lake Erie. *Journal of Great Lakes Research* 35:190-198.

- Prince, E. D., and C. P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography* 15:451-464.
- Quevedo, M., R. Svanback, and P. Eklov. 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology* 90:2263-2274.
- Rao, Y. R., N. Hawley, M. N. Charlton, and W. M. Schertzer. 2008. Physical processes and hypoxia in the central basin of Lake Erie. *Limnology and Oceanography* 53:2007-2020.
- Roberts, J. J., and coauthors. 2009. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. *Journal of Experimental Marine Biology and Ecology* 381:S132-S142.
- Rosen, R. 1981. Length-dry weight relationships of some freshwater zooplankton. *Journal of Freshwater Ecology* 1:225-229.
- Ryan, P. A., and coauthors. 2003. Fish-community goals and objectives for Lake Erie. *Great Lakes Fishery Commission Special Publication* 03-02:56.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49:704-726.
- Stief, P., L. Nazarova, and D. de Beer. 2005. Chimney construction by *Chironomus riparius* larvae in response to hypoxia: microbial implications for freshwater sediments. *Journal of the North American Benthological Society* 24:858-871.
- Stierhoff, K. L., T. E. Targett, and J. H. Power. 2009. Hypoxia-induced growth limitation of juvenile fishes in an estuarine nursery: assessment of small-scale temporal dynamics using RNA:DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1033-1047.
- Suthers, I. M., and J. H. Gee. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1562-1570.
- Svanback, R., and P. Eklov. 2003. Morphology dependent foraging efficiency in perch: a trade-off for ecological specialization? *Oikos* 102:273-284.
- Svanback, R., and L. Persson. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *Journal of Animal Ecology* 73:973-982.
- ter-Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57:255-289.

- Tyson, J. T., and R. L. Knight. 2001. Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. *Transactions of the American Fisheries Society* 130:766-782.
- Vanderploeg, H. A., and coauthors. 2009. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *Journal of Experimental Marine Biology and Ecology* 381:S92-S107.

Chapter 4

Growth and condition of yellow perch (*Perca flavescens*) in response to hypoxia

Abstract

Similar to other freshwater and coastal marine ecosystems worldwide, seasonal bottom water hypoxia ($<2 \text{ mg O}_2 \cdot \text{l}^{-1}$) has been a recurring phenomenon in Lake Erie, and evidence has been mounting to indicate that hypoxia can negatively affect both benthic and pelagic species in such systems. To explore these issues, we used field- and laboratory-based approaches to estimate the effects of reduced dissolved oxygen (DO) availability on yellow perch (*Perca flavescens*), a species of economic and ecological importance in Lake Erie that has been shown to avoid bottom hypoxia in the field. Our laboratory experiments revealed a temperature-specific decrease in yellow perch growth and consumption with declining DO conditions. A strong response of RNA:DNA content (an index of short-term growth) to DO or ration was not observed in our experiments, although fish growth and RNA:DNA content were correlated. Field collections made in hypoxic and normoxic regions of central Lake Erie during 2005 and 2007 revealed that yellow perch RNA:DNA ratios varied spatiotemporally, suggesting that other factors may influence short-term growth as much as or perhaps more than hypolimnetic hypoxia. While hypolimnetic hypoxia appears to alter yellow perch habitat use and foraging our data suggest that, through various behavioral mechanisms, yellow perch can mitigate effects on short-term growth.

Introduction

Hypoxia ($<2 \text{ mg O}_2\cdot\text{L}^{-1}$) is a recurring phenomena in both marine and freshwater ecosystems worldwide (Diaz 2001; Diaz and Rosenberg 2008). Previous studies have demonstrated that hypoxia can influence fish distributions, foraging behavior, and food web interactions both directly and indirectly (e.g., Pihl 1994; Eby and Crowder 2002; Craig and Crowder 2005; Roberts et al. 2009). However, the effects of hypoxia on fish growth are less clear (but see Stewart et al. 1967; Brandt et al. 2009).

Although laboratory experiments have clearly demonstrated the direct effects of low oxygen concentrations on fish physiology (Kramer 1987; Thomas et al. 2005; Stierhoff et al. 2006), the impacts of hypoxia are not as evident in natural ecosystems because many fishes can detect and avoid hypoxic areas. Laboratory studies have demonstrated that hypoxia can negatively influence consumption and growth of fishes (e.g., Stewart et al. 1967; Brandt et al. 2009) and may lead to responses such as increased ventilation rates and altered distributions (Petrosky and Magnuson 1973; Suthers and Gee 1986). Various field studies have suggested that avoidance of hypoxic conditions can influence distributions of fishes and indirectly affect diet patterns (Pihl 1994; Aku et al. 1997; Taylor et al. 2007). While such effects on diet and movement into novel habitats may be expected to influence growth, few field studies have demonstrated actual hypoxia-induced growth consequences for fish in natural systems (but see Eby et al. 2005; Stierhoff et al. 2009).

Traditional methods of examining fish growth (e.g., chronometric structures) integrate conditions over long periods (e.g., annually, lifetime). Such methods are not

ideal for examining growth responses to hypoxia, given the relatively short persistence (hours to months) of hypoxia in most systems. Ratios of nucleic acids (RNA:DNA) are relatively useful indices of short-term growth since DNA concentrations in cells are relatively static, whereas RNA concentrations are more dynamic. Greater amounts of RNA are indicative of increased protein synthesis and therefore increased growth (Bulow 1987). RNA:DNA ratios have been used to examine short-term growth of various aquatic organisms including zooplankton (Gorokhova and Kyle 2002; Gorokhova 2003), larval fish (Clemmesen 1994; Pepin et al. 1999; Höök et al. 2008) and juvenile/adult fish (Gwak et al. 2003; Smith and Buckley 2003; Stierhoff et al. 2009), including our study species yellow perch *Perca flavescens* (Audet and Couture 2003; Tardif et al. 2005; Glemet and Rodriguez 2007). Several laboratory studies have also developed species- and temperature-specific relationships between growth and RNA:DNA ratios (Clemmesen 1994; Grant 1996; Ali and Wootton 2003; MacLean and Caldarone 2008; Stierhoff et al. 2009), thereby facilitating a clear linkage between RNA:DNA ratios and somatic growth. RNA:DNA ratios are sensitive to temperature because for most fish species more RNA is required at lower temperatures than at higher temperatures to induce similar growth rates (Buckley 1982; Goolish et al. 1984).

The combined use of laboratory experiments, targeted field sampling, and relevant measures that can capture short-term changes in growth dynamics, offers an integrative approach to determine whether hypoxia affects fish growth. To this end, we conducted a field- and laboratory-based study to test the hypothesis that hypolimnetic hypoxia can lead to short-term reductions in yellow perch growth and condition. We would expect to find evidence supporting this hypothesis given that 1) a previous

laboratory study demonstrated that yellow perch growth declined when dissolved oxygen concentration approached $2 \text{ mg O}_2 \cdot \text{l}^{-1}$ at $\sim 20^\circ\text{C}$ (Carlson et al. 1980) and 2) a previous field study demonstrated that bottom hypoxia could alter habitat-use (i.e., reduced use of bottom waters) and foraging (i.e., reduced consumption of benthic macroinvertebrates) patterns of yellow perch in Lake Erie's central basin (LECB) (Roberts et al. 2009). We evaluated this hypothesis in LECB, a system that experiences hypolimnetic hypoxia during summer in most years (Rosa and Burns 1987; Bertram 1993; Burns et al. 2005; Edwards et al. 2005; Hawley et al. 2006) and in which yellow perch is a species of vital ecological and economic importance (Ryan et al. 2003).

To explore specific growth consequences of hypoxia for LECB yellow perch, we integrate laboratory experiments with field results. Through one laboratory experiment, we examine how growth responded to different levels of ration and temperature, and explored relationships among consumption, growth, and nucleic acid ratios within these treatments. We use a second laboratory experiment to evaluate the interactive effects of dissolved oxygen concentrations and temperature on consumption, somatic growth, and RNA:DNA ratios. The relationship between maximum consumption and dissolved oxygen is noteworthy given that relationships between abiotic variables and maximum consumption are a central component of fish bioenergetics models (Kitchell et al. 1977). Finally, we examine both spatial and temporal variation in short-term growth and condition (*via* RNA:DNA ratios) of yellow perch collected from hypoxic and normoxic sites in LECB during summers of 2005 and 2007.

Methods

Laboratory experiments: overall experimental design

We conducted controlled laboratory experiments to examine how temperature, ration, and dissolved oxygen concentration may affect yellow perch consumption, growth, and RNA:DNA ratios interactively. Experiments were completed at the Michigan Department of Natural Resources' Fisheries Research Station (Saline, MI). Juvenile (i.e., age-1) yellow perch (100-180 mm total length, TL) were obtained from a local fish hatchery, housed in holding tanks, and fed thawed mysis (*Mysis relicta*) shrimp until the experiments began. Experimental chambers consisted of two ~18-L compartments within a single 40-L tank. Compartments were separated by two opaque mesh plastic sheets, between which were housed a heater, air-stones, and an underwater internal filter (Fluval 1 Plus©). Each experimental tank also contained a copper cooling coil buried underneath a bottom substrate layer (~30 mm) of sand. In low temperature (11 °C) treatment tanks, these cooling coils were connected to chiller units that circulated cooled water to maintain the desired temperature. The cooling coils in the middle (21 °C) and high (26 °C) temperature treatment tanks were not connected to a chiller, acting as sham objects. We manipulated dissolved oxygen concentrations by injecting combinations of nitrogen and atmospheric gas through air-stones until the desired dissolved oxygen concentrations were obtained. We measured and recorded the temperature (°C), pH, and dissolved oxygen concentration ($\text{mg O}_2 \cdot \text{l}^{-1}$) of each experimental tank once daily using an Accumet® Portable PH/°C Meter and YSI Model 55 DO System, respectively.

At the beginning of each experiment, randomly selected individual yellow perch were removed from holding tanks, measured (total length (TL) to nearest 1 mm and mass to nearest 0.01 g) and placed in experimental compartments. Two fish were placed in

each tank, on opposite sides of the plastic mesh dividers. While the two yellow perch in each tank did not interact directly, we used mean tank observations as our sample unit, taking a conservative approach to avoid any possible pseudoreplication (Hurlbert 1984). Experiments consisted of three tank acclimation days, followed by five experimental days. Fish were fed thawed mysids on acclimation day 1 and then starved during acclimation days 2 and 3. During experimental days, food was left in tanks for six hours (from 9:00 to 15:00), and then removed (using small aquarium nets), blotted dry, and weighed (nearest 0.01 g). We determined consumption by measuring the difference between the amount of food introduced to the tank chamber and the amount of food remaining uneaten after six hours. These measures of remaining food were corrected for loss of material to solution by multiplying the remaining amount of food by temperature-specific correction factors (Appendix 1). To calculate mean consumption for individual fish, we averaged observed consumption during experimental days 3-5. We used consumption measures only from experimental days 3-5 because we found that mean consumption during experimental day 1 (following two days of starvation) and experimental day 2 were greater and less, respectively, than during other experimental days. No differences in consumption rates were found during experimental days 3-5.

Following the six-hour feeding trials on experimental day 5, individuals were removed and anesthetized. We then recorded the TL (to 1 mm) and mass (to 0.01 g) of each individual. To determine RNA:DNA ratios, white epaxial muscle tissue (~40 mg) was extracted using dissection techniques and placed into individual microcentrifuge tubes containing a storage solution (RNAlater®) to preserve nucleic acids (both RNA and

DNA) for subsequent analysis (See *Nucleic acid analysis*). These data were used to quantify three response variables: consumption, growth, and RNA:DNA ratio.

Laboratory experiments: ration and temperature effects

Using a similar calibration method to Clemmesen (1994), we explored the relationship between yellow perch RNA:DNA ratios and growth rate. We used three different rations (high, medium, and low) and three temperatures (11 °, 20 °, and 26 °C) to induce different growth rates and subsequently measured RNA:DNA from the muscle tissue of individuals. We used a full factorial design with three replications per treatment (54 yellow perch, i.e., n=27 total). We lost one yellow perch due to mortality during our experimental trial (Table 4.1; n=26). We used a bioenergetics model (Kitchell et al. 1977) to calculate a theoretical temperature-specific maximum consumption rate and maintenance ration rate (i.e., the amount of daily consumption predicted to result in no gain or loss of mass) to define our three ration treatments. Our high ration level was 150% of maximum daily consumption, medium ration was 150% of maintenance consumption, and the low ration was 50% of maintenance consumption. To account for mass loss during the starvation periods of acclimation days 2-3, we took additional length and mass measurements of each experimental yellow perch before the feeding trial on experimental day 1. We did not manipulate dissolved oxygen concentrations for this experiment beyond simply injecting atmospheric air through air-stones into each aquarium sufficient to maintain normoxic conditions in all experimental chambers. Other experimental specifics followed the overall experimental design listed above (see *overall experimental design*).

Laboratory experiments: dissolved oxygen and temperature effects

We also measured yellow perch consumption, growth, and RNA:DNA ratio under different temperatures and dissolved oxygen concentrations. These experiments were patterned after ones conducted to parameterize bioenergetics models. We used this experimental design to investigate the effects of dissolved oxygen on yellow perch growth and consumption. Experimental treatments included three temperatures (11 °, 20 °, and 26 °C) and three dissolved oxygen concentrations (2, 5, and 8 mg·l⁻¹) for the 20 and 26 °C temperature treatments and four oxygen concentrations (2, 5, 8, and 11 mg·l⁻¹) for the 11 °C treatment. During experiments, all individuals were fed thawed mysids *ad libitum* for 6 hours, based on estimated maximum consumption rates from a bioenergetics model (Kitchell et al. 1977). During the experiment, no fish consumed all the food during the six hour feeding trial. Due to limited tank space, we repeated this experimental design three times from June-August 2007. For each experimental trial, we included all treatments for a full factorial design with two replicates for every treatment per experimental trial. To adjust for potential mortality loss, we allocated four additional replicates to each of the low oxygen treatments at medium and high temperatures. Thus, an experiment consisted of 48 fish distributed among 48 experimental compartments within 24 experimental tanks (n = 72 across three experimental trials).

Field collections

During 2005, four sites (A, B, D, and H) in LECB were sampled for a suite of biological and physical information on a monthly basis during June-October (excluding July; Table 4.2, Figure 4.1). The set of sites sampled varied by month, and only site B was sampled every month (see Table 4.2; for more details see Roberts et al. 2009). During June and August, all sample sites (B and D) were thermally stratified with a

normoxic hypolimnion, except for site H, which was stratified with a hypoxic hypolimnion during August. During September, all sample sites were stratified with a hypoxic hypolimnion. Site H varied in depth; thus, given the depth of the thermocline, shallower areas along this site transect may have experienced normoxic conditions during September while other areas were hypoxic (for further details see, Roberts et al. 2009).

During 2007, LECB was sampled twice during hypoxic conditions (August and September) for a suite of biological and physical information. During August, we sampled one stratified hypoxic sites (B), one stratified normoxic site (U), and one unstratified (T) site. During September, we sampled one stratified normoxic site (SS) and two unstratified sites (D2 and D3; Table 4.2; Figure 4.1). At each site, yellow perch were collected with bottom (7.6 m semi-balloon: 13 mm stretched-mesh cod-liner) and mid-water (9.1 x 9.1 m: 13 mm stretched-mesh cod-liner) trawls. These collection techniques were performed identically during 2005 and 2007. Once collected yellow perch were counted and measured for total length and mass. To determine RNA:DNA ratios, white epaxial muscle tissue (~40 mg) was extracted using dissection techniques and placed into individual microcentrifuge tubes containing a storage solution (RNAlater®) to preserve nucleic acids (both RNA and DNA) for subsequent analysis (See *Nucleic acid analysis*).

Nucleic acid analysis

We quantified ratios of RNA:DNA from experimental and field-collected yellow perch ranging in size from 100-180 mm TL. From each individual, we removed epaxial white muscle tissue (~40 mg), placing this tissue into individual microcentrifuge tubes containing a storage solution (RNAlater®) to preserve nucleic acids (both RNA and

DNA). Samples were stored at 4°C until analysis (Gorokhova 2005). We quantified nucleic acids fluorometrically using a microplate fluorescence reader (FL_x800, Bio-Tek instruments with KCjunior software) and an established protocol for extracting and quantifying nucleic acids (Gorokhova and Kyle 2002; Höök et al. 2008), which is described below.

Working reagents, standards and controls

To perform nucleic acid analyses we used the following list of working reagents, standards and controls: RNAlater™ (Sigma, cat. # R 0901); RiboGreen™ Quant_it RNA Assay Kit (Molecular Probes, cat. # R11490); Ribosomal RNA for standards (from *Escherichia coli*, Component C of the RNA Assay Kit); DNA for standards (calf thymus, Sigma, cat. # D-8515); RNase, DNase free (Molecular probes cat. # RNAS0500) working solution was 5 µg·ml⁻¹; N-lauroyl sarcosine sodium salt (MP Biomedicals cat. # 190289); TE buffer, DNase/RNase/Protease free (Fisher cat. # BP2474-1). RNA and DNA standards were diluted with TE Buffer into working solutions, aliquots were created and stored at -20 °C until analysis: RNA concentrations of 0.08-2.57 µg·ml⁻¹ and DNA concentrations of 0.03-1.02 µg·ml⁻¹.

Using a sterile scalpel blade cleaned with RNase erase (MP Biomedicals, cat. # 821682), we removed two subsamples of ~10 mg from each yellow perch muscle sample stored in RNAlater. These subsamples were placed into individual microcentrifuge tubes containing 500 µl of extraction buffer (1% N-lauroyl sarcosine sodium salt in TE buffer). Samples were then homogenized using RNase/DNase-free pestles (Fisher, cat. # K749521 1590). After homogenization, samples were subjected to repeated (n = 3) sequences of ultrasonic (30 s) and ice (1 min) baths. Samples then were allowed to shake

at room temperature for two hours. Each subsample was assayed in duplicate using a microplate fluorescence reader (FL_x800 Biotek instruments, filters: 485 nm for excitation and 528 nm for emission) and 96 well black flat bottom plates (Costar 3915). Plates were scanned with one second well measurement time and ten measurements per well. Plates were loaded in duplicate with RNA and DNA standards, blanks, negative controls, and tissue subsamples. The fluorescence of each well was first quantified after RiboGreen addition ($70 \mu\text{l}\cdot\text{well}^{-1}$; 5 minute incubation at room temperature) and then for a second time after RNase addition ($5 \mu\text{l}\cdot\text{well}^{-1}$) and incubation for 30 minutes at 37 °C. The first fluorescence gave a measure of total nucleic acids, whereas the second gave a measure of DNA since RNA in each well was digested by RNase. The difference between these two measures, minus residual fluorescence, was our measure of RNA fluorescence. Each RNA and DNA fluorescence estimate was then compared to the plate-specific standard curve to quantify the amount of both nucleic acids in each subsample. To correct for any variation in our standards and working reagents over the two years in which our samples were collected and analyzed, we calculated the standard curve ratio (m_{DNA}/m_{RNA}) for each plate as described by (Caldarone et al. 2006), and standardized all our RNA:DNA values using the overall mean curve slope ratio (mean=2.87) as our reference.

Data analysis

Ration and temperature effects. Over the size range of yellow perch analyzed, we did not find a significant linear relationship between yellow perch length and RNA:DNA ratio (Fig 4.2a), and thus we used a 2-way Analysis of Variance (ANOVA) to separately analyze our three response variables (consumption, growth, and RNA:DNA ratio) in relation to two factors (temperature and ration) and an interaction term. We also

performed a post hoc Tukey pairwise comparison of each unique treatment ($\alpha=0.05$) to further analyze treatment differences. Similar to Stierhoff et al. (2009), we used specific growth rate (SGR: % biomass $\cdot d^{-1}$; Equation 1) as our measure of growth (Ricker 1975; Houde and Schekter 1981). We determined SGR using the instantaneous growth rate (G; Equation 2):

$$1) \quad SGR=(e^G-1)*100$$

$$2) \quad G=(\ln(W_f)-\ln(W_i))/d$$

where W_i is initial mass, W_f is final mass, and d is the number of days between measurements. To quantify growth as the change in somatic tissue free of recently consumed stomach contents, we determined W_f by subtracting the amount of food consumed on experimental day 5 from the observed mass of a given yellow perch.

A goal of these experiments was to evaluate the ability of RNA:DNA ratios to index consumption and growth. Studies of other species suggest that such relationships are temperature-dependent (Buckley et al. 1999). We used ordinary least squares (OLS) regression analysis with temperature treatment and RNA:DNA as independent variables. We observed a strong correlation between temperature and RNA:DNA ratio ($r=-0.875$), and due to this colinearity, we repeated this analysis using RNA:DNA as the sole independent variable. We performed these regression analyses with consumption, and growth each as a separate dependent variable.

Dissolved oxygen and temperature effects. Results were generated for each week-long experimental trial independently, and we therefore performed a series of one-way ANOVAs to evaluate if we could combine the results from all three experimental trials for our final analysis. For each ANOVA, we separately analyzed our three response

variables (consumption, growth, and RNA:DNA) for each of our nine treatments (3 temperatures \times 3 oxygen concentrations). Since we used 27 ANOVAs to evaluate potential trial effects, we set a conservative level of significance ($\alpha=0.01$). In so doing, we found no significant effects of experimental trial on response variables and therefore grouped data across trials for subsequent analyses.

