

THE ROLE OF ENVIRONMENTAL CHARACTERISTICS ON FISH
COMMUNITY STRUCTURE AND FOOD WEB INTERACTIONS IN LAKE
ONTARIO EMBAYMENTS

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Cornell University 2008

Aquatic ecosystems are influenced by physical, chemical, and biological processes operating at multiple spatial scales, from landscape through microhabitats. Processes operating at the landscape level, such as watershed land use or precipitation, are external factors that influence an aquatic ecosystem. Internal factors are processes operating on an aquatic ecosystem from within the system, such as habitat. I explored how external and internal factors influenced fish community structure and function in Lake Ontario embayments. With my research, I aimed to address the following questions: (1) which internal and external factors influence how much and where biomass is distributed in the fish community (i.e., structure); (2) which factors influence energy sources utilized by the fish communities (i.e., function); (3) are structural and functional responses related to each other? Structural characteristics responded to both external and internal factors. Biomass increased with phosphorus loading (external factor) and area (internal factor), whereas abundance increased and size structure decreased with percent vegetation (internal factor). Similarly, both external and internal factors influenced energy sources incorporated by the fish communities, including connectivity to adjacent habitats (external factor), depth profile (internal factor), and vegetation (internal factor). Fish communities in embayments with stronger connections to their watersheds (versus Lake Ontario)

incorporated greater energy and nutrients from the watershed, and vice versa. Fish communities in deep embayments relied primarily on energy sources from pelagic habitat; fish communities in shallow embayments utilized energy sources from both pelagic and littoral habitats. Finally, structural and functional responses appeared to be related through their effects on trophic interactions, as indicated by a study of yellow perch (*Perca flavescens*) populations. A comparison of observed yellow perch growth versus energy budget model predictions suggested that embayment morphometry could influence the relative importance of trophic interactions. Yellow perch populations in shallow, littoral embayments, where vegetation provides protection from predation, were sensitive to prey availability and composition. In contrast, yellow perch growth and size structure in deep, pelagic embayments might have been influenced to a greater extent by predation. Overall, internal factors influenced fish communities to a greater extent than external factors, primarily by influencing trophic interactions.

BIOGRAPHICAL SKETCH

Kristin (Kristi) Arend was born in Columbus, OH, on March 30, 1974. She received her B.A. in Biology from Oberlin College in 1996. From March 1997 – August 1998, Kristi was a Research Aid in the Department of Natural Resources at Cornell University. Kristi received her M.S. in Evolution, Ecology and Organismal Biology, with a concentration in Aquatic Ecology, from The Ohio State University in 2002. While pursuing her doctoral degree, Kristi received a first-year fellowship from the university and held research and teaching assistantships. During June – July 2007, Kristi taught Ichthyology (EEOB 621) at The Ohio State University's F. T. Stone Laboratory.

For my grandmother, Frances Clapp Arend (1902-2006), whose love of learning and
life has inspired two generations.

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LIST OF ABBREVIATIONS

ESRI	Environmental Systems Research Institute
NOAA	National Oceanic and Atmospheric Administration
TIN	Triangulated irregular network
EZD	Euphotic zone depth
GIS	Geographic information system
GPS	Global positioning system
DC	Direct current
OLS	Ordinary Least Squares
TL	Total length
°C	Celsius
CPUE	Catch per unit effort
BPUE	Biomass per unit effort
NSS	Normalized size spectra
C, ¹³ C	Carbon, carbon-13
N, ¹⁵ N	Nitrogen, nitrogen-15
ANOVA	Analysis of variance
IQR	Interquartile range
DIC	Dissolved organic carbon
EtOH	Ethanol
HCl	Hydrochloric acid
COIL	Cornell University Stable Isotope Laboratory
SE	standard error
NLS	Nonlinear least squares
YOY	Young-of-year