We did not find a significant linear relationship between yellow perch length and RNA:DNA (Fig 4.2b), and thus we used a 2-way ANOVA to separately analyze three response variables (consumption, RNA:DNA, and growth) in relation to two factors (temperature and oxygen concentration) and an interaction term. We also performed a post hoc Tukey pairwise comparison of each unique treatment ($\alpha=0.05$) to further analyze differences between treatments. Growth was determined using the methods described above with one modification; since our initial measure of yellow perch mass was taken before the three tank acclimation days, we calculated growth for a period encompassing all acclimation (i.e., period of starvation) and experimental days (i.e., 8 days). We excluded the high-oxygen by low-temperature treatment from our ANOVA analysis to keep a balanced design and simplify the results of this test.

To visualize experimental results and the associated non-linear relationships, we used quadratic multiple-regression to develop response surfaces using our three response variables (consumption, growth, and RNA:DNA ratio) as dependent variables, and temperature and dissolved oxygen (percent saturation) as independent variables. We used percent saturation for our measure of dissolved oxygen concentration to normalize oxygen measures across all temperatures.

Field collections. Length and RNA:DNA ratios were uncorrelated among field-collected individuals during 2005 and 2007 (Fig 4.2 c-d). Therefore, we did not include length as a covariate and used a series of one-way ANOVAs with post-hoc Tukey comparisons ($\alpha=0.05$) to evaluate differences in RNA:DNA between yellow perch collected in normoxic versus hypoxic sites. We grouped our field-collected yellow perch RNA:DNA data from 2005 and 2007 by month and ran two ANOVAs (one for each year) to evaluate coarse temporal patterns. We also compared 2005 and 2007 RNA:DNA ratios by sites 1) within months (4 ANOVA's for 2005 and 2 for 2007) to evaluate spatial patterns and 2) among months by site (4 tests, one for each site) to evaluate site-specific temporal patterns (2005 only).

Results

Ration and temperature effects

Although consumption increased with increasing ration (Figure 4.3), no differences in RNA:DNA ratios and growth were found among ration treatments (Figure 4.3). By contrast, all three of our response variables were affected by temperature. RNA:DNA ratios and growth tracked one another, being lower at higher temperatures. The interaction effect between our two factors was significant for consumption suggesting this response variable was affected interactively by temperature and ration treatments (Figure 4.3). The post-hoc pairwise comparison suggests that consumption at the low-ration treatment is significantly less than the high-ration within the high-temperature treatment (Figure 4.3). Growth within the high-temperature treatment and the low-ration treatment is significantly less than the medium-ration

treatment (Figure 4.3). There are no other temperature-specific significant differences between ration treatments.

Although temperature and RNA:DNA data were strongly correlated in our experiments ($r = -0.875$), the relationship between RNA:DNA and growth was stronger than the relationship between temperature and growth (univariate regression: $p_{\text{temp}}=0.001$, $R^2 = 0.35$; $p_{\text{RNA:DNA}} < 0.001$, $R^2=0.48$), and a two-variable model with both temperature and RNA:DNA as independent variables did not improve our predictive ability, owing to multicollinearity (multiple regression: $p_{\text{temp}} = 0.93$, $p_{\text{RNA:DNA}} = 0.04$; $R^2=0.48$, $p = 0.001$). Regression results with consumption as our dependent variable were similar and both univariate regressions were significant and explained nearly the same amount of variation ($p_{\text{RNA:DNA}}=0.007$; $r^2=0.26$ and $p_{\text{temp}}=0.004$; $r^2=.26$). Therefore, by grouping growth measures across temperature treatments, we found a significant positive relationship with RNA:DNA (Figure 4.4a), and conversely the relationship between RNA:DNA and consumption was significant and negative (Figure 4.4b).

Dissolved oxygen and temperature effects

Our temperature and dissolved oxygen experiments yielded results for 64 tank means (Table 4.4). Eight individuals died during the experiments and an additional 11 fish were excluded from our RNA:DNA analysis due to faulty reagents and sample contamination. All three response variables varied significantly across temperature treatments, whereas only consumption and growth varied significantly across oxygen treatments (Figure 4.5). The interaction effect was only significant for consumption suggesting that only this response variable was affected interactively by temperature and oxygen. The post-hoc pairwise comparison suggests that at high temperature

consumption was significantly lower for the low-oxygen treatment than the high-oxygen treatment (Figure 4.5). There were no other temperature-specific significant differences between oxygen treatments.

We developed significant response surfaces for our three dependent variables (Figure 4.6), with the growth response surface explaining the greatest amount of variation, 62% (Figure 4.6b).

Equations 1-3:

$$1)C(D,T) = -0.051 + 0.0078T - 0.0002T^2 - 0.00008D + 0.00004D \cdot T - 0.000004D^2$$

$$2)G(D,T) = 0.208 - 0.0505T - 0.0014T^2 + 0.0254D + 0.000007D \cdot T - 0.0002D^2$$

$$3)RD(D,T) = 12.260 - 0.211T - 0.0061T^2 + 0.0098D + 0.0034D \cdot T - 0.00064D^2$$

where, D is dissolved oxygen concentration ($\text{mg O}_2 \cdot \text{l}^{-1}$), T is temperature ($^{\circ}\text{C}$), C is wet weight consumption ($\text{g}^{-1} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), G is growth ($\% \text{ biomass} \cdot \text{d}^{-1}$), and RD is RNA:DNA ratio. These results help us visualize the parabolic relationship between both temperature and oxygen concentration (Figure 4.6). Consumption is maximized at high temperature and dissolved oxygen concentration (Figure 4.6a), whereas RNA:DNA and growth are maximized at low temperature and intermediate dissolved oxygen concentration (Figure 4.6b and c).

Field measurements

When sites were pooled across months during 2005, RNA:DNA ratios varied through time (one-way ANOVA: $F_{2,78}=4.10$; $p=0.02$), with nucleic acid ratios higher in August ($n = 32$ individuals) than June ($n = 21$ individuals) (Figure 4.7a). Nucleic acid ratios from yellow perch collected during September ($n = 34$) did not differ from either June or August (Figure 4.7a). During June, mean RNA:DNA ratio at site D was less than site B and in September mean ratio at site H was significantly less than sites B and A

(Figure 4.7b). However, we found no significant differences in mean RNA:DNA ratio among sites during August ($F_{2,29}=1.06$; $p=0.36$). Within-site temporal variation was only significant at site D, with August higher than June ($F_{1,23}=6.52$; $p=0.02$; Figure 4.7c). RNA:DNA ratios did not differ across sample months at sites B ($F_{2,28}=1.88$; $p=0.17$) or H ($F_{1,15}=1.29$; $p=0.27$; Figure 4.7c).

During 2007, yellow perch were sampled in August and September at the height of hypoxic conditions in LECB. Sites with normoxic and hypoxic hypolimnetic conditions were sampled during both months (Table 4.2). Eighteen perch were analyzed from hypoxic areas (August=18, September=0), 12 were analyzed from normoxic areas (August=4, September=8) and 35 were analyzed from unstratified areas (August=5, September=30; Table 4.5). Thus, the power to detect differences between our three habitat types through this analysis was relatively low. Nonetheless, with data grouped across sites with normoxic, hypoxic, and unstratified habitat conditions, we found significantly higher short-term growth during August than during September ($F_{1,62}=14.028$; $p<0.001$; Figure 4.8a). However, during August ($F_{2,23}=0.235$; $p=0.792$) and September ($F_{2,35}=1.867$; $p=0.170$), RNA:DNA did not differ between sites (Figure 4.8b).

Discussion

Hypoxia has the potential to negatively affect yellow perch in LECB as our laboratory results suggest both consumption and growth are reduced at low dissolved oxygen concentrations. However, we observed no difference in yellow perch short-term growth and condition due to hypoxia. Collectively these results suggest yellow perch within LECB are able to mitigate the negatively affects of hypoxia.

Our laboratory experiments demonstrated that both temperature and dissolved oxygen levels can influence yellow perch consumption and growth. Consumption and growth were lower at low dissolved oxygen ($2 \text{ mg O}_2 \cdot \text{l}^{-1}$) levels relative to medium and high oxygen levels across medium- and high-temperature treatments. Carlson et al. (1980) reported that yellow perch growth decreased when oxygen concentrations approach $2 \text{ mg O}_2 \cdot \text{l}^{-1}$ over a 71-day experiment at one temperature ($\sim 20^\circ\text{C}$). Similarly, Stewart et al. (1967) found that both consumption and growth of largemouth bass (*Micropterus salmoides*) declined when exposed to oxygen levels below $3 \text{ mg O}_2 \cdot \text{l}^{-1}$, and also found reduced consumption when oxygen levels approached 100% saturation. Similar findings (Hermann et al. 1962) have been used in aquaculture studies to develop bioenergetics growth models incorporating a suite of abiotic factors (including temperature and oxygen) to predict fish growth (Cuenco et al. 1985a; Cuenco et al. 1985b).

A review and synthesis of studies examining hypoxia's effect on Atlantic cod (*Gadus morhua*), a demersal marine species, suggest that metabolic scope (difference between routine and maximum metabolic rate) is reduced at low oxygen levels, leading to decreased activity and growth (Chabot and Claireaux 2008). Our results are similar, since we showed a decrease in growth and consumption of yellow perch at low oxygen conditions, which could potentially be related to physiological processes influenced by reductions in metabolic scope. In a similar laboratory study, Brandt et al. (2009) examined the interactive effects of temperature and dissolved oxygen on growth and consumption of juvenile striped bass (*Morone saxatilis*). Both growth and consumption

were lower at lower ($\sim < 4 \text{ mg O}_2 \cdot \text{l}^{-1}$) oxygen treatments, particularly at higher temperatures (Brandt et al. 2009).

RNA:DNA ratios have been validated (Clemmesen 1994; Grant 1996; Ali and Wootton 2003) and successfully used to examine short-term growth of larval (Clemmesen 1994; Höök et al. 2008), juvenile (MacLean and Caldarone 2008), and adult fishes (Aday et al. 2000; Gwak et al. 2003; Glemet and Rodriguez 2007). Our results suggest short-term growth is positively related to RNA:DNA ratios for juvenile/adult yellow perch. However, given the influence of temperature on RNA:DNA ratios (Buckley 1984; Goolish et al. 1984; Stierhoff et al. 2009), this relationship needs to be interpreted with caution. We did not observe sufficient variation in growth within a temperature treatment to effectively evaluate the effect of temperature on the RNA:DNA relationship. Our results also suggest a negative relationship between consumption and RNA:DNA ratios. However, due to the strong positive relationships between temperature and consumption and between temperature and RNA:DNA, this relationship is difficult to interpret.

Various studies (Grant 1996; Ali and Wootton 2003; MacLean and Caldarone 2008) have found strong relationships between somatic growth and RNA:DNA ratios for adult and juvenile fishes. However, these studies lasted for 30 (MacLean and Caldarone 2008), 35 (Grant 1996) and 56 (Ali and Wootton 2003) days. Stierhoff et al. (2009) used RNA:DNA ratios to investigate the growth response of two juvenile estuarine species (weakfish -*Cynoscion regalis* and summer flounder-*Paralichthys dentatus*) to hypoxia in a coastal Delaware bay and found a strong relationship between RNA:DNA ratios and growth after a seven-day period. Further laboratory results from Stierhoff et al. (2009)

suggest a response of RNA:DNA ratios after about one day without food. We suspect a combination of factors (prolonged effects of our starvation period, relatively short treatment period (5 days), and small growth differences between our ration treatments) are responsible for the relatively poor fit of our growth to RNA:DNA ratio relationship. While we were able to detect a positive relationship between these two measures of yellow perch growth over only five days, we would expect the strength of this relationship to be more robust with increased exposure time. Moreover, including a starvation period in our experimental design followed by this relatively short period of experimental feeding may have negatively influenced the strength of our RNA:DNA ratio to growth relationship. Therefore, our laboratory measures of RNA:DNA ratios may reflect both negative growth associated with the starvation period and the experimental feeding treatments. Nonetheless, the positive relationship between growth and RNA:DNA suggests that RNA:DNA ratios are at the least qualitatively indicative of relative short-term growth and condition of yellow perch, even if not in a predictive capacity. To fully use RNA:DNA ratios as measures of short-term growth and condition of yellow perch and other temperate freshwater species, further research exploring the temperature-specific relationship between this measure and growth is necessary. Additional examination of these relationships should allow for development of predictable relationships between RNA:DNA ratios and somatic growth rates.

LECB yellow perch RNA:DNA ratios show little or no change in response to hypoxic hypolimnetic conditions. Previous studies examining seasonal variation in yellow perch growth suggest a continued increase in growth and condition of these fish through September (Diana and Salz 1990; Henderson et al. 2000). Our data suggest no

change in yellow perch RNA:DNA ratios from August to September, which may be indicative of a system-wide hypoxia effect, possibly suggesting that within LECB there are limited areas serving as growth refuges during hypoxic conditions. However, the uncertainty surrounding how temperature may be influencing these observed RNA:DNA ratios confounds our results. During hypoxia, yellow perch continue to consume benthic prey, albeit at a lower rate than under normoxic conditions (Hergenrader and Hasler 1966; Roberts et al. 2009), and evidence suggests that yellow perch frequently move from warm epilimnetic temperatures to cool hypolimnetic temperatures (Roberts et al. 2009; Vanderploeg et al. 2009). Thus, even if a temperature-specific relationship existed between RNA:DNA and growth, it is unclear how this relationship may change in response to short-term movements of fish among different temperatures.

It is unclear if differences in RNA:DNA ratios of field collected yellow perch are actually indicative of growth patterns or simply seasonal thermal patterns. Roberts et al. (2009) also observed no increase in percent dry weight of LECB yellow perch from August to September, which is a relatively longer-term condition measure and a proxy of energy density (Hartman and Brandt 1995b). However, the lack of spatial differences in RNA:DNA between hypoxic and normoxic sites suggest that yellow perch might be able to behaviorally mitigate the short-term negative effects of low oxygen levels indicated by our lab results.

Previous studies have shown links between the presence of hypoxic habitat conditions and fish growth in freshwater (Aku and Tonn 1997), estuarine (Eby et al. 2005) and coastal marine (Pihl 1994; Petersen and Pihl 1995) systems. Aku and Tonn (1997) demonstrated that total biomass of cisco (*Coregonus artedii*) in Amisk Lake,

Alberta, Canada increased in response to artificial hypolimnetic oxygenation, but also suggested that individual growth rates decreased due to resulting density-dependent effects. Petersen and Pihl (1995) used both field and laboratory studies to examine the effects of hypoxia on plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*) in the Kattegat, an area between the Baltic and North Seas. Field collections revealed reduced sizes of both species during hypoxia while laboratory studies found decreases in specific growth rates in response to hypoxia. Eby et al. (2005) used field enclosures to directly observe how periodic hypoxia in the Neuse River estuary influenced growth patterns of juvenile Atlantic croaker (*Micropogonias undulates*). They found reduced growth of juvenile estuarine fishes with increased duration and frequency of hypoxic conditions through a variety of pathways (e.g., density-dependent competition and increased benthic prey mortality). Aday et al. (2000) used RNA:DNA ratios to suggest that bluegill (*Lepomis macrochirus*) exposed to hypoxic conditions within the lower Atchafalaya River Basin, Louisiana had lower short term growth rates (i.e., RNA:DNA ratios) than those in normoxic ($>2 \text{ mg O}_2 \cdot \text{l}^{-1}$) habitats. However, laboratory studies by Aday et al. (2000) reported no difference in RNA:DNA ratios of bluegill exposed to hypoxic or normoxic conditions. These studies demonstrate the difficulty in examining growth responses of fish to hypoxic conditions in natural systems and emphasize the utility of both laboratory and field explorations to evaluate relationships between hypoxia and fish growth and condition.

Our results also should have implications for bioenergetics modeling of fish growth and consumption. While standard bioenergetics models (e.g., Kitchell et al. 1977; Hansen et al. 1997) do not include dissolved oxygen effects, several studies have

incorporated dissolved oxygen into bioenergetics analyses (Cuenco et al. 1985a; Cuenco et al. 1985b; Neill et al. 2004). As our experiments were patterned after those used to parameterize (Hartman and Brandt 1995a; Lee and Johnson 2005) the widely-used Wisconsin bioenergetics model (Hansen et al. 1997) our results could be incorporated into such models in multiple ways. One option would be to replace temperature-dependent equations for maximum consumption (C_{MAX}) with the temperature- and dissolved oxygen-dependent equation we developed for consumption. However, the temperature range we used in our experiments was narrower than those used to develop temperature-dependent predictions of C_{MAX}, so incorporating our dissolved oxygen equation in the existing temperature-dependent model may be for effective. For example, results could identify critical oxygen levels at which C_{MAX} starts to decline and then assume a linear decrease of C_{MAX} with oxygen concentration.

Overall, dissolved oxygen appears to influence growth, consumption, and condition (Roberts et al. 2009) of yellow perch. Observed changes in yellow perch RNA:DNA occur during a period when individuals accumulate critical energy reserves as they prepare for resource scarce overwinter conditions and upcoming spring spawning events. However, our field results are rather enigmatic and could suggest yellow perch do not experience the potential negative effects observed in our laboratory studies, but rather they appear to mitigate these negative effects through behavioral and distribution changes. Therefore, it is difficult to determine if short-term consequences exist and it remains debatable if these hypoxia-induced ecological changes (Roberts et al. 2009) scale-up to affect population-level dynamics and influence yellow perch production. On the other hand, laboratory results suggest that effects of low oxygen diminish with lower

temperature and, since hypoxia in LECB occurs predominantly in the deep, cool, hypolimnion, physiological consequences may be less severe than they would be at warmer temperatures. Nonetheless, collectively our results stress the importance of incorporating dissolved oxygen into studies aimed at quantifying or predicting fish growth and habitat quality.

Acknowledgments

We would like to thank the captains and crew of the R/V *Laurentian* for their tireless work and dedication during our field excursions onto Lake Erie. For their assistance with laboratory and experimental work, we thank Kara Lindelof, Tom Johengen, Kristi Sabo, Damon Krueger, Solomon David, Greg Jacobs, and Christie Roberts. We especially salute the contributions of Brad Utrup to the design and implementation of our laboratory experiments. We also thank Drs. Lizu Wang and Jim Breck from the Michigan Department of Natural Resources-Institute for Fisheries Research for allowing our use of their facilities and their advice. I would also like to thank my co-authors Stephen B. Brandt, David Fanslow, Stuart A. Ludsin, Steven A. Pothoven, Donald Scavia, and Tomas O. Höök for their help conducting this research and preparing this manuscript. This work was conducted as part of the International Field Years on Lake Erie (IFYLE) program, supported by NOAA-GLERL, NOAA National Sea Grant (to T. Höök), and the US EPA Great Lakes National Program Office and in part by NOAA Center for Sponsored Coastal Ocean Research grant NA07OAR432000. This manuscript is a GLERL-NOAA contribution and EcoFore Lake Erie publication # 09-006.

Table 4.1 Mean abiotic habitat characteristics of sites sampled in Lake Erie’s central basin during summers 2005 and 2007. Sites are categorized: Hypoxic (H), Normoxic (N), and Unstratified (U). Groupings based on the presence (H or N) or absence (U) of a thermocline, and the hypolimnetic dissolved oxygen concentration ($>2 \text{ mg O}_2 \cdot \text{l}^{-1} = \text{N}$, $\leq 2 \text{ mg O}_2 \cdot \text{l}^{-1} = \text{H}$). The absence of any vertical thermal structure at unstratified sites is denoted by (--)’s within specific cells. *The depth at site H varied along a west to east transect. Range of depths are presented for site H.

Month (dates)	Site	Depth (m)	Epilimnion temp. (°C)	Epilimnion DO (mg O ₂ ·l ⁻¹)	Thermocline depth (m)	Hypolimnion temp. (°C)	Hypolimnion DO (mg O ₂ ·l ⁻¹)	Category
2005								
June (17-21)	B	23.2	17.9	8.8	10.8	8.7	10.5	N
	D	20.5	18.3	8.8	12.0	10.2	11.1	N
August (15-18)	B	23.2	25.0	7.1	12.8	10.3	4.6	N
	D	20.5	25.2	7.1	17.9	13.0	4.8	N
	H	14.2 (11-21)*	23.3	6.6	8.0	11.7	2.7	N
September (17-19)	A	20.7	21.6	6.3	14.7	11.6	1.1	H
	B	23.2	21.7	6.4	16.8	11.3	1.5	H
	H	14.2 (11-21)*	21.9	6.8	14.5	15.4	0.9	H
2007								
August (27-30)	B	24.0	23.1	7.5	15.0	11.8	2.1	H
	U	13.5	23.4	7.5	11.5	20.5	4.1	N
	T	13.0	23.9	6.6	--	--	--	U
September (17-20)	D2	21.0	20.9	6.7	--	--	--	U
	D3	17.5	20.9	6.8	--	--	--	U
	SS	18.0	21.0	6.8	18.0	18.6	4.5	N

Table 4.2 Summary statistics of yellow perch, abiotic treatments, and results for ration and temperature experiment, which consisted of three acclimation days followed by five experimental days. Yellow perch total length and weight are final value means. Temperature and ration values are means from the five experimental days

Treatment		Yellow perch		Temperature	Ration
Temperature	Ration	Total Length (mm)	Weight (g)	°C	g•day ⁻¹
Low	Low	130.8	22.9	11.6	0.01
	Medium	137.2	28.2	11.4	0.03
	High	141.0	30.2	11.5	0.08
Medium	Low	137.8	24.7	22.1	0.02
	Medium	136.2	25.4	22.0	0.06
	High	129.5	22.5	21.7	0.15
High	Low	129.3	22.4	26.5	0.02
	Medium	133.7	23.6	26.1	0.09
	High	141.5	30.1	26.4	0.13

Table 4.3 Summary statistics of yellow perch and abiotic treatments averaged across three trials of dissolved oxygen and temperature experiments with each trial consisting of three acclimation days followed by five experimental days. Yellow perch total length and weight are final value means. Temperature and dissolved oxygen values are means from the five experimental days.

Treatment		Yellow perch		Abiotic	
Temperature	Dissolved O ₂	Total Length (mm)	Weight (g)	Temperature (°C)	Dissolved Oxygen (mg O ₂ ·l ⁻¹)
Low	Low	128.9	20.3	11.3	2.1
	Medium-low	130.3	21.1	11.2	4.9
	Medium-high	133.9	23.9	10.9	8.3
	High	132.1	22.2	11.2	11.1
Medium	Low	129.1	19.9	20.9	2.3
	Medium	128.0	20.7	20.8	5.0
	High	129.7	20.5	19.9	8.4
High	Low	126.9	17.5	26.5	2.7
	Medium	129.1	19.9	26.4	4.9
	High	127.9	20.0	26.9	7.0

Table 4.4 Summary statistics for RNA:DNA measured yellow perch (total length 100-180 mm) collected using trawling at different sites within Lake Erie's central basin during 2005 and 2007.

2005								
Site	June		August			September		
	D	B	B	D	H	A	B	H
Total length (mm)	123.5	122.7	140.7	124.3	119.7	148.3	134.6	153.5
Wet mass (g)	19.7	17.6	34.3	20.9	27.3	35.9	32.9	40.1
n	10	11	12	15	5	12	10	12

2007						
Site	August			September		
	B	T	U	D2	D3	SS
Total length (mm)	123.4	135.8	166.8	145.5	128.0	148.3
Wet mass (g)	22.3	32.0	55.6	38.8	25.7	23.5
n	17	5	4	19	11	8

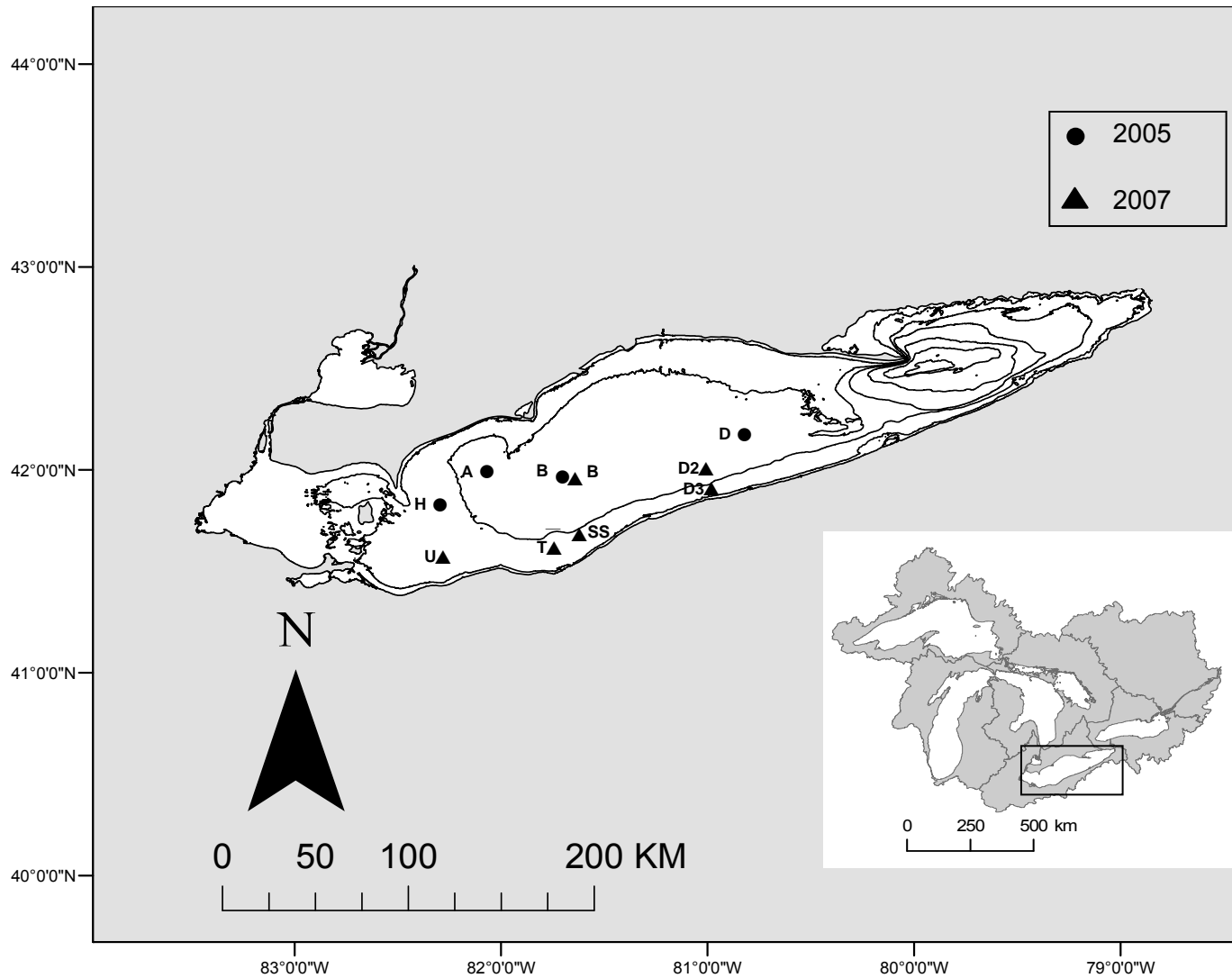
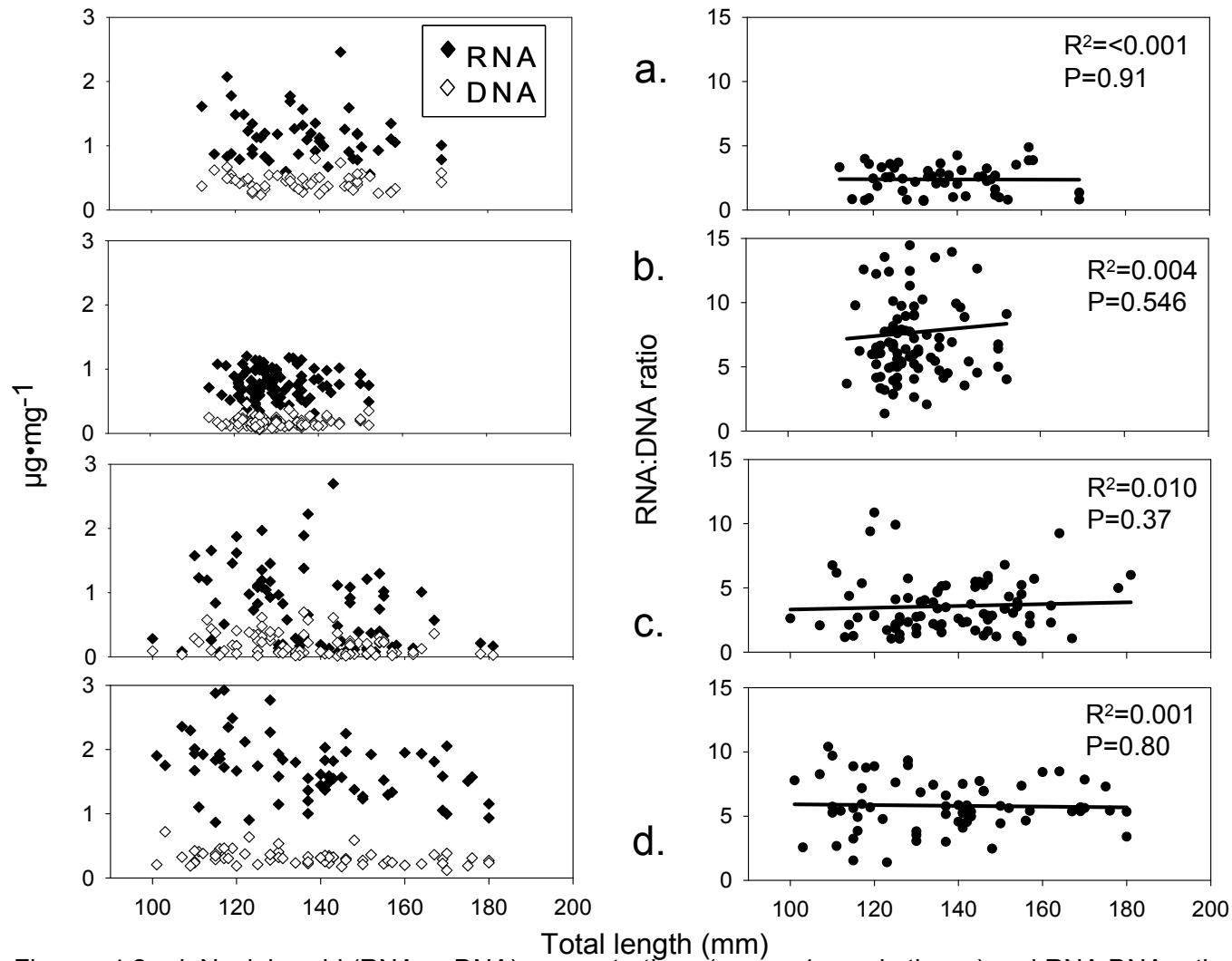
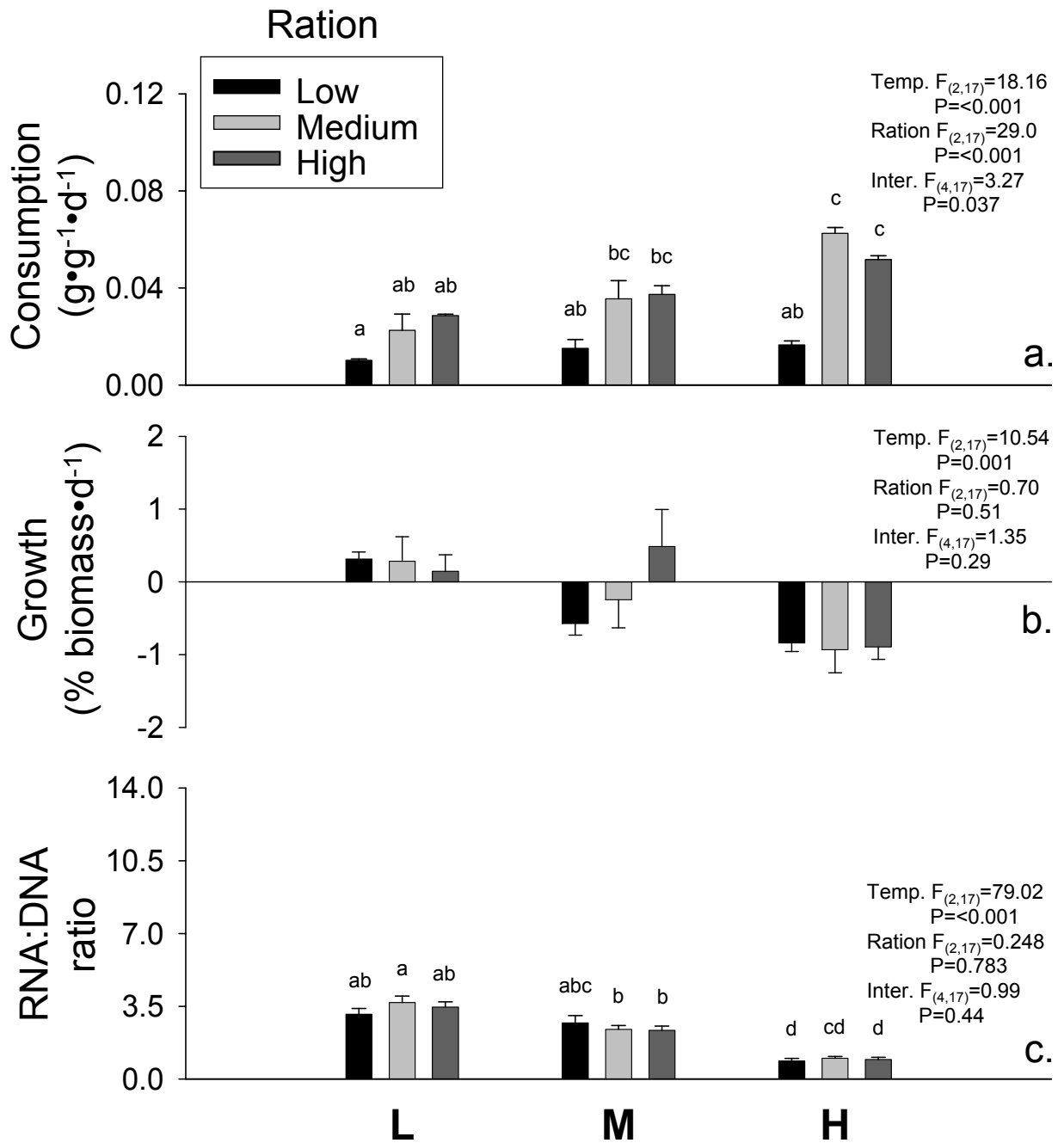


Figure 4.1 The location of Lake Erie within the Laurentian Great Lakes (and our 2005 and 2007 sample sites). Lake Erie bathymetry is depicted with 10 meter depth contours.

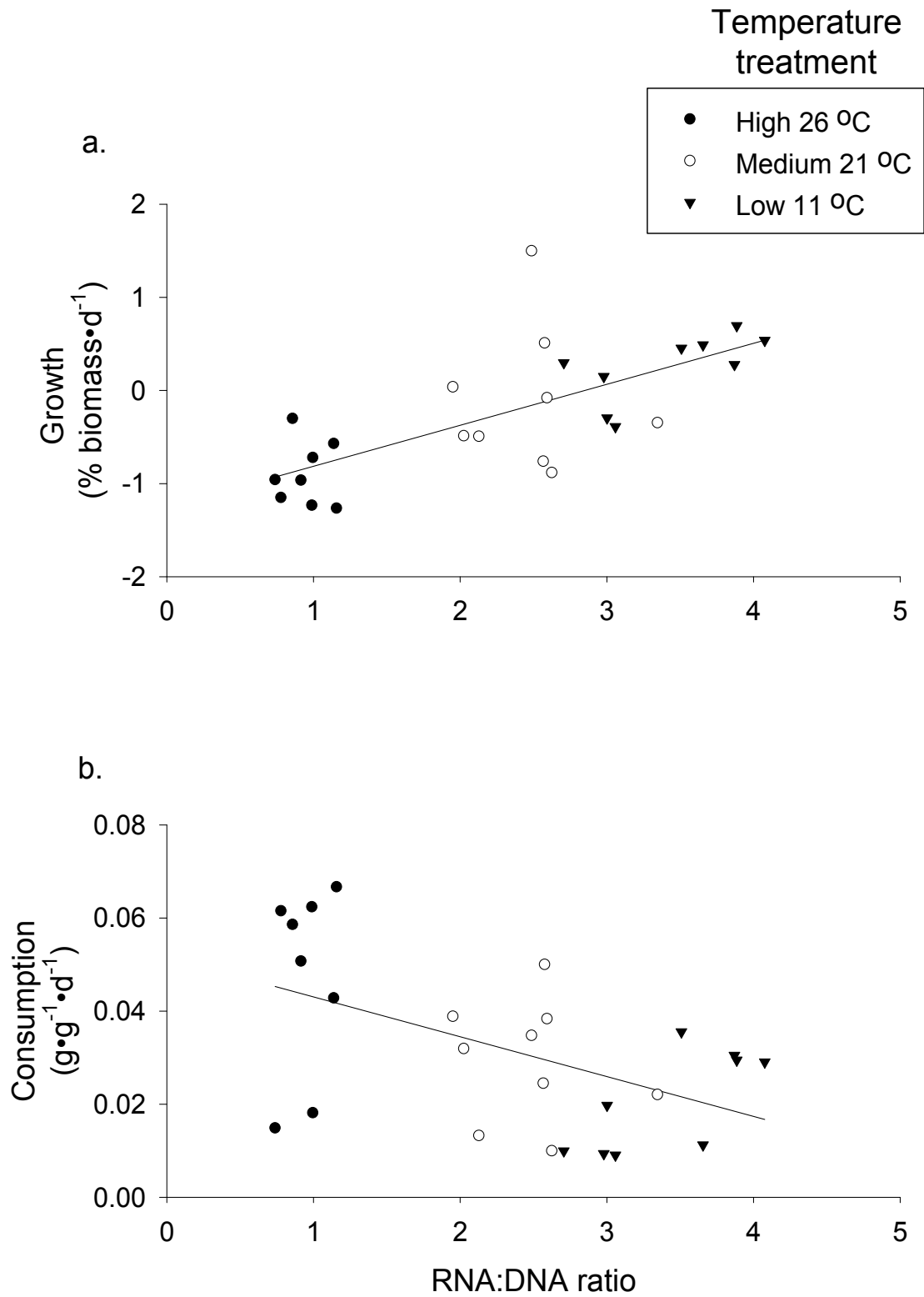


Figures 4.2a-d Nucleic acid (RNA or DNA) concentrations ($\mu\text{g}\cdot\text{mg}^{-1}$ muscle tissue) and RNA:DNA ratios versus total length of yellow perch from *a.* ration and temperature experiment, *b.* dissolved oxygen and temperature experiment, *c.* 2005 field samples, and *d.* 2007 field samples. Statistics related to linear relationships between RNA:DNA ratio and length are presented.