LIST OF SYMBOLS

z_{sd}	Secchi disk depth
χ^2	Chi-square
p	p-value
$\%$	Percent
δ	Delta; stable isotope ratio
λ	Lambda; trophic position of food web base
α	Alpha; proportion of seston C assimilated
‰	Parts per mille
C_{24}	Daily ration
R	Evacuation rate
S_{mean}	Mean biomass of stomach contents
a, b	Regression coefficients for estimating ration
T	Temperature
W	Weight; waste
B_{cons}	Assimilated biomass consumed
E_{cons}	Assimilated energy consumed
PP_i	Mean proportion of prey i consumed
ED_i	Energy density of prey i
l_n	Otolith-based length at age
d_n	Distance from otolith focus to annulus n
d_T	Distance from otolith focus to edge of otolith
l_T	Fish length at capture
$0+$	$0 < \text{age} < 1$ year
C	Consumption

<i>G</i>	Gonadal growth
<i>M</i>	Metabolism

PREFACE

Aquatic ecosystems are influenced by physical, chemical, and biological processes operating at multiple spatial scales, from the landscape through microhabitats. Processes operating at the landscape level, such as watershed land use or precipitation, can be thought of as external factors that influence an aquatic ecosystem. Internal factors are attributes operating on an aquatic ecosystem from within the ecosystem, such as habitat availability and ecosystem size. Fish communities are sensitive to both external and internal factors. For example, nutrient loading (external) and habitat type and availability (internal) influence fish community structure, such as species composition and size structure (Brazner and Beals 1997, Ludsine et al. 2001). Nutrient loading and habitat also influence fish community function, for example energy flow and maximum food chain length (Post et al. 2000, Sierszen et al. 2006). A number of studies have looked at how particular environmental variables influence either fish community structure or function (e.g., Randall et al. 1996, Vander Zanden et al. 1999b, Post et al. 2000). A smaller group of studies has addressed multiple drivers or both structure and function simultaneously (e.g., Carpenter et al. 1985, Stein et al. 1995, Carpenter et al. 2001). These more comprehensive studies, while logistically and conceptually challenging, are important for advancing our understanding of the role of fish communities in aquatic ecosystems. For example, understanding the relative strength of top-down versus bottom-up control in freshwater ecosystems, the pathways by which energy flows through a food web, and nutrient cycling and flow through aquatic ecosystems will provide important basic and applied insights into aquatic communities.

Structural descriptors of fish communities include species composition, species diversity, and population and community abundance, biomass, and size structure.

Previous research has shown that abundance and biomass of individual fish species and fish communities as a whole increase with nutrient loading (an external factor), particularly phosphorus in freshwater systems; in contrast, species diversity decreases or intolerant species are replaced with tolerant species with greater nutrient loading (Bachmann et al. 1996, Ludsin et al. 2001). System morphometry (an internal factor) also influences fish abundance and biomass by determining both habitat and prey availability. A lake's area and depth profile establish the relative amount of potentially inhabitable shallow and deep habitat. A more varied profile offers greater habitat diversity that different species can occupy (Eadie and Keast 1984, Benson and Magnuson 1992). Finally, vegetated habitat (an internal factor) increases habitat heterogeneity by offering different types of structure that support prey communities and offer small-bodied fish refuge from predation (Zambrano et al. 2006).

Fish community function includes trophic interactions (competitive and predator-prey), energy flow, and nutrient cycling. Energy flow and trophic interactions are influenced to varying degrees by the nutrients and energy (including prey) that move into an aquatic ecosystem and between habitats within that ecosystem. As such, both watershed inputs (external factors) and morphometric characteristics (internal factors), such as size and depth profile, are important determinants of the sources from which a fish community obtains energy (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). For example, nutrient inputs and long water residence time may increase fish community reliance on pelagic energy (Vadeboncoeur et al. 2002, Sierszen et al. 2006). Fish in larger, deeper lakes are likely to rely more heavily on pelagic energy than littoral energy (Vadeboncoeur et al. 2002). Watershed and system controls on energy flow are tightly linked with trophic interactions and, subsequently, the strength of top-down versus bottom-up control within the entire food web. However, this

relationship can be complex and difficult to predict. For example, the availability of resource subsidies can either dampen or enhance top-down effects within a food web. A food web's response to subsidies depends on which trophic level utilizes the subsidy, the amount of subsidization, or the degree to which the consumer preferentially consumes the local resource versus the resource subsidy (Huxel et al. 2002, Vander Zanden and Vadeboncoeur 2002).