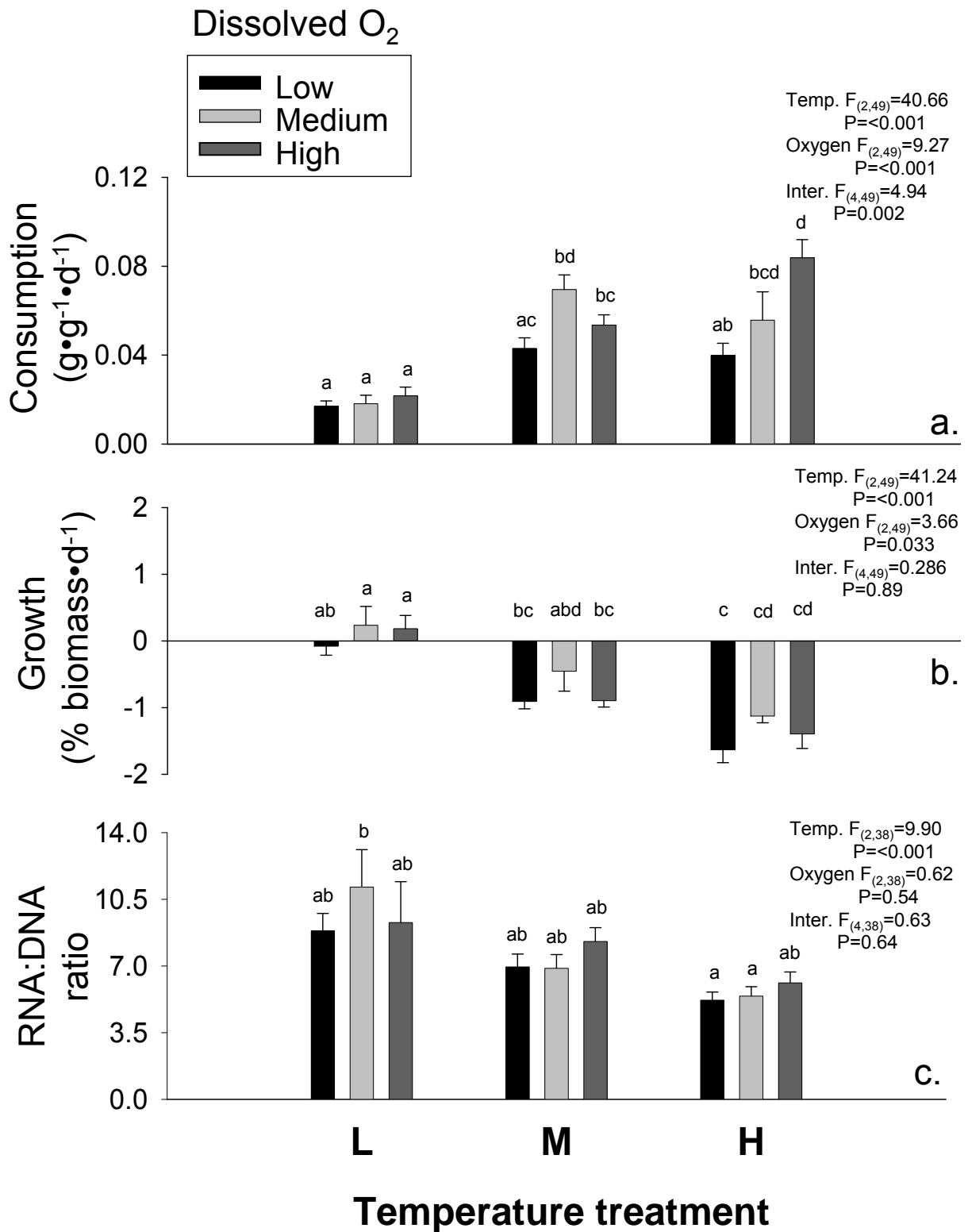


Temperature treatment

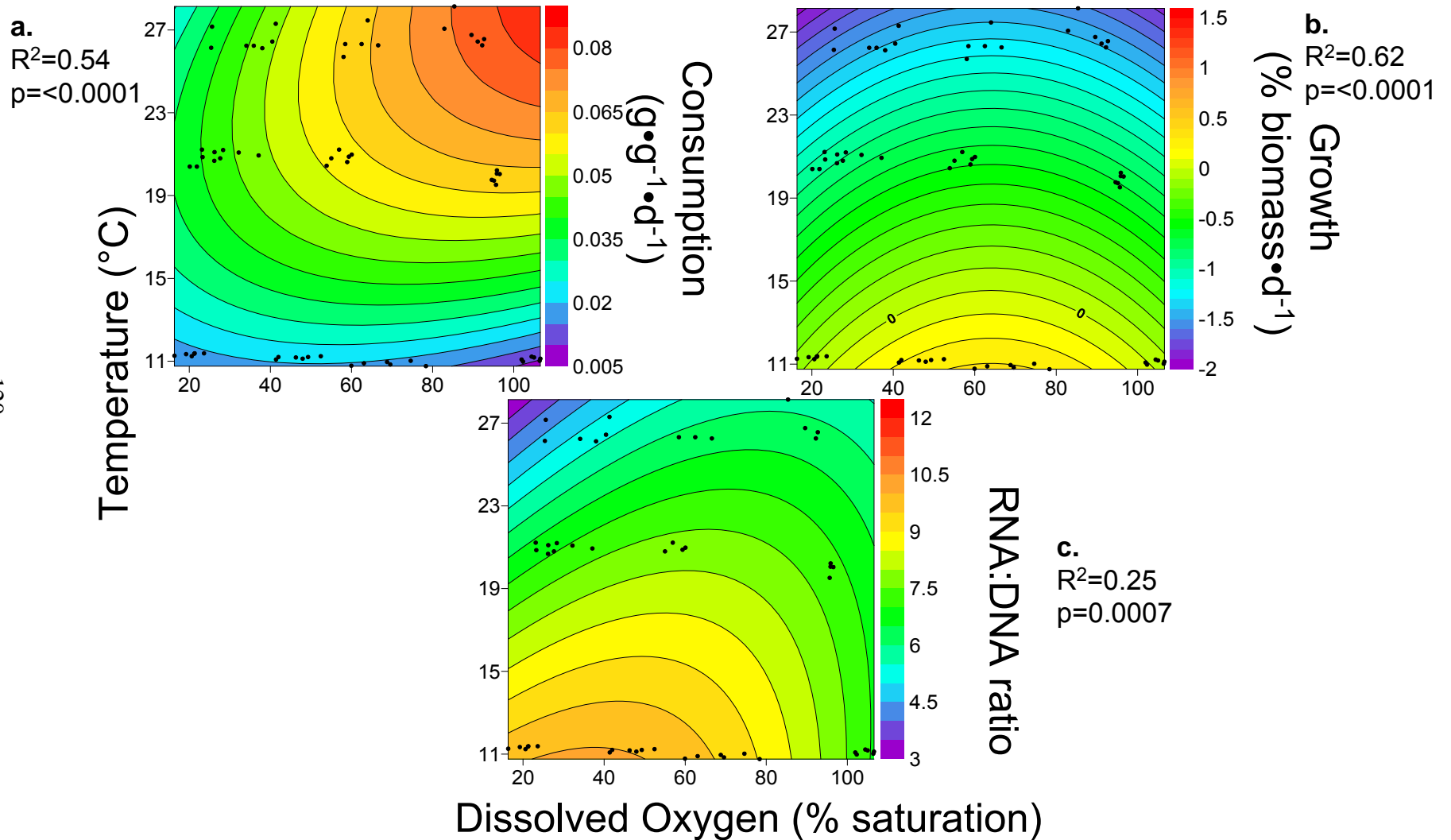
Figures 4.3a-c Results from ration and temperature experiment and corresponding 2-way ANOVA statistics and post-hoc Tukey comparison ($\alpha=0.05$). Unique letters denote significant statistical difference while the absence of letters denotes $p>0.05$. Each plot corresponds to a separate response variable (a. consumption, b. growth, and c. RNA:DNA ratio). ANOVA statistics are presented for the two factors (temperature and ration) and the interaction between the two factors.



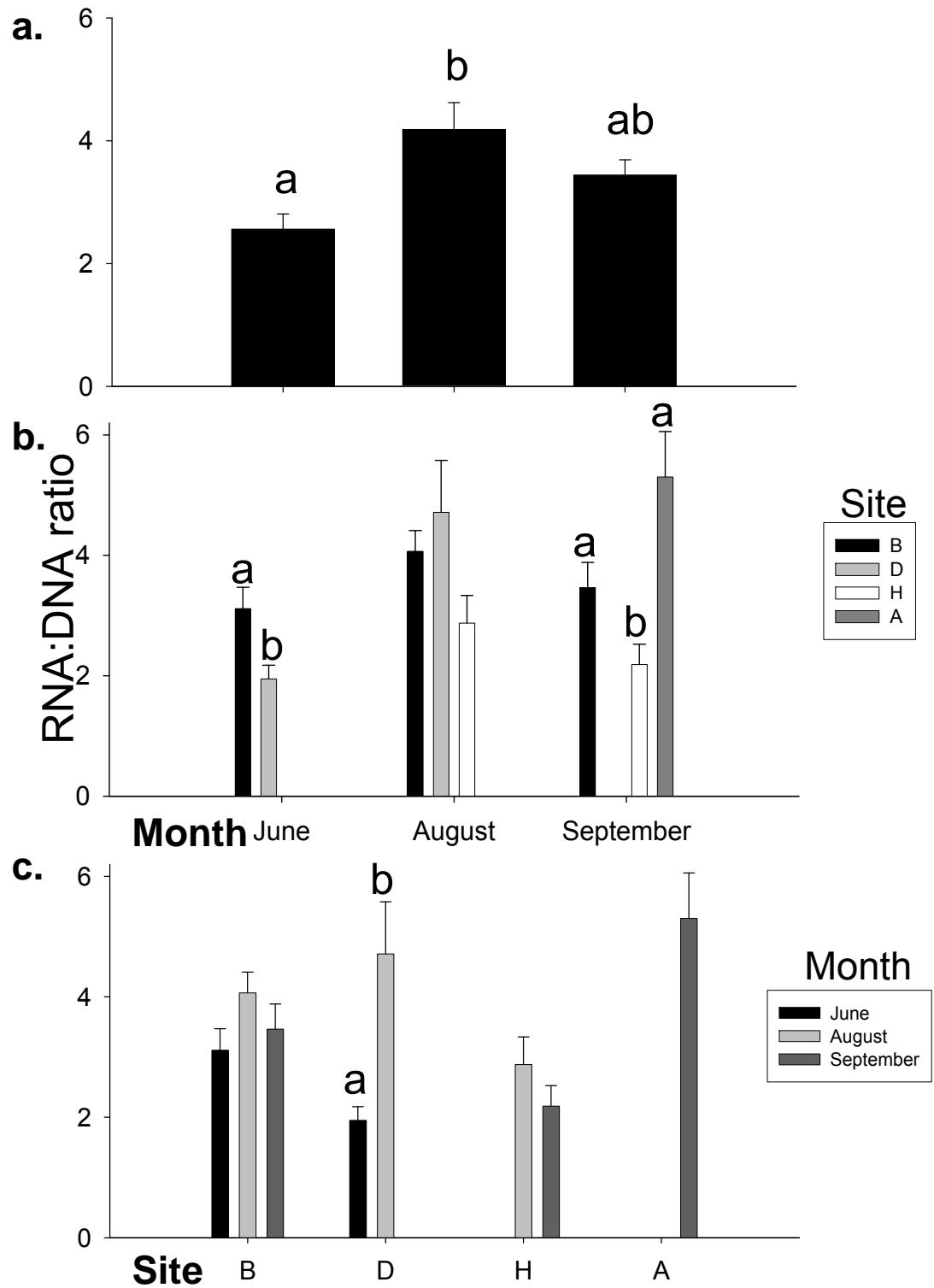
Figures 4.4a & b Scatter plot and corresponding regression statistics from ration and temperature effects experiment with observed growth (a) and consumption (b) as dependent variables. Glyph type corresponds to each point's temperature treatment. Observations were grouped across temperature treatments for regression analyses.



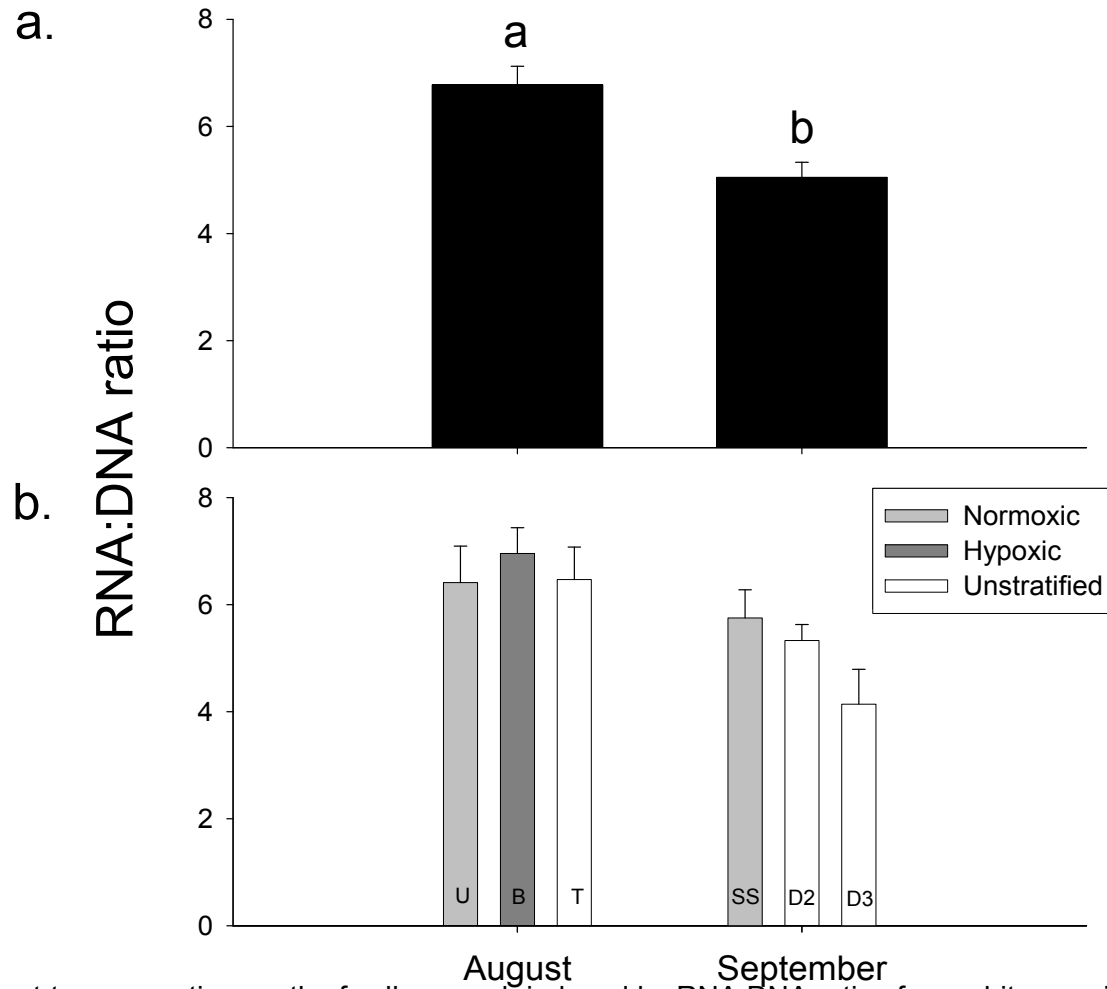
Figures 4.5a-c Results from dissolved oxygen and temperature experiment and corresponding 2-way ANOVA statistics and post-hoc Tukey comparison ($\alpha=0.05$). Unique letters denote significant statistical difference while the absence of letters denotes $p>0.05$. Each plot corresponds to a separate response variable (a. consumption, b. growth, and c. RNA:DNA ratio). ANOVA statistics are presented for the two factors (temperature and ration) and the interaction between the two factors.



Figures 4.6a-c Contour plots depicting response surfaces generated from a quadratic multiple-regression analysis. The two independent variables are temperature (X) and percent saturation of dissolved oxygen (Y) while the dependent variable is yellow perch (a. consumption, b. growth, and c. RNA:DNA ratio). Data points from experiment are depicted as ●'s.



Figures 4.7a-c Short-term somatic growth of yellow perch indexed by RNA:DNA ratios from white epaxial muscle tissue collected during summer 2005 from Lake Erie's central basin. Values were compared using a one-way ANOVA and Tukey post-hoc comparison ($\alpha=0.05$). To evaluate temporal and spatial variation we performed three analyses using month (a) and sites within months (b) and sites between months (c) as factors. Unique letters denote significant statistical difference while the absence of letters denotes $p>0.05$.



Figures 4.8a and b Short-term somatic growth of yellow perch indexed by RNA:DNA ratios from white epaxial muscle tissue collected during summer 2007 from Lake Erie's central basin. Sites were grouped into three categories: hypoxic stratified water-column (Hypoxic), normoxic stratified water-column (Normoxic), and unstratified water-column (Unstratified). Values were compared using a one-way ANOVA and Tukey post-hoc comparison ($\alpha=0.05$). To evaluate temporal and spatial variation in the data we performed two analyses using month (a) and sites within a month (b) as factors. Unique letters denote significant statistical difference while the absence of letters or shared letters denote $p>0.05$.

Appendix 1.

To obtain correction factors of the uneaten collected experimental food, we conducted trials at three temperatures (11, 21, 26°C) during which we placed known amounts of thawed mysids (0.127 g to 1.233 g) in empty experimental compartments and then attempted to recover this food after six hours. We consistently found that we were unable to recover all the food, but we were able to recover a greater percentage of food placed in cooler tanks (Table A1). To account for this, we multiplied the amount of food recovered from a tank during experimental runs by a temperature-specific correction factor ($\text{Temp}_{\text{high}}\text{-}26^{\circ}\text{C}=1.27$, $\text{Temp}_{\text{med.}}\text{-}21^{\circ}\text{C}=1.20$, and $\text{Temp}_{\text{low}}\text{-}11^{\circ}\text{C}=1.15$), and we used this as our final measure of uneaten food for calculating observed consumption (Table A1).

Table A.1 Summary statistics from *Mysis* spp. consumption calibration experiment performed to determine amount of *Mysis* spp. wet mass lost to solution after six hours in experimental chambers. Resulting temperature-specific correction factors were multiplied by observed remaining food to estimate wet weight of uneaten food.

Percent mysids lost	Temperature treatment		
	H	M	L
Mean	27.1	20.6	15.0
N	15.0	16.0	16.0
SD	2.3	2.6	2.5
Correction factor	1.27	1.21	1.15

Literature cited

- Aday, D. D., D. A. Rutherford, and W. E. Kelso. 2000. Field and laboratory determinations of hypoxic effects on RNA-DNA ratios of bluegill. *American Midland Naturalist* 143:433-442.
- Aku, P. M. K., L. G. Rudstam, and W. M. Tonn. 1997. Impact of hypolimnetic oxygenation on the vertical distribution of cisco (*Coregonus artedi*) in Amisk Lake, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2182-2195.
- Aku, P. M. K., and W. M. Tonn. 1997. Changes in population structure, growth, and biomass of cisco (*Coregonus artedi*) during hypolimnetic oxygenation of a deep, eutrophic lake, Amisk Lake, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2196-2206.
- Ali, M., and R. J. Wootton. 2003. Correlates of growth in juvenile three-spined sticklebacks: potential predictors of growth rates in natural populations. *Ecology of Freshwater Fish* 12:87-92.
- Audet, D., and P. Couture. 2003. Seasonal variations in tissue metabolic capacities of yellow perch (*Perca flavescens*) from clean and metal-contaminated environments. *Canadian Journal of Fisheries and Aquatic Sciences* 60:269-278.
- Bertram, P. E. 1993. Total phosphorus and dissolved oxygen trends in the central basin of Lake Erie, 1970-1991. *Journal of Great Lakes Research* 19:224-236.
- Brandt, S. B., M. Gerkin, K. J. Hartman, and E. Demers. 2009. Effects of hypoxia on food consumption and growth of juvenile striped bass (*Morone saxatilis*). *Journal of Experimental Marine Biology and Ecology* 381:S143-S149.
- Buckley, L., E. Caldarone, and T.-L. Ong. 1999. RNA-DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. *Hydrobiologia* 401:265-277.
- Buckley, L. J. 1982. Effects of temperature on growth and biochemical composition of larval winter flounder *Pseudopleuronectes americanus* *Marine Ecology-Progress Series* 8:181-186.
- Buckley, L. J. 1984. RNA-DNA ratio: an index of larval fish growth in the sea. *Marine Biology* 80:291-298.
- Bulow, F. J. 1987. RNA:DNA ratios as indicators of growth in fish: a review. Pages 45-64 in R. C. Summerfelt, editor. *The Age and Growth of Fish*. The Iowa State University Press, Ames, Iowa.
- Burns, N. M., D. C. Rockwell, P. E. Bertram, D. M. Dolan, and J. J. H. Ciborowski. 2005. Trends in temperature, secchi depth, and dissolved oxygen depletion rates

- in the central basin of Lake Erie, 1983-2002. *Journal of Great Lakes Research* 31:35-49.
- Caldarone, E. M., and coauthors. 2006. Intercalibration of four spectrofluorometric protocols for measuring RNA/DNA ratios in larval and juvenile fish. *Limnology and Oceanography: Methods* 4:153-163.
- Carlson, A. R., J. Blocher, and L. J. Herman. 1980. Growth and survival of channel catfish and yellow perch exposed to lowered constant and diurnally fluctuating dissolved oxygen concentrations. *The progressive fish-culturist* 42:73-78.
- Chabot, D., and G. Claireaux. 2008. Environmental hypoxia as a metabolic constraint of fish: The case of Atlantic cod, *Gadus morhua*. *Marine Pollution Bulletin* 57:287-294.
- Clemmesen, C. M. 1994. The effects of food availability, age or size on the RNA/DNA ratios of individual herring larvae: laboratory calibration. *Marine Biology* 118:377-382.
- Craig, J. K., and L. B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series* 294:79-94.
- Cuenca, M. L., R. R. Stickney, and W. E. Grant. 1985a. Fish bioenergetics and growth in aquaculture ponds: I. Individual fish model development. *Ecological Modelling* 27:169-190.
- Cuenca, M. L., R. R. Stickney, and W. E. Grant. 1985b. Fish bioenergetics and growth in aquaculture ponds: II. Effects of interactions among, size, temperature, dissolved oxygen, unionized ammonia and food on growth of individual fish. *Ecological Modelling* 27:191-206.
- Diana, J. S., and R. Salz. 1990. Energy storage, growth, and maturation of yellow perch from different location in Saginaw Bay, Michigan. *Transactions of the American Fisheries Society* 119:976-984.
- Diaz, R. J. 2001. Overview of hypoxia around the world. *Journal of Environmental Quality* 30:275-281.
- Diaz, R. J., and R. Rosenberg. 2008. Spreading Dead Zones and Consequences for Marine Ecosystems. *Science* 321:926-929.
- Eby, L. A., and L. B. Crowder. 2002. Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Canadian Journal of Fisheries and Aquatic Sciences* 59:952-965.

- Eby, L. A., L. B. Crowder, C. M. McClellan, C. H. Peterson, and M. J. Powers. 2005. Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Marine Ecology-Progress Series* 291:249-261.
- Edwards, W. J., J. D. Conroy, and D. A. Culver. 2005. Hypolimnetic oxygen depletion dynamics in the central basin of Lake Erie. *Journal of Great Lakes Research* 31:262-271.
- Glemet, H., and M. A. Rodriguez. 2007. Short-term growth (RNA/DNA ratio) of yellow perch (*Perca flavescens*) in relation to environmental influences and spatio-temporal variation in a shallow fluvial lake. *Canadian Journal of Fisheries and Aquatic Sciences* 64:1646-1655.
- Goolish, E. M., M. G. Barron, and I. R. Adelman. 1984. Thermoacclimatory response of nucleic acid and protein content of carp muscle-tissue: influence of growth rate and relationship to glycine uptake by scales. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 62:2164-2170.
- Gorokhova, E. 2003. Relationships between nucleic acid levels and egg production rates in *Acartia bifilosa*: implications for growth assessment of copepods *in situ*. *Marine Ecology Progress Series* 262:163-172.
- Gorokhova, E. 2005. Effects of preservation and storage of microcrustaceans in RNA later on RNA and DNA degradation. *Limnology and Oceanography: Methods* 3:143-148.
- Gorokhova, E., and M. Kyle. 2002. Analysis of nucleic acids in *Daphnia*: development of methods and ontogenetic variations in RNA-DNA content. *Journal of Plankton Research* 24:511-522.
- Grant, G. C. 1996. RNA-DNA ratios in white muscle tissue biopsies reflect recent growth rates of adult brown trout. *Journal of Fish Biology* 48:1223-1230.
- Gwak, W. S., Y. Tanaka, O. Tominaga, T. Tsusaki, and M. Tanaka. 2003. Field evaluation by RNA/DNA ratios on post-release nutritional status of released and wild Japanese flounder *Paralichthys olivaceus* juveniles. *Journal of Experimental Marine Biology and Ecology* 293:107-124.
- Hansen, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish Bioenergetics 3.0. University of Wisconsin-Madison Center for Limnology and University of Wisconsin Sea Grant Institute, Madison, WI.
- Hartman, K. J., and S. B. Brandt. 1995a. Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1647-1666.
- Hartman, K. J., and S. B. Brandt. 1995b. Estimating energy density of fish. *Transactions of the American Fisheries Society* 124:347-355.

- Hawley, N., and coauthors. 2006. Lake Erie hypoxia prompts Canada-U.S. study. *Eos, Transactions, American Geophysical Union* 87:313-315.
- Henderson, B. A., T. Trivedi, and N. Collins. 2000. Annual cycle of energy allocation to growth and reproduction of yellow perch. *Journal of Fish Biology* 57:122-133.
- Hergenrader, G. L., and A. D. Hasler. 1966. Diel activity and vertical distribution of yellow perch (*Perca flavescens*) under the ice. *Journal of the Fisheries Research Board of Canada* 23:499-509.
- Hermann, R. B., C. E. Warren, and P. Doudoroff. 1962. Influence of oxygen concentration on the growth of juvenile coho salmon. *Transactions of the American Fisheries Society* 91:155-167.
- Höök, T. O., E. Gorokhova, and S. Hansson. 2008. RNA:DNA ratios of Baltic Sea herring larvae and copepods in embayment and open sea habitats. *Estuarine, Coastal and Shelf Science* 76:29-36.
- Houde, E. D., and R. C. Schekter. 1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. *Rapports et Proces-verbaux des Réunions. Conseil International pour l'Exploration de la Mer* 178:441-453.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of Fisheries Research Board of Canada* 34:1922-1935.
- Kramer, D. L. 1987. Dissolved oxygen and fish behavior. *Environmental Biology of Fishes* 18:81-92.
- Lee, V. A., and T. B. Johnson. 2005. Development of a bioenergetics model for the round goby. *Journal of Great Lakes Research* 31:125-134.
- MacLean, S. A., and E. M. Caldarone. 2008. Estimating recent growth rates of Atlantic salmon smolts using RNA-DNA ratios from nonlethally sampled tissues. *Transactions of the American Fisheries Society* 137:1279-1284.
- Neill, W. H., and coauthors. 2004. Ecophys.Fish: A simulation model of fish growth in time-varying environmental regimes. *Reviews in Fisheries Science* 12:233-288.
- Pepin, P., G. T. Evans, and T. H. Shears. 1999. Patterns of RNA/DNA ratios in larval fish and their relationship to survival in the field. *ICES Journal of Marine Science* 56:697-706.

- Petersen, J. K., and L. Pihl. 1995. Responses to hypoxia of plaice, *Pleuronectes platessa* and dab, *Limanda limanda*, in the south-east Kattegat: distribution and growth. *Environmental Biology of Fishes* 43:311-321.
- Petrosky, B. R., and J. J. Magnuson. 1973. Behavioral responses of northern pike, yellow perch and bluegill to oxygen concentrations under simulated winterkill conditions. *Copeia* 1:124-133.
- Pihl, L. 1994. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. *Canadian Journal of Fisheries and Aquatic Sciences* 51:321-336.
- Ricker, W. E. 1975. *Computation and interpretation of biological statistics of fish populations*, Ottawa.
- Roberts, J. J., and coauthors. 2009. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. *Journal of Experimental Marine Biology and Ecology* 381:S132-S142.
- Rosa, F., and N. M. Burns. 1987. Lake Erie central basin oxygen depletion changes from 1929-1980. *Journal of Great Lakes Research* 13:684-696.
- Ryan, P. A., and coauthors. 2003. Fish-community goals and objectives for Lake Erie. *Great Lakes Fishery Commission Special Publication* 03-02:56.
- Smith, T. R., and L. J. Buckley. 2003. RNA-DNA ratio in scales from juvenile cod provides a nonlethal measure of feeding condition. *Transactions of the American Fisheries Society* 132:9-17.
- Stewart, N. E., D. L. Shumway, and P. Doudoroff. 1967. Influence of oxygen concentration on the growth of juvenile largemouth bass. *Journal of Fisheries Research Board of Canada* 24:475-494.
- Stierhoff, K. L., T. E. Targett, and K. Miller. 2006. Ecophysiological responses of juvenile summer and winter flounder to hypoxia: experimental and modeling analyses of effects on estuarine nursery quality. *Marine Ecology Progress Series* 325:255-266.
- Stierhoff, K. L., T. E. Targett, and J. H. Power. 2009. Hypoxia-induced growth limitation of juvenile fishes in an estuarine nursery: assessment of small-scale temporal dynamics using RNA:DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1033-1047.
- Suthers, I. M., and J. H. Gee. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1562-1570.

- Tardif, D., H. Glemet, P. Brodeur, and M. Mingelbier. 2005. RNA/DNA ratio and total length of yellow perch (*Perca flavescens*) in managed and natural wetlands of a large fluvial lake. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2211-2218.
- Taylor, J. C., P. S. Rand, and J. Jenkins. 2007. Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. *Marine Biology* 152:939-957.
- Thomas, P., M. S. Rahman, J. A. Kummer, and S. Lawson. 2005. Reproductive endocrine dysfunction in Atlantic croaker exposed to hypoxia. Pages S249-S252 in 13th International Symposium on Pollutant Responses in Marine Organisms (PRIMO 13). Elsevier Sci Ltd, Alessandria, ITALY.
- Vanderploeg, H. A., and coauthors. 2009. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *Journal of Experimental Marine Biology and Ecology* 381:S92-S107.

Chapter 5

Sub-daily behavioral response and associated consequences of hypolimnetic hypoxia for yellow perch (*Perca flavescens*)

Abstract

Hypolimnetic hypoxic ($< 2 \text{ mg O}_2\text{ l}^{-1}$) conditions develop in Lake Erie's central basin during late summer, and previous results suggest that yellow perch (*Perca flavescens*) diets and distributions in Lake Erie are affected by bottom hypoxia. To explore subtle behavioral mechanisms leading to these ecological consequences, we integrated field and laboratory methods. 1) We used drifting hydroacoustics and trawl sampling to assess sub-daily vertical movement of yellow perch within hypoxic and normoxic habitats in Lake Erie. 2) In the laboratory, we exposed yellow perch to various static and fluctuating oxygen conditions and examined effects on consumption. Collectively, our results suggest that yellow perch will undertake brief foraging forays into hypoxic habitats, but that consumption potential is not significantly affected by sharp changes in ambient oxygen concentrations associated with such behavior. Detailed understanding of such sub-daily behavior may be crucial for determining interactive individual- and ecosystem-level effects of stressors such as hypoxia.

Introduction

Fine-scale behavioral patterns may have important implications for individual and population fitness (Quevedo et al. 2009). For instance, subtle changes in individual distributions and foraging can influence growth and thereby mediate long-term survival of organisms (Delibes et al. 2001; Bolnick et al. 2003; Mueller and Fagan 2008). Such ecological subtleties may have important mediating effects on population- and ecosystem-level responses. Therefore, elucidation of behavioral responses is important for predicting the consequences of environmental stressors (e.g., invasive species, climate change, and eutrophication) on fish populations (Rose 2000; Railsback 2001).

Hypoxic ($< 2 \text{ mg O}_2 \cdot \text{l}^{-1}$) stratified waters may promote important interactive impacts at various levels of biological organization. For example, hypoxia can influence sub-daily foraging and distribution patterns at the individual level (Rahel and Nutzman 1994; Taylor et al. 2007) while simultaneously altering ecosystem function and services (Turner 2001; Breitburg 2002; Diaz and Rosenberg 2008). Elucidating individual-level consequences of hypoxia can be an important first step towards understanding impacts at population-, community- and ecosystem-levels. Rose et al. (2009) suggested that a lack of information on individual fish exposure and avoidance of hypoxic conditions confounds development and application of models aimed at predicting population level consequences of hypoxia.

Under hypoxic conditions, many fishes are exposed to very low oxygen concentrations, while others avoid hypoxic habitats and as a result may occupy habitats with novel abiotic (e.g., elevated temperature, low water clarity) and biotic (e.g., increased competition, enhanced predation pressure) conditions (Eby and Crowder 2002;

Craig and Crowder 2005; Eby et al. 2005). Previous studies demonstrate that in systems with a hypoxic bottom layer, some fish will undertake brief foraging forays into hypoxic habitats (Rahel and Nutzman 1994; Taylor et al. 2007). However, the energetic costs of such forays are unclear and may have longer-term ramifications for seasonal growth and condition.

Yellow perch (*Perca flavescens*) in Lake Erie are ecologically important and support valuable sport and commercial fisheries (Ryan et al. 2003). The hypolimnion in Lake Erie's central basin (LECB) provides a cool thermal habitat and energetically favorable prey that yellow perch target during normoxic conditions (Roberts et al. 2009). However, LECB's hypolimnion becomes hypoxic in late summer, and previous studies suggest that in response to hypoxia yellow perch migrate vertically or horizontally to avoid potentially lethal oxygen concentrations (Roberts et al. 2009). Interestingly, some yellow perch continue to forage on benthic prey even though they seemingly spend the majority of their time higher in the water column, above the hypoxic habitat (Roberts et al. 2009). These results suggest that yellow perch in LECB undertake foraging forays into hypoxic waters.

Herein, we explored subtle behavioral responses of yellow perch to hypolimnetic hypoxia and evaluated associated costs of such behavior. Specifically, we used drifting hydroacoustics, transect hydroacoustics, bottom trawls, and mid-water trawls to describe spatial distributions and short term behavior of yellow perch. In the laboratory, we exposed yellow perch to various static and fluctuating oxygen conditions and quantified their effects on consumption. These data are used to test the hypothesis that hypoxia-induced alteration of sub-daily behaviors negatively affects yellow perch.

Methods

Physical variables

We sampled LECB (Figure 5.1) three times during August and September 2007 (when hypoxia was most pronounced) onboard the R/V *Laurentian* (August and September) and *Lake Guardian* (August). We visited seven sites with a stratified water column and either a normoxic ($>2 \text{ mg O}_2 \cdot \text{l}^{-1}$) or hypoxic ($<2 \text{ mg O}_2 \cdot \text{l}^{-1}$) hypolimnion. A sampling site consisted of a 5-km transect (for examples of sampling sites see Pothoven et al. 2009, Vanderploeg et al. 2009a, Roberts et al. 2009). To quantify abiotic environmental conditions (temperature, dissolved oxygen, and PAR) of the entire water column, vertical casts of a CTD/fluorometer/oxygen sensor package were deployed, and physical variables were measured once per 24-hr sampling period at $\sim 0.03\text{-m}$ intervals at the east, west, and middle of each station transect. For analyses, measurements were grouped into 1-m depth bins. We used these data to split the water column into two approximately isothermal layers above (epilimnion) and below (hypolimnion) the thermocline. We then used the layer-specific measures of depth, temperature, and dissolved oxygen to represent depth-specific abiotic conditions within each of these layers.

Hydroacoustics

Field

To index distributions of fish, we used a split-beam DTX 120 kHz echosounder (BioSonics Inc, Seattle, WA, USA) (ping rate of 4 pings s^{-1} , 0.4-ms pulse width, and -130 dB acquisition threshold) mounted and lowered into the water on a towfish. Hydroacoustic data were collected with a laptop computer running acquisition software.

We collected these data while drifting within the 5-km site transects (Table 5.1). During drift sampling, our research vessel had no engines running and no anchor was deployed, similar to procedures previously suggested for use in the Great Lakes (Parker-Stetter et al. 2009). Data were collected during dusk (± 2 hrs civil twilight) as previous studies of yellow perch diel foraging patterns within LECB suggested this is the period of greatest food consumption (Hayward et al. 1991). We collected 5-hrs 30-mins of drifting acoustic data during 2007 at four hypoxic sites (B, S, SN, and Y) and two normoxic sites (U and SS).

We also sampled these six sites (B, U, S, SN, SS, and Y) with simultaneous night-time trawling (bottom and mid-water) and hydroacoustics to determine which fishes were present throughout the water column. Bottoms trawls (7.6 m semi-balloon: 13 mm stretched-mesh cod-liner) were deployed for an average of 9.5-mins, whereas mid-water trawls (9.1 x 9.1 m: 13 mm stretched-mesh cod-liner) were deployed for an average of 19.7-mins. At every site each trawl type was deployed at least once at night. While each trawl net was in the water, hydroacoustic data were simultaneously collected using the same transducer, settings, software, and towfish described above. These trawl data were used to determine the distribution of fish biomass throughout the water column, as well as the fish assemblage (species and size) present at each site.

Data processing

Our drifting hydroacoustic data were processed to determine the number of hypolimnetic foraging forays as well as the difference in swimming behavior between normoxic and hypoxic habitats. We followed established Great Lakes acoustic protocols for data processing (Parker-Stetter et al. 2009). We used Echoview 4.3 (EV; Sonar Data,

[Http://www.sonardata.com](http://www.sonardata.com)) software to analyze acoustic data, and quantified changes in depth, temperature, and dissolved oxygen concentrations from individual fish tracks collected during drifting hydro-acoustic sampling to examine yellow perch swimming behavior. Both the volume backscattering (S_v) and backscattering cross-section or target strength (TS) echograms were used to perform a single target analysis (single target method 2) using parameters from Parker-Stetter et al. (2009). We used the fish-tracking module within the EV software platform to identify single targets pertaining to an individual fish's movement or track within the acoustic beam, using parameters previously reported by Johnson et al. (2005). Output from this fish-tracking module included the track-specific maximum and minimum TS (-dB) and depth (m). The abiotic data collected from our CTD casts were used in conjunction with the depth-specific location and range of the individual fish tracks to quantify site-specific abiotic conditions experienced by these targets (Figure 5.2).

Figure 5.2 depicts how we quantified properties of the recorded fish tracks. Tracks could start at points A, B, or C and terminate at B, C, D, or E. Tracks that traveled into the hypolimnion at any point were included in that layer for analysis purposes. We used a track's maximum and minimum depth values and site-specific profiles of temperature and oxygen to determine the minimum and maximum abiotic conditions experienced by a specific acoustic target. Tracks that never crossed into the hypolimnion were assigned to the epilimnetic layer for analysis. We determined the change in depth, temperature, and dissolved oxygen using the difference between the maximum and minimum values of each of the three previously listed abiotic track

measurements. These results were summarized and used as our fish track descriptive statistics.

To determine the distribution of yellow perch biomass throughout the water column, we used the trawl and transect hydroacoustic data. We used the S_v , TS, and single target detection echograms to determine yellow perch density using equation 1:

$$N_v = \frac{c \tau \psi R^2 \rho_v}{2} \quad \text{Equation 1.}$$

$$\rho = \frac{S_v}{\sigma_{bs}} \quad \text{Equation 2.}$$

$$\sigma_{bs} = 10^{(TS/10)} \quad \text{Equation 3.}$$

$$s_v = 10^{(S_v/10)} \quad \text{Equation 4.}$$

where c is the speed of sound ($\text{m}\cdot\text{sec}^{-1}$), τ is the pulse duration (0.40 msec), ψ is the equivalent beam angle (23.5 steradians), R is the range (i.e., maximum depth of the cell; m), and ρ_v is the density of targets ($\#\cdot\text{m}^{-3}$) from equations 2-4 (Parker-Stetter et al. 2009). The S_v and TS values were exported directly from the respective echograms by regions and one meter bin sizes using the EV software. We identified the epilimnetic and hypolimnetic regions using temperature profiles from our CTD data.

We used trawl catch data to determine the species-specific target strength for each site. We used the species-specific range of lengths from the trawl catches along with previously published results on species- and size-specific total length (TL) to target strength relationships. Our most abundant fishes and the source for their respective TL to target strength relationships are gizzard shad (*Dorosoma cepedianum*; Foote et al. 1987), rainbow smelt (*Osmerus mordax*; Rudstam et al. 2003), yellow perch (obtained from Eurasian perch, *Perca fluviatilis*; Frouzova et al. 2005), and Moronidae (i.e., white bass-*Morone chrysops* and white perch-*Morone americana*; Hartman and Nagy 2005). We

used the lengths and species composition from our trawls along with length to target strength relationships to identify ranges of target strength at each site specific to yellow perch (Table 5.2). Once the site-specific yellow perch target strength ranges were determined, we applied these as data filters in all our acoustic analyses.

Laboratory

We performed experiments to evaluate the response of yellow perch consumption rates to static and sub-daily fluctuating oxygen concentrations. Experiments were conducted at the University of Delaware's College of Marine and Earth Sciences (Lewes, DE). The experimental setup consisted of five systems of ten tanks each. Within each system, we were able to measure and adjust oxygen concentrations in 30 minute time blocks. Systems were controlled by one central computer in which the desired oxygen concentrations for every 30-min time block over 24-hrs were set and stored. The experimental setup is described in Gre cay and Stierhoff (2002) and has been used in previous studies (Stierhoff et al. 2003; Stierhoff et al. 2006). These experimental units allowed for five oxygen treatments each with ten fish, resulting in 50 total yellow perch per experimental trial. A constant temperature of 20 °C was used for each treatment.

Yellow perch were obtained from the aquaculture facilities at Delaware State University where they were reared in hatchery-type conditions. Individuals used for our experiment were age-1 and of similar size (TL (mm)_{mean}=108.8, range=80-122; mass (g)_{mean}=17.3, range=9.5-27.7). Yellow perch were fed pelletized fish food (Melick aquafeed, 1.5 mm slow sinking pellet) and experimental trials did not begin until yellow perch were acclimated as indicated by regular feeding behavior within the experimental

chambers. Once acclimated, fish were starved for two days (acclimation days) before we started our feeding trials on days 3-7 (experimental days 1-5).

Our experimental design included two static oxygen treatments (high-8 mg•l⁻¹ and low-2 mg•l⁻¹), two diurnally fluctuating treatments (high-night/low-day O₂ and low-night/high-day O₂), and one rapidly fluctuating treatment. The rapidly fluctuating treatment had a 1.5-hr transition period from high to low and a 30-min transition period from low to high O₂ (Figure 5.3a-e). A 12-hr on (6:00-18:00) 12-hr off (18:00-6:00) light regime was used for all treatments. During the experimental period, fish were fed *ad libitum* during the day and given 6-hrs (8:00-14:00) to consume feed. Uneaten food pellets were removed after 6-hrs and counted to quantify fish consumption. We also recorded fish lengths (nearest 0.1mm) and mass (nearest 0.01 g) after the experimental trial to correct for differences in fish size.

Data analysis

Field

To determine how distributions of yellow perch biomass were influenced by hypoxia we used the volumetric (g•m⁻³) and areal (g•m⁻²) expressions of total biomass found within the hypolimnion at each trawl transect sample site. We performed regression analyses using site-specific hypolimnetic yellow perch biomass as the dependent variable and hypolimnetic dissolved oxygen concentration as our independent variable. A one-way ANOVA with a post-hoc Tukey comparison ($\alpha=0.05$) was used to compare the variation in fish track statistics among sites (Table 5.3): 1) including all tracks from the entire water column and 2) only including tracks which occupied the hypolimnion.

Laboratory

We converted our consumption measures from counts of pellets to mass using the average dry mass per pellet which was 0.011 g (SE=0.0004). To standardize for perch size, we divided our consumption measures by the mass of individual fish. Our mean consumption measure for each perch was calculated using experimental days 3-5 since we observed higher and lower consumption on experimental days one and two respectively, which was probably an artifact of starvation during the previous acclimation days. This experimental design is similar to our previous laboratory experiments (see Chapter 4 for details). To analyze our laboratory results we used a one-way ANOVA analysis with a post-hoc Tukey comparison ($\alpha=0.05$). All statistical analyses were performed using SYSTAT© 12 software.

Results

Physical variables

We sampled one normoxic site (U) and two hypoxic sites (S and Y) in August and we sampled two normoxic sites (NWX and SS) and two hypoxic sites (B and SN) in September. We sampled every site except for (NWX and SS) with both drifting and transect hydroacoustics in coordination with bottom and mid-water trawls to collect fish for identification. Site NWX was sampled using only drifting hydroacoustics and site SS was only sampled with trawls and transect hydroacoustics (Table 5.1).

Hydroacoustics

We were able to determine a range in target strengths unique to yellow perch at all but two of our sample sites (Table 5.2). Size ranges of white perch and white bass at sites SS and U overlapped with yellow perch, and we thus used a target strength range

that included both Moronidae and yellow perch targets for sites U and SS (Table 5.2). Our nighttime transect hydroacoustic biomass estimates suggest that across months, proportionally more yellow perch are found in the hypolimnion at sites with normoxic conditions while more yellow perch occupy the epilimnion at hypoxic sites (Figure 5.4). Our regression results suggest that the relative amount of yellow perch biomass within the hypolimnion increases with increasing oxygen concentration (Figure 5.5). However, this relationship is only significant for yellow perch biomass expressed per unit volume (and not per unit area), likely due to the large differences in epilimnetic vs. hypolimnetic volume at our sample sites (Table 5.1; Figure 5.5). This suggests that during nighttime the majority of yellow perch are found lower in the water column during normoxic conditions and vice versa during hypoxic conditions.

We relied on the trawls to index the size range of yellow perch at a site, and we used the same target strength ranges for our analysis of drifting hydroacoustics data (Table 5.2). With drifting hydroacoustics, we observed fish diving into and out of hypoxic areas; however, some fish statically occupied specific areas of the water column (Figure 5.6). Furthermore, these tracks were all incomplete observations of this behavior; that is, we only recorded targets returning from hypoxic regions or diving into hypoxic regions. The mean change of depth (ΔD) was not significantly different when including all tracks or when only including hypolimnetic tracks (Figure 5.7). Site S was excluded from our analysis of hypolimnetic fish tracks because only one track was observed within this layer. Sites U and Y were both excluded from the analyses of track-specific change in temperature and oxygen because neither site had a target move between layers. However, the change in temperature (ΔT) significantly varied among our sites when we

analyzed tracks across all layers or within the hypolimnion (Figure 5.7). The change in dissolved oxygen (ΔDO) varied significantly among our sites only within the hypolimnion (Figure 5.7). The ΔT and ΔDO of tracks among sites are not consistently different among hypoxic and normoxic sites (Figure 5.7). In fact, across all layers the only significant difference between hypoxic and normoxic sites, was between ΔT at sites SN and NWX (Figure 5.7). Within the hypolimnetic layer, all hypoxic sites (B and SN) experience a greater ΔT than the normoxic site NWX (Figure 5.7). Site B is the only hypoxic site within the hypolimnetic layer whose ΔDO is not significantly greater than the normoxic site NWX (Figure 5.7).

Laboratory

Our laboratory results suggest that different oxygen treatments significantly affect yellow perch consumption rates ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$; Figure 5.8; $F_{4,45}=2.723$; $p=0.041$). However, mean consumption rates only differed significantly when comparing between the static-low treatment and the high-day, low-night treatment (Figure 5.8), suggesting that yellow perch consumption potential responds most negatively to consistently low oxygen conditions. Interestingly, mean consumption rate in the rapidly fluctuating oxygen treatment was not significantly different from mean consumption for the static high oxygen treatment.

Discussion

Hypoxic conditions may influence fishes' foraging, movement, and growth (Pihl 1994; Breitburg et al. 2001; Eby and Crowder 2002; Stanley and Wilson 2004; Craig and Crowder 2005; Roberts et al. 2009; Vanderploeg et al. 2009b). Within LECB, previous studies have suggested yellow perch shift their distribution and foraging patterns in the

presence of a hypoxic hypolimnion (Roberts et al. 2009). However, if these ecological responses negatively impact yellow perch consumption or growth is unclear. Yellow perch may mitigate potential negative consequences of hypoxia by altering their sub-daily behavioral patterns. The ability of freshwater fishes to avoid hypoxic habitats, but still forage within this region, has been reported in previous studies of yellow perch (Hergenrader and Hasler 1966; Roberts et al. 2009) and central mudminnow (*Umbra limi*; Rahel and Nutzman 1994). Our study confirms yellow perch in LECB are undertaking such foraging forays and, in so doing, are subjected to highly variable temperature and oxygen conditions. Our laboratory results suggest that short exposures to hypoxic conditions do not significantly affect consumption potential of yellow perch. However, our experiments were performed at one temperature (20°C) and our field results suggest that foraging yellow perch experience changes in both oxygen and temperature conditions.

Rose (2000) suggested that understanding fine spatio-temporal scale responses to changes in environmental quality is crucial to determining the overall impact of environmental changes. This is particularly important when trying to quantify the impacts of hypoxia on fish populations because fish can sense low oxygen concentrations and avoid most direct negative effects (Kramer 1987; Pollock et al. 2007). However, by avoiding a preferred habitat when it becomes hypoxic, fish may move to novel habitats characterized by less suitable abiotic (e.g., temperature) and biotic (e.g., prey densities) conditions.

To mitigate the negative effects of hypoxia these displaced fishes could either forage on alternative prey items or continuing foraging on the same prey items in a

different manner. Across a range of aquatic systems, studies demonstrate that fish will shift distributions in response to hypoxia and thereby either alter prey consumption or undertake foraging forays into hypoxic waters to consume preferred prey. Within marine (Stanley and Wilson 2004; Prince and Goodyear 2006) and estuarine (Eby and Crowder 2002; Taylor and Rand 2003; Ludsin et al. 2009) systems, evidence suggests fish avoid hypoxic habitats and alter their prey consumption (Craig and Crowder 2005; Eby et al. 2005; Zhang et al. 2009). However, some fish are able to maintain consumption of preferred prey through novel foraging strategies. For instance, in the Neuse River estuary, Taylor et al. (2007) report short forays into hypoxic habitats by anchovies (*Anchoa spp.*) to forage on preferred zooplankton prey. Similarly, freshwater fish also avoid hypoxic habitats, and shift consumption patterns (Aku and Tonn 1997; Baldwin et al. 2002; Roberts et al. 2009). Aku and Tonn (1999) report that cisco (*Coregonus artedi*) increase foraging on pelagic zooplankton when avoiding hypoxic bottom waters. Moreover, laboratory and field observations by Rahel and Nutzman (1994) suggest central mudminnow will make short forays into hypoxic habitats to forage on preferred prey items. Collectively, these studies suggest that across vastly different aquatic systems (i.e., coastal marine, estuarine, and lentic freshwaters) fish responses to hypoxia are fairly consistent.

Our *in-situ* observations of yellow perch hypoxic foraging forays provide previously unknown, detailed accounts of hypoxic foraging foray behavior in natural freshwater systems. Our acoustic tracks quantified abiotic conditions experienced during such behaviors, and demonstrate that yellow perch experience pronounced variation in temperature and oxygen conditions during hypoxic forays. In addition, our drifting

acoustic measures suggest that these behaviors were fairly common, which is consistent with evidence that yellow perch consume benthic prey items despite hypoxic conditions (Roberts et al. 2009).

The frequency of yellow perch diving behavior appears to vary spatially. Even among hypoxic sites, yellow perch do not consistently exhibit this diving behavior. This behavior is likely regulated by a combination of abiotic (temperature, dissolved oxygen, and hypolimnetic thickness) and biotic (pelagic prey, benthic prey, and fish assemblage) conditions. Similarly, a study of Stellar sea lions (*Eumetopias jubatus*) suggests diving behavior is regulated synergistically by resources and predators (Frid et al. 2009). Frid et al (2009) used both empirical data and models to suggest Stellar sea lion foraging behavior is related to tradeoffs between foraging profitability and predation risk. The diving behavior of large pelagic marine fishes (Dagorn et al. 2006; Kraus and Rooker 2007; Schaefer and Fuller 2007; Schaefer et al. 2007; Hays et al. 2009) has been documented, but, only limited insights into mechanisms regulating these behaviors exist for fishes. While our studies provide important insights into potential mechanisms regulating yellow perch hypoxic foraging behavior, more detailed information on the fine-scale characteristics, associated energetic costs, and benefits are required to fully understand and predict these behaviors.

Our experimental results suggest that yellow perch consumption at fluctuating oxygen conditions is not significantly different from consumption at static normoxic conditions, however these experiments do not strictly mimic conditions experienced by perch during hypoxic forays because such forays also lead to sharp changes in temperature. While many studies have evaluated the effects of fluctuating temperature

on fish growth and survival (Donaldson et al. 2008), the interactive effects of fluctuating temperature and oxygen are more equivocal.

Studies of estuarine fish responses to fluctuating oxic conditions have demonstrated that fluctuating hypoxic conditions may negatively influence growth (Stierhoff et al. 2006) and alter swimming behavior (Brady et al. 2009). Stierhoff et al. (2006) studied exposure of two estuarine species to fluctuating oxygen conditions and reported a larger decrease in growth rate due to diel cycling of hypoxic conditions compared to static high oxygen conditions for summer flounder (*Paralichthys dentatus*), but no difference between the two oxygen regimes for winter flounder (*Paralichthys americanus*). Brady et al. (2009) explored the behavioral swimming response of weakfish (*Cynoscion regalis*) to diel cycling of hypoxic conditions. Two groups of fish were used in the laboratory portion of this study (hypoxia-acclimated and saturation-acclimated). However, they found a large locomotion response (i.e., swim speed and angular correlation) in only the saturation-acclimated weakfish to cycling hypoxic conditions. These studies suggest cycling hypoxic conditions may negatively affect fish growth and swimming patterns. However, these responses are species-specific and appear to be mediated by previous exposure to hypoxic conditions. As suggested by the results of our laboratory studies, juvenile yellow perch in a freshwater prairie marsh migrate diurnally to avoid cycling hypoxic conditions (Suthers and Gee 1986). Overall, results from our study, and previous investigations, suggest fluctuating hypoxic conditions may influence the distribution of fishes but brief exposures to hypoxic conditions through foraging forays do not always negatively affect growth.

Within LECB, yellow perch experience significant changes in both temperature and oxygen when foraging in the hypolimnion during hypoxic conditions. Sudden and drastic changes in temperature can have acute (i.e., mortality) and chronic negative effects (i.e., stress responses) on fish (Donaldson et al. 2008). Donaldson et al. (2008) reviewed the effects of sudden decreases in temperature for fishes or “cold shock” and suggest there are three levels of responses (primary, secondary, and tertiary) to these sudden changes in temperature. These three levels represent the initial (primary) neuro-chemical response which can cascade into physiological processes (secondary) and finally result in growth and behavioral (tertiary) consequences. The realized response of fish to cold shock is dependent on the degree of change in temperature and species specific thermal tolerances (Donaldson et. al. 2008). Nonetheless, the sharp temperature changes experienced by yellow perch undertaking hypoxic forays may have chronic non-lethal effects.

In summary, hypoxic hypolimnia appear to shift yellow perch biomass horizontally (to areas without hypoxic bottom waters) and vertically (higher in the water column; Roberts et al. 2009). This change in distribution can induce some yellow perch to undertake forays into the cooler hypoxic habitat to forage on their preferred benthic prey. Our experimental results suggest there is little effect of these fluctuating oxygen conditions on yellow perch consumption, however long-term consequences of repeated forays into low oxygen environments, in concert with temperature changes, remain equivocal. Understanding sub-daily responses of fishes like yellow perch to hypoxia is important to fully understand the impact of this type of phenomenon in LECB and other aquatic systems.

Acknowledgments

I would first like to thank my co-authors Stuart A. Ludsin, Paul A. Greco, Steven A. Pothoven, and Tomas O. Höök who helped perform this research. I would also like to thank all those who helped with field portions of this study including, Greg Jacobs, Brad Utrup, Dave Fanslow, Joann Cavaletto and Aaron Adamack. I would like to extend a special thanks to the captains and crew of the R/V *Laurentian* who were a tremendous help. I would also like to thank those who help with the laboratory portion of this study including Jennifer Metes and Catherine House. Lastly, I would also like to thank Dr. Tim Targett who facilitated our use of his dynamic experimental system which made our experimental design possible. This work was conducted as part of the International Field Years on Lake Erie (IFYLE) program, supported by NOAA-GLERL, NOAA National Sea Grant and the US EPA Great Lakes National Program Office and in part by NOAA Center for Sponsored Coastal Ocean Research grant NA07OAR432000.

Table 5.1 Abiotic conditions observed at sample sites within the central basin of Lake Erie during 2007. These data were collected from CTD (conductivity-temperature-depth) casts at the east, central and west points of each site's 5km transect over a single 24 hour period. All sites were sampled with drifting (DA) and transect acoustics and trawls (Tr), except SS, where no DA were conducted, and NWX where no Tr were conducted.

Month	Site	Depth (m)	Epilimnetic temperature (°C)	Epilimnetic DO (mg O ₂ ·l ⁻¹)	Thermocline depth (m)	Hypolimnetic temperature (°C)	Hypolimnetic DO (mg O ₂ ·l ⁻¹)	Sampling
August	S	20.0	23.9	7.2	16.0	12.8	1.4	DA, Tr
	U	13.5	23.4	7.5	11.5	20.5	4.1	DA, Tr
	Y	19.0	23.6	7.1	14.0	11.8	0.6	DA, Tr
September	B	23.5	19.4	6.9	19.0	12.1	1.0	D,A Tr
	SN	22.5	19.9	7.1	20.0	12.7	1.4	DA, Tr
	SS	18.0	21.0	6.8	18.0	18.6	4.5	Tr
	NWX	16.0	22.8	7.8	14.0	21.0	5.6	DA

Table 5.2 Summary of yellow perch size and species compositions at sites sampled in Lake Erie's central basin during 2007, where BTR represents bottom trawl and MTR represent mid-water trawl. Using the size of the yellow perch and other species caught at each site (via MTR and BTR trawling) and published species-specific relationships between fishes' total length and maximum target strength (decibels; dB), we determined a site-specific range of target strengths that are specific to yellow perch. At sites U and SS, we could not use a target strength range exclusive of Moronidae species. The species caught at each site are indicated by three letter species codes: emerald shiner (EMS; *Notropis atherinoides*), freshwater drum (FRD; *Aplodinotus grunniens*), gizzard shad (GIS; *Dorosoma cepedianum*), rainbow smelt (RAS; *Osmerus mordax*), yellow perch (YEP; *Perca flavescens*), white bass (WHP; *Morone chrysops*), and white perch (WHP; *Morone americana*). No YEP were collected in trawls at site B so we used a TS range that did not overlap any fishes that we did collect. No trawls were deployed at NWX, and instead, we assumed that every target within the TS range corresponding to yellow perch between 100-300 mm were yellow perch.

Month	Site	Speed of sound (c; m•sec ⁻¹)	Gear (# of trawls)	Trawl yellow perch TL (mm; min./ mean/ max.)	Yellow perch dB range (TL; min-max)	Species assemblage
August	S	1486.86	BTR (2)/ MTR (2)	(109/ 227/ 390)	-44.5 to -36.0 (100-180)	EMS, GIS, RAS, WHP, YEP
	U	1480.49	BTR (1)/ MTR (1)	(142/ 203/ 258)	>-40.7 (w/ Moronidae; > 130)	YEP, WHP, WHB, ROG, RAS, GIS, EMS
	Y	1482.05	BTR (2)/ MTR (2)	(53/ 187/ 232)	-54.4 to -31.9 (120-240)	YEP, RAS, FRD, EMS
September	B	1476.17	BTR (2) /MTR (2)	None sampled	-46.0 to -35.0 (90-190)	WHB, WHP, RAS, GIS, EMS
	NWX	1489.59	N/A		-44.5 to -28.7 (100-300)	N/A
	SN	1479.29	BTR (2) /MTR (3)	6(95/ 185.6/ 256)	-46.0 to -34.0 (90-200)	EMS, FRD, RAS, WHB, WHP, YEP
	SS	1484.77	BTR (2) /MTR (2)	(192/ 224.8/ 313)	>-48.0 (w/ Moronidae; > 80)	EMS, FRD, GIS, RAS, WHB, WHP, YEP

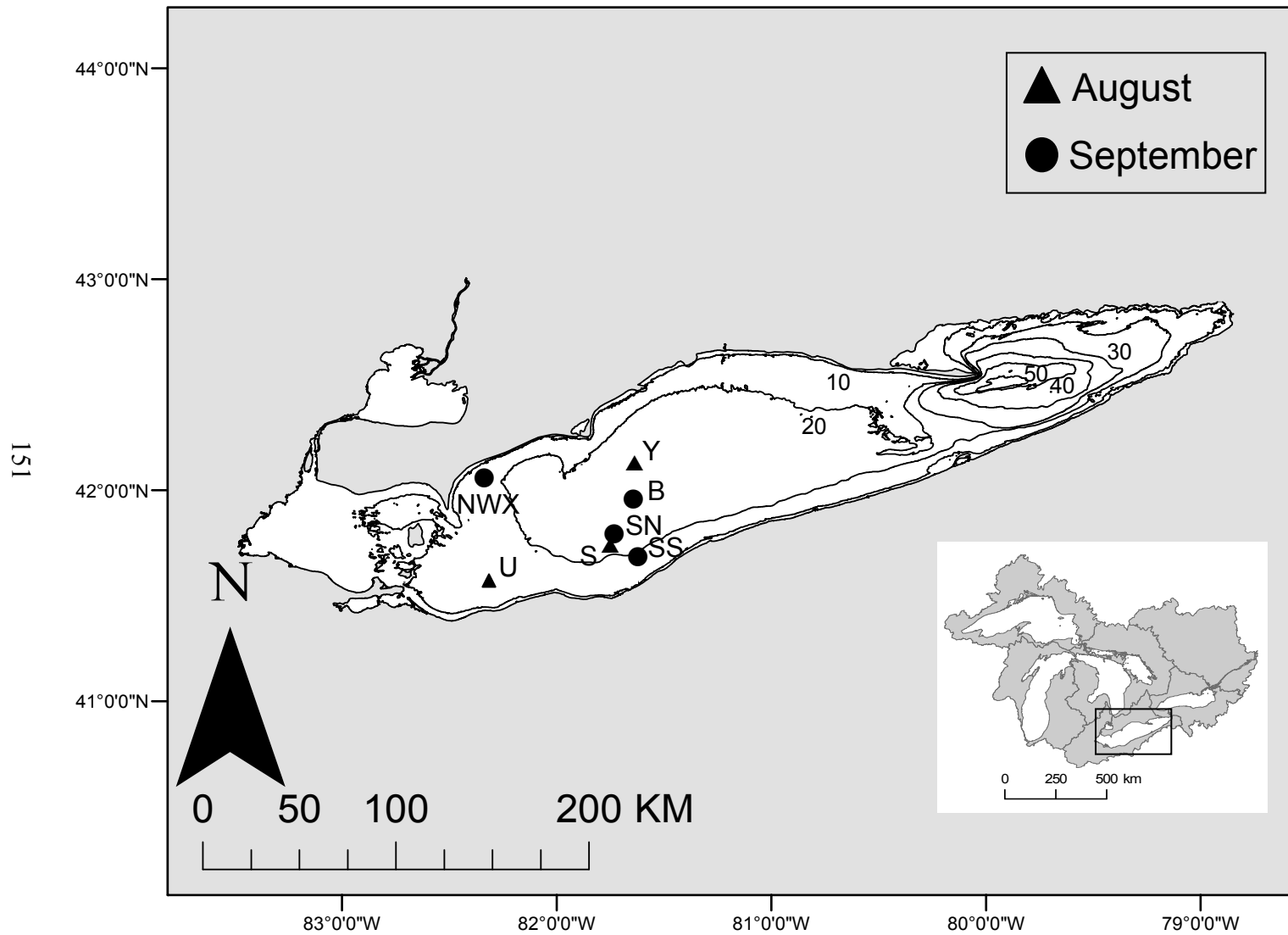


Figure 5.1 The location of Lake Erie within the Laurentian Great Lakes and 2007 August and September sample sites. Lake Erie bathymetry is depicted with 10 meter depth contours.

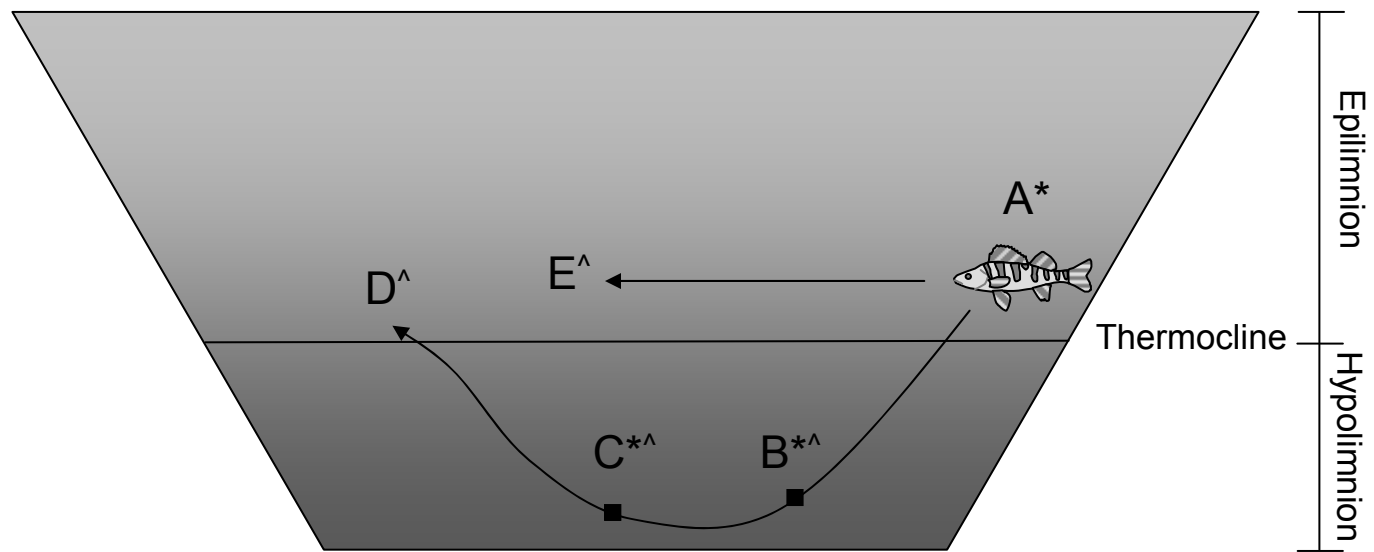
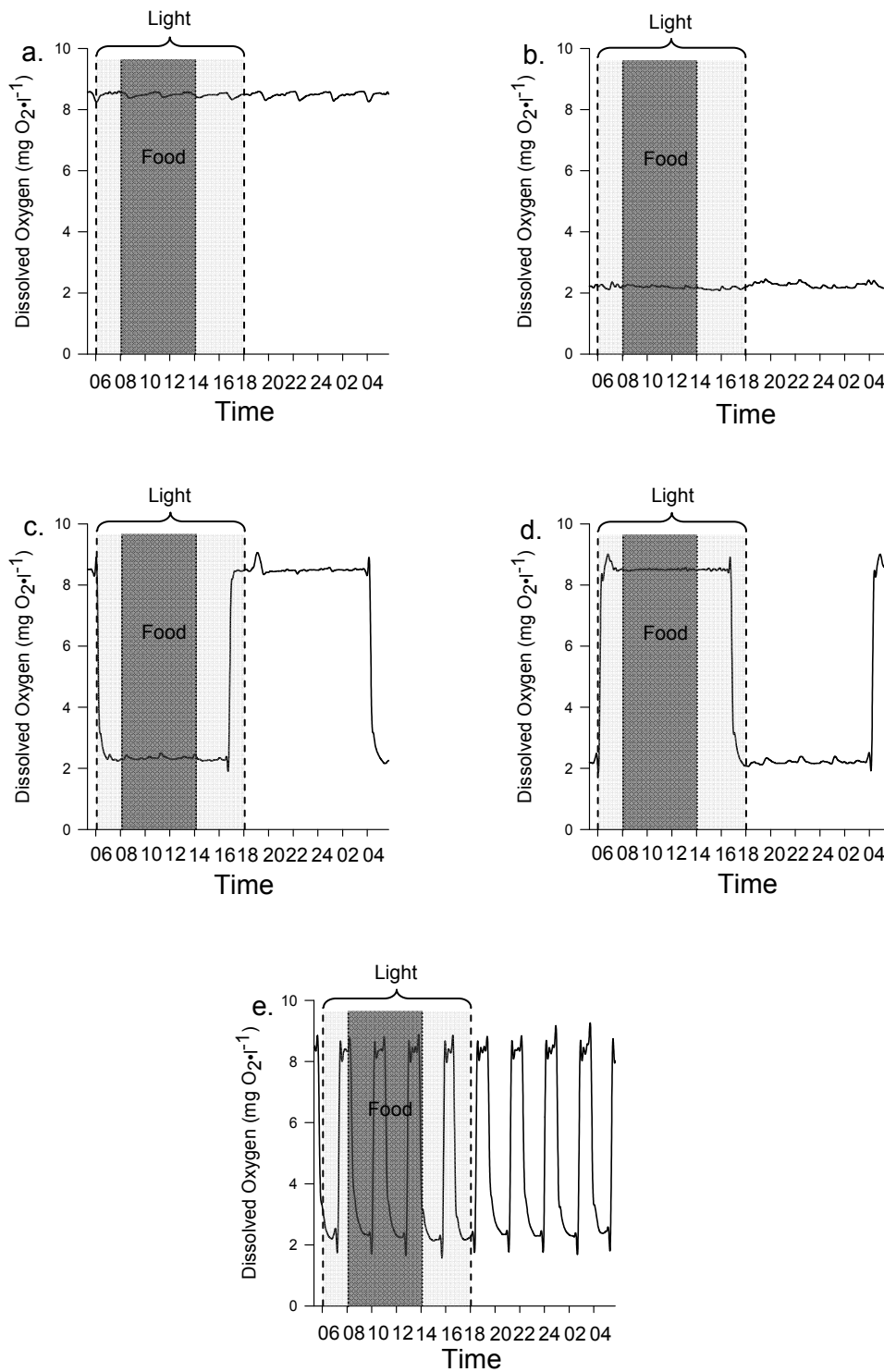
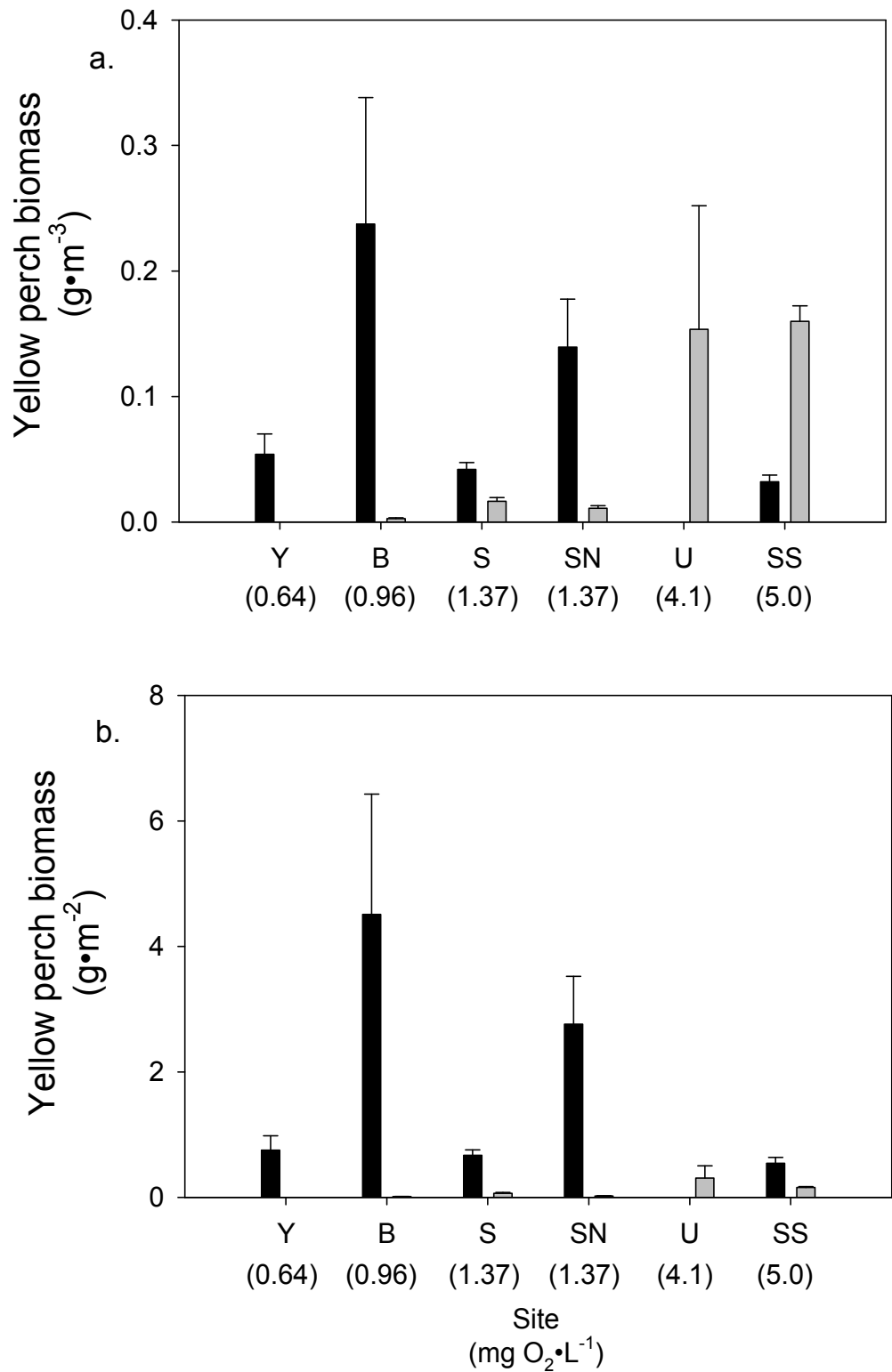


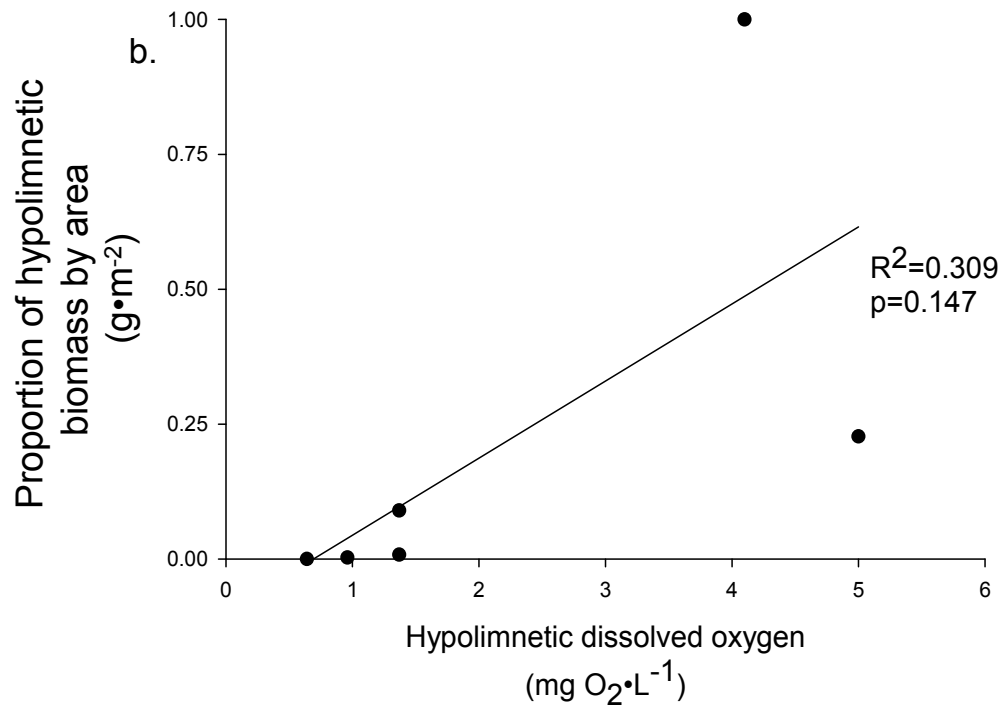
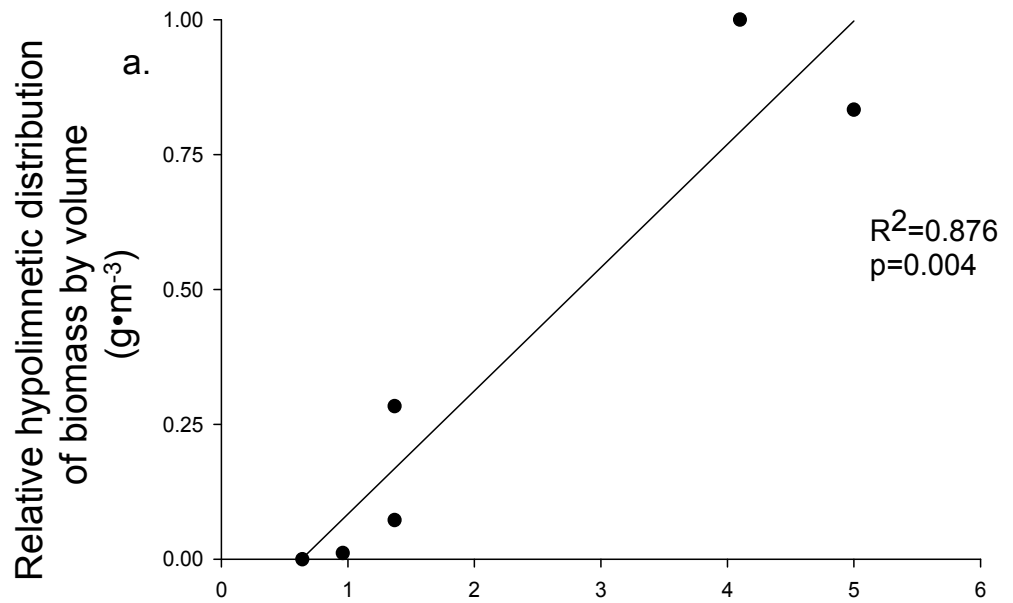
Figure 5.2 A hypothetical stratified water column and the potential movements of yellow perch as observed with our drifting hydroacoustic sampling method. All letters with *'s indicate potential start points and those with ^'s indicate potential end points of fish tracks (multiple single targets deemed to belong to one individual fish) captured within our sample beam.



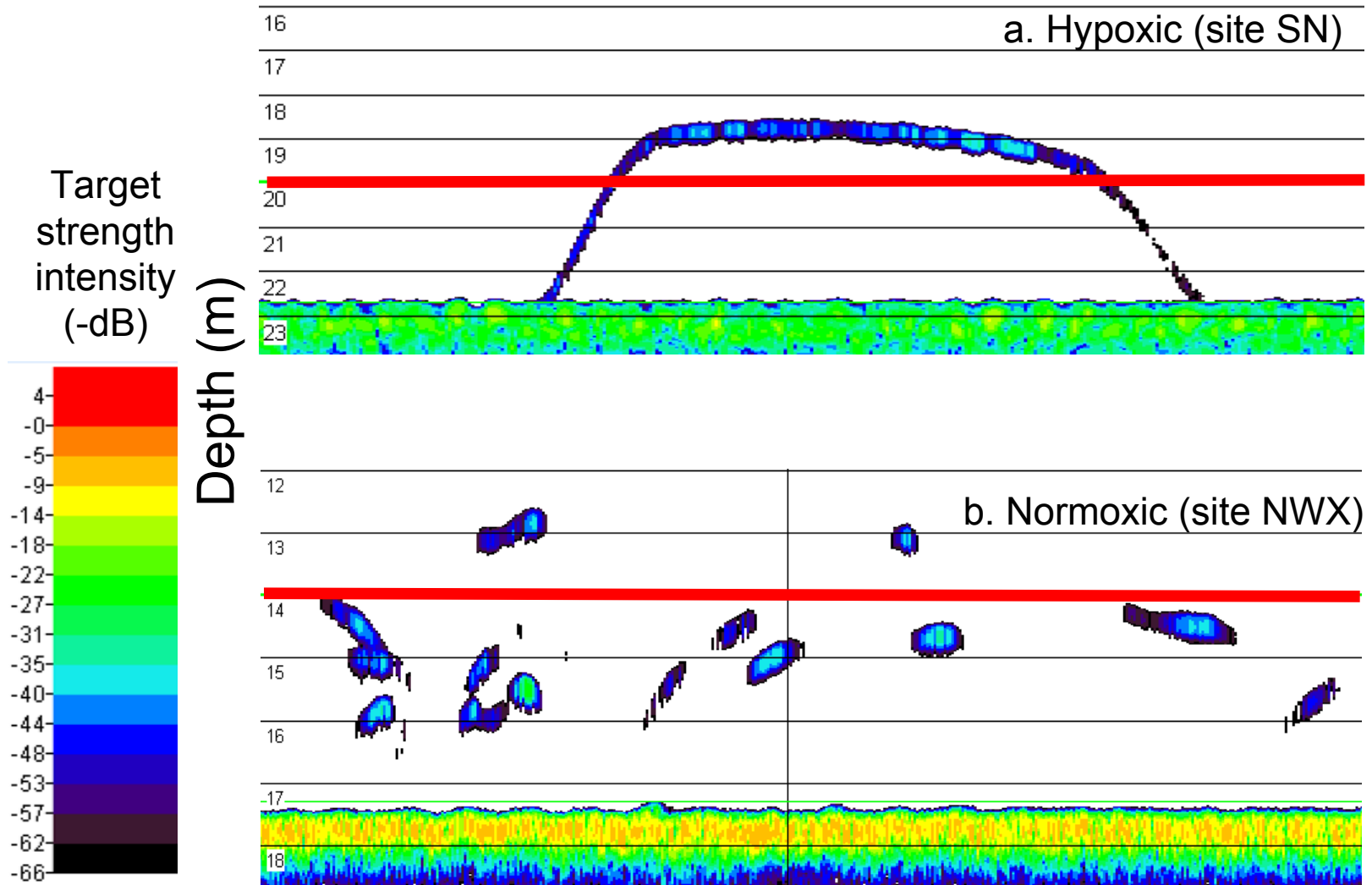
Figures 5.3a-e Example of the oxygen concentrations from our five treatment regimes throughout one 24-hr day of our experimental trial. Six hours for which food was available to yellow perch indicated by grey shading and 12 hours of light indicated by light grey shading. Our five treatments consisted of a) static high oxygen, b) static low oxygen, c) 12-hr high-day low-night oxygen, d) 12-hr low-day high-night oxygen, and e) rapidly fluctuating oxygen conditions.



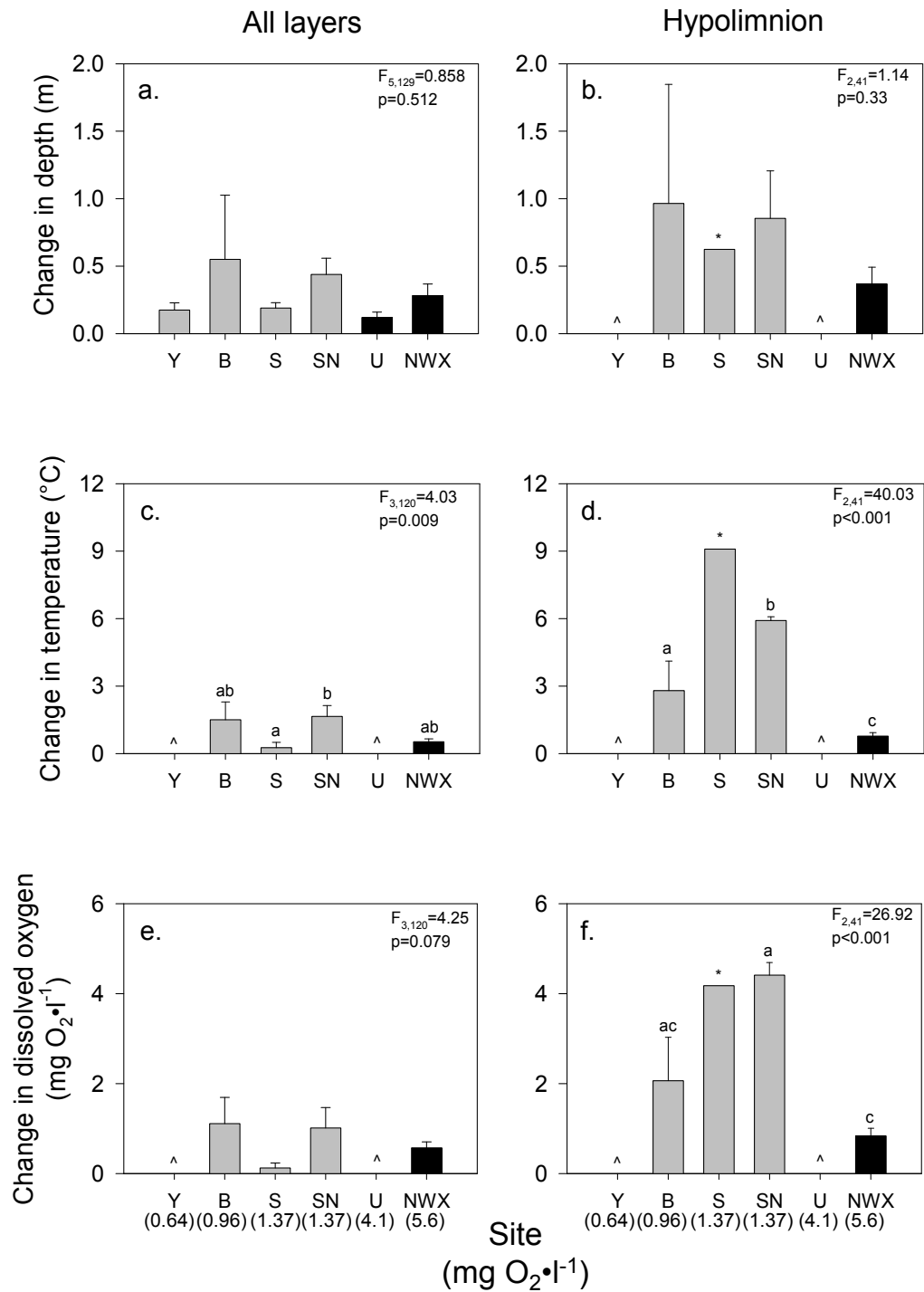
Figures 5.4a & b Vertical distribution of mean yellow perch biomass determined from transect hydroacoustic and trawl estimates collected in Lake Erie's central basin during 2007, with data presented within epilimnetic (black) and hypolimnetic (gray) vertical layers(+SE). Sites are arranged by increasing hypolimnetic dissolved oxygen concentration. Vertical distribution of yellow perch biomass are presented by volume (g·m⁻³; a) and area (g·m⁻²; b).



Figures 5.5a & b Regression results relating proportional vertical distribution of hydroacoustically estimated yellow perch biomass from both normoxic and hypoxic habitats versus dissolved oxygen concentration. This analysis was performed using volumetric biomass ($\text{g}\cdot\text{m}^{-3}$; a) and areal biomass ($\text{g}\cdot\text{m}^{-2}$; b). Data was collected in Lake Erie's central basin during 2007.



Figures 5.6a & b Sample TS echograms displaying yellow perch fish tracks from Lake Erie's central basin during 2007. Sample echogram's are presented from hypoxic site SN (a) normoxic site NWX (b). Redlines denote the vertical location of the thermocline within these water columns.



Figures 5.7a-f Summary of mean fish track statistics (change in depth, change in temperature and change in dissolved oxygen concentration) and corresponding one-way ANOVA results (+SE). Analyses were performed for tracks within all vertical layers of the water column (a, c, and e) and tracks only within the hypolimnion (b, d, and f). Sites are arranged in increasing hypolimnetic dissolved oxygen concentration. Sites Y and U were removed from the all layer analysis of changes in temperature and oxygen and all hypolimnetic layer analyses since no tracks switching layers were observed at these sites (denoted by '^'). Statistically significant differences among sites are indicated by unique combinations of letters which were determined from our post-hoc Tukey comparison ($\alpha=0.05$). We excluded site S were from our hypolimnetic analysis since only one was track observed (denoted by '*').

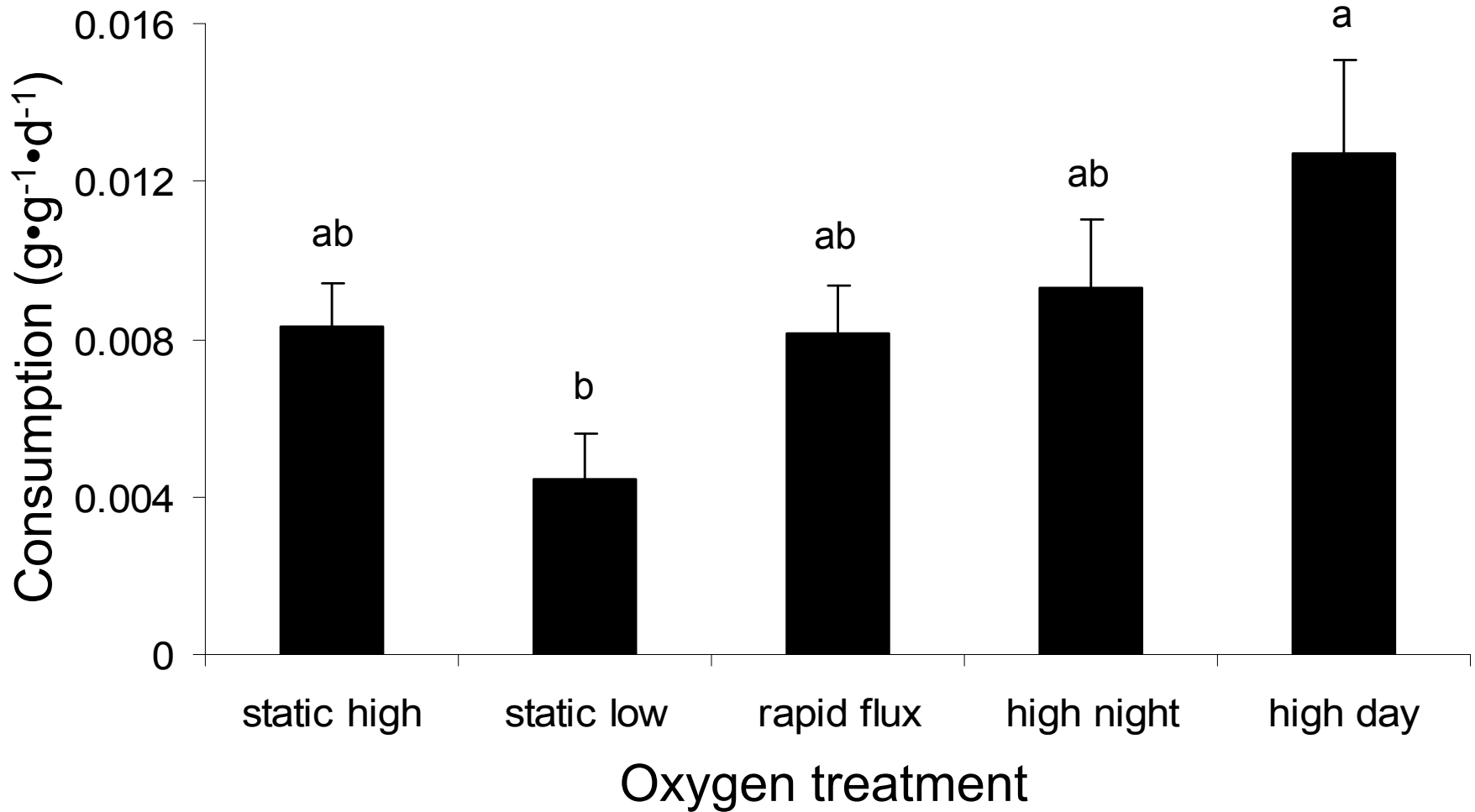


Figure 5.8 Consumption results from our laboratory experiments where yellow perch were exposed to different fluctuating oxygen regimes. Significant differences denoted by unique letters as determined by a one-way ANOVA analysis and post-hoc Tukey comparison ($\alpha=0.05$).

Literature Cited

- Aku, P. M. K., and W. M. Tonn. 1997. Changes in population structure, growth, and biomass of cisco (*Coregonus artedi*) during hypolimnetic oxygenation of a deep, eutrophic lake, Amisk Lake, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2196-2206.
- Aku, P. M. K., and W. M. Tonn. 1999. Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. *Transactions of the American Fisheries Society* 128:17-30.
- Baldwin, C. M., D. A. Beauchamp, and C. P. Gubala. 2002. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. *Transactions of the American Fisheries Society* 131:143-158.
- Bolnick, D. I., and coauthors. 2003. The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist* 161:1-28.
- Brady, D. C., T. E. Targett, and D. M. Tuzzolino. 2009. Behavioral responses of juvenile weakfish (*Cynoscion regalis*) to diel-cycling hypoxia: swimming speed, angular correlation, expected displacement, and effects of hypoxia acclimation. *Canadian Journal of Fisheries and Aquatic Sciences* 66:415-424.
- Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25:767-781.
- Breitburg, D. L., L. Pihl, and S. E. Kolesar. 2001. Effects of low dissolved oxygen on the behavior, ecology and harvest of fishes: a comparison of the Chesapeake Bay and Baltic-Kattegat systems. Pages 241-268 in N. N. Rabalais, and R. E. Turner, editors. *Coastal hypoxia: consequences for living resources and ecosystems*. American Geophysical Union, Washington DC.
- Craig, J. K., and L. B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series* 294:79-94.
- Dagorn, L., and coauthors. 2006. Deep diving behavior observed in yellowfin tuna (*Thunnus albacares*). *Aquatic Living Resources* 19:85-88.
- Delibes, M., P. Ferreras, and P. Gaona. 2001. Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters* 4:401-403.
- Diaz, R. J., and R. Rosenberg. 2008. Spreading Dead Zones and Consequences for Marine Ecosystems. *Science* 321:926-929.
- Donaldson, M. R., S. J. Cooke, D. A. Patterson, and J. S. Macdonald. 2008. Cold shock and fish. *Journal of Fish Biology* 73:1491-1530.

- Eby, L. A., and L. B. Crowder. 2002. Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Canadian Journal of Fisheries and Aquatic Sciences* 59:952-965.
- Eby, L. A., L. B. Crowder, C. M. McClellan, C. H. Peterson, and M. J. Powers. 2005. Habitat degradation from intermittent hypoxia: impacts on demersal fishes. *Marine Ecology-Progress Series* 291:249-261.
- Frid, A., J. Burns, G. G. Baker, and R. E. Thorne. 2009. Predicting synergistic effects of resources and predators on foraging decisions by juvenile Stellar sea lions. *Oecologia* 158:775-786.
- Frouzova, J., J. Kubecka, H. Balk, and J. Frouz. 2005. Target strength of some european fish species and its dependence on fish body parameters. *Fisheries Research* 75:86-96.
- Greccay, P. A., and K. L. Stierhoff. 2002. A Device for Simultaneously Controlling Multiple Treatment Levels of Dissolved Oxygen in Laboratory Experiments. *Journal of Experimental Marine Biology and Ecology* 280:53-62.
- Hartman, K. J., and B. W. Nagy. 2005. A target strength and length relationship for striped bass and white perch. *Transactions of the American Fisheries Society* 134:375-380.
- Hays, G. C., M. R. Farquhar, P. Luschi, S. L. H. Teo, and T. M. Thys. 2009. Vertical niche overlap by two ocean giants with similar diets; Ocean sunfish and leatherback turtles. *Journal of Experimental Marine Biology and Ecology* 370:134-143.
- Hayward, R. S., F. J. M. Jr., D. L. Parrish, and B. Vondracek. 1991. Low-cost field estimation of yellow perch daily ration. *Transactions of the American Fisheries Society* 120:589-604.
- Hergenrader, G. L., and A. D. Hasler. 1966. Diel activity and vertical distribution of yellow perch (*Perca flavescens*) under the ice. *Journal of the Fisheries Research Board of Canada* 23:499-509.
- Johnson, B. L., T. M. Keevin, E. A. Laux, and T. B. Miller. 2005. Seasonal fish densities in the lock chamber at lock and dam 25, upper Mississippi River. U.S. Army Corps of Engineers, ENV Report 57, St. Louis, MO.
- Kramer, D. L. 1987. Dissolved oxygen and fish behavior. *Environmental Biology of Fishes* 18:81-92.
- Kraus, R. T., and J. R. Rooker. 2007. Patterns of vertical habitat use by Atlantic blue marlin (*Makaira nigricans*) in the Gulf of Mexico. *Gulf and Caribbean Research* 19:89-97.

- Ludsin, S. A., and coauthors. 2009. Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: implications for food web interactions and fish recruitment. *Journal of Experimental Marine Biology and Ecology* 381:S121-S131.
- Mueller, T., and W. F. Fagan. 2008. Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos* 117:654-664.
- Parker-Stetter, S. L., L. G. Rudstam, P. J. Sullivan, and D. M. Warner. 2009. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Great Lakes Fishery Commission Special Publication 01.
- Pihl, L. 1994. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. *Canadian Journal of Fisheries and Aquatic Sciences* 51:321-336.
- Pollock, M. S., L. M. J. Clarke, and M. G. Dube. 2007. The effects of hypoxia on fishes: from ecological relevance to physiological effects. *Environmental Reviews* 15:1-14.
- Pothoven, S. A., H. A. Vanderploeg, S. A. Ludsin, T. O. Höök, and S. B. Brandt. 2009. Feeding ecology of emerald shiners and rainbow smelt in central Lake Erie. *Journal of Great Lakes Research* 35:190-198.
- Prince, E. D., and C. P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. *Fisheries Oceanography* 15:451-464.
- Quevedo, M., R. Svanback, and P. Eklov. 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology* 90:2263-2274.
- Rahel, F. J., and J. W. Nutzman. 1994. Foraging in a lethal environment: fish predation in hypoxic water of a stratified lake. *Ecology* 75:1246-1253.
- Railsback, S. F. 2001. Concepts from complex adaptive systems as a framework for individual-based modeling. *Ecological Modelling* 139:47-62.
- Roberts, J. J., and coauthors. 2009. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. *Journal of Experimental Marine Biology and Ecology* 381:S132-S142.
- Rose, K. A. 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecological Applications* 10:367-385.
- Rose, K. A., and coauthors. 2009. Does hypoxia have population-level effects on coastal fish? Musing from the virtual world. *Journal of Experimental Marine Biology and Ecology*.

- Rudstam, L. G., and coauthors. 2003. Application of *in situ* target-strength estimations in lakes: example from rainbow-smelt surveys in Lake Erie and Champlain. ICES Journal of Marine Science 60:500-507.
- Ryan, P. A., and coauthors. 2003. Fish-community goals and objectives for Lake Erie. Great Lakes Fishery Commission Special Publication 03-02:56.
- Schaefer, K. M., and D. W. Fuller. 2007. Vertical movement patterns of skipjack tuna (*Katsuwonus pelamis*) in the eastern equatorial Pacific Ocean, as revealed with archival tags. Fishery Bulletin 105:379-389.
- Schaefer, K. M., D. W. Fuller, and B. A. Block. 2007. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. Marine Biology 152:503-525.
- Stanley, D. R., and C. A. Wilson. 2004. Effect of hypoxia on the distribution of fishes associated with a petroleum platform off coastal Louisiana. North American Journal of Fisheries Management 24:662-671.
- Stierhoff, K. L., T. E. Targett, and P. A. Greco. 2003. Hypoxia tolerance of the mummichog: the role of access to the water surface. Journal of Fish Biology 63:580-592.
- Stierhoff, K. L., T. E. Targett, and K. Miller. 2006. Ecophysiological responses of juvenile summer and winter flounder to hypoxia: experimental and modeling analyses of effects on estuarine nursery quality. Marine Ecology Progress Series 325:255-266.
- Suthers, I. M., and J. H. Gee. 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. Canadian Journal of Fisheries and Aquatic Sciences 43:1562-1570.
- Taylor, J. C., and P. S. Rand. 2003. Spatial overlap and distribution of anchovies (*Anchoa* spp.) and copepods in a shallow stratified estuary. Aquatic Living Resources 16:191-196.
- Taylor, J. C., P. S. Rand, and J. Jenkins. 2007. Swimming behavior of juvenile anchovies (*Anchoa* spp.) in an episodically hypoxic estuary: implications for individual energetics and trophic dynamics. Marine Biology 152:939-957.
- Turner, R. E. 2001. Some effects of eutrophication on pelagic and demersal marine food webs. Pages 371-398 in N. N. Rabalais, and R. E. Turner, editors. Coastal hypoxia: consequences for living resources and ecosystems. American Geophysical Union, Washington DC.
- Vanderploeg, H. A., and coauthors. 2009a. Hypoxic zones as habitat for zooplankton in Lake Erie: refuges from predation or exclusion zones? Journal of Experimental Marine Biology and Ecology 381:S108-S120.

- Vanderploeg, H. A., and coauthors. 2009b. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *Journal of Experimental Marine Biology and Ecology* 381:S92-S107.
- Zhang, H., and coauthors. 2009. Hypoxia-driven changes in the behavior and spatial distribution of pelagic fish and mesozooplankton in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology* 381:s80-s91.

Chapter 6

Conclusion

Summary

Understanding the ecological consequences of large-scale limnological phenomena such as seasonal hypolimnetic Hypoxia ($< 2 \text{ mg O}_2 \cdot \text{l}^{-1}$) are important to assess the influence hypoxia has on ecosystem functioning. Lake Erie's central basin (LECB) is seasonally affected by hypolimnetic hypoxia, but the influence of hypoxia on LECB biota is unknown. Fishery production is an ecologically and economically important ecosystem attribute within LECB. Previous studies of the Lake Erie fish community concluded that fish species richness and composition are influenced by nutrient enrichment, a driver of hypoxic conditions in LECB (Ludsin et al. 2001). Yellow perch (*Perca flavescens*) support both commercial and recreational fisheries, making them an important component of the LECB fish assemblage (Ryan et al. 2003). Therefore, exploring the ecological consequences of hypoxia for yellow perch in LECB is of interest to managers and fishery ecologists. To this end my dissertation research, using both laboratory and field studies, examined the hypothesis that hypoxia negatively affects yellow perch within LECB. My laboratory results suggest hypoxia has the potential to reduce yellow perch growth (*Perca flavescens*; Chapter 4). However, it appears by avoiding low oxygen conditions and modifying their foraging behavior yellow perch can mitigate these potential negative effects in LECB (Chapters 2, 3, and 5)

Temporal patterns suggest that yellow perch alter their distributions and diet during hypoxic conditions. Specifically, I observed reduced bottom trawl catches and an accompanied shift from benthic to pelagic foraging in hypoxic areas (Chapter 2). In addition, I found a decrease in total food within yellow perch stomachs, but surprisingly, no change in the condition of these fish during the hypoxic period (Chapter 2). Comparisons of spatial patterns in the response of yellow perch to hypoxia during 2007 also revealed clear shifts in distributions (Chapter 3). For example, yellow perch bottom trawl catches increased linearly with hypolimnetic oxygen conditions (Chapter 3). However, spatial patterns of yellow perch diets were inconsistent. While some yellow perch evidently targeted pelagic zooplankton at hypoxic sites, others continued to forage on benthic prey items despite the presence of hypoxic conditions (Chapter 3). Investigation of these diet patterns suggests intrapopulation variation within and across sites. In general, at normoxic sites, individual yellow perch appear to specialize on different subsets of diet items, whereas at hypoxic sites individuals exhibit similar site-specific proportional diet patterns (Chapter 3).

Results from laboratory experiments demonstrate that yellow perch consumption and growth (somatic growth and RNA:DNA ratios) are influenced by both temperature and oxygen concentrations, suggesting that hypoxia can negatively affect yellow perch (Chapter 4). However, field results show no reduction in short-term growth (RNA:DNA ratios) of yellow perch at hypoxic sites, suggesting that these fish are somehow able to mitigate the potential negative effects of hypoxia (Chapter 4).

I used drifting acoustics to demonstrate that yellow perch perform short-term forays into hypoxic hypolimnetic habitats, presumably to forage upon energy rich benthic prey items (Chapter 5). Moreover, by exposing yellow perch to fluctuating oxygen conditions in the laboratory, I found that such conditions do not reduce yellow perch consumption, indicating hypoxic foraging forays are a potential behavioral modification to mitigate the negative consequences of hypoxia (Chapter 5). It is unclear how accompanying drastic changes in temperature influence yellow perch consumption as I performed these experiments at a constant temperature.

Implications

Overall, my dissertation research addressed how hypoxia, a phenomenon affecting freshwater and marine environments throughout the world, influences a fish population of economic and ecological importance. My research suggests that hypoxia affects fish through various direct and indirect pathways, which are likely related to underlying patterns of growth and consumption.

Specifically, it is evident that yellow perch avoid hypoxic conditions by migrating either vertically (higher in the water column to warmer, more well oxygenated areas) or horizontally (to shallower, well oxygenated nearshore areas) (Chapters 2, 3 and 5). These alterations in the distribution of yellow perch appear to mitigate individual growth consequences (Chapter 4) but could have other implications. For example, these altered distribution patterns could change the food-web structure and dynamics of discrete areas within LECB by concentrating yellow perch into normoxic habitats. By changing the distribution of yellow perch, hypoxia could also influence the interpretation of

monitoring efforts of US and Canadian agencies aimed at managing stocks of yellow perch within Lake Erie.

Management agencies from the US and Canada annually sample Lake Erie fishes during summer (August) and fall (October) (Tyson et al. 2006). Data from these binational sampling efforts are used to create population estimates, which are crucial to determining annual fishery catch quotas for Lake Erie (Tyson et al. 2006). To assess specific spatial regions of Lake Erie, the Great Lakes Fishery Commission Lake Erie Committee (GLFC-LEC) has established four management units (MU) used to manage and summarize spatially explicit groups of Lake Erie fishes (Ryan et al. 2003). Tyson et al. (2006) examined these sampling methods in an effort to standardize techniques across agencies and create correction factors for any biases. My results suggest that hypoxia may influence agency catches during these summer and fall sampling periods by concentrating yellow perch in nearshore normoxic areas during hypoxic conditions in late summer (August-September). Specifically, hypoxia-induced yellow perch distribution patterns could inflate nearshore population estimates and result in cross MU movement. Given the majority of harvest and monitoring efforts for yellow perch occur in the nearshore areas of Lake Erie, hypoxia could influence data crucial to management decisions. Given the possibility for these hypoxia-induced movements of yellow perch to have implications for Lake Erie monitoring and management, there is a need to further explore these movement patterns and potentially incorporate them into Lake Erie monitoring efforts and management decisions.

These results should be widely applicable, to both freshwater and marine systems, to individuals ranging from managers charged with ensuring sustainable fisheries in Lake

Erie to scientists investigating basic ecological questions (e.g., identifying abiotic drivers of biotic processes and patterns). Results from my research will ultimately help to advance efforts aimed at understanding and protecting ecologically and economically important aquatic resources such as yellow perch.

Literature Cited

- Ludsin, S. A., M. W. Kershner, K. A. Blocksom, R. L. Knight, and R. A. Stein. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecological Applications* 11:731-746.
- Ryan, P. A., and coauthors. 2003. Fish-community goals and objectives for Lake Erie. Great Lakes Fishery Commission Special Publication 03-02:56.
- Tyson, J. T., T. B. Johnson, C. T. Knight, and M. T. Bur. 2006. Intercalibration of research survey vessels on Lake Erie. *North American Journal of Fisheries Management* 26:559-570.