Given that both fish community structure and function can respond to the same suite of external and internal environmental factors, I was interested in the following questions: (1) which internal and external factors influence how much and where biomass is distributed in the fish community (i.e., structure); (2) which factors influence energy sources utilized by the fish communities (i.e., function); (3) are structural and functional responses related to each other? The three chapters of my dissertation address these questions by evaluating relationships between Lake Ontario embayment physicochemical factors and several aspects of fish community structure and function (Figure 0.1). Lake Ontario embayments provide an ideal setting for looking at external and internal environmental effects on fish communities, because they drain watersheds that vary in agricultural land use and thus nutrient loading, they range in hydrologic connections to their watersheds and Lake Ontario, and they differ in several morphological characteristics. Despite these physical and chemical differences, they support fish communities that are quite similar in species composition but different in community structure and function. As such, these embayments provide the opportunity to assess how similar groups of fish species respond to environmental conditions that differ at multiple spatial scales.

In Chapter 1, I identified external and internal physicochemical and hydrologic factors

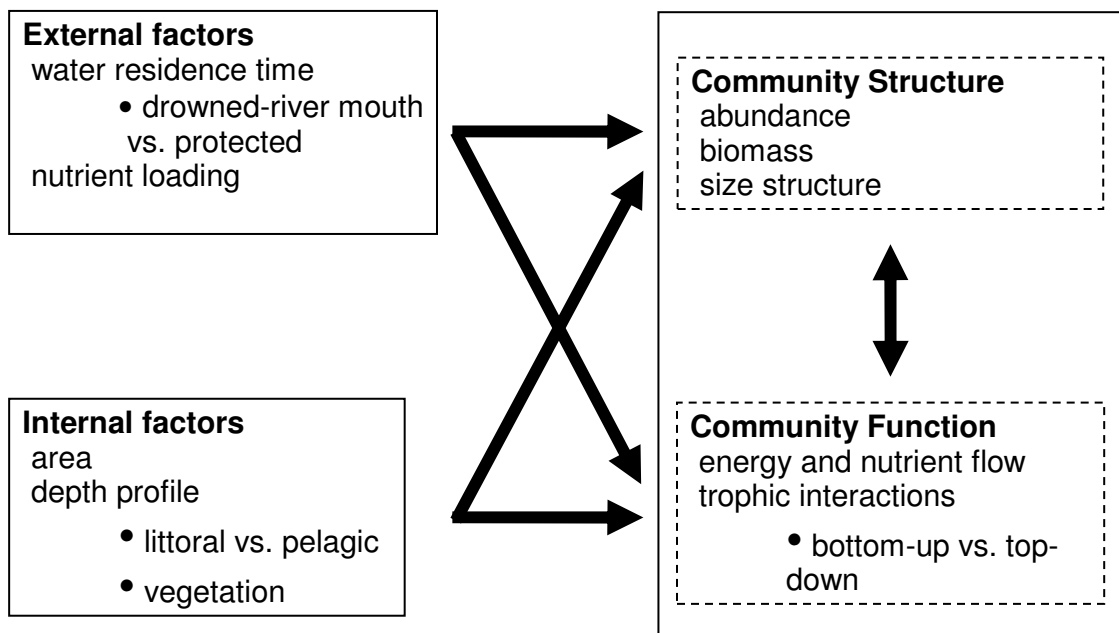


Figure 0.1. Conceptual diagram of possible interactions among external and internal physicochemical factors and fish community structure and function.

that are related to embayment fish community relative abundance, biomass, size structure, and species diversity across eight embayments. I tested hypotheses regarding effects of several factors on fish community structure that are grounded in previous findings reported in the literature. The external factors I focused on included water residence time and nutrient loading. The internal factors included embayment area, the proportion of littoral versus pelagic habitat, and vegetated habitat availability. To better understand the relative importance of external versus internal factors to fish community structure, I grouped the embayments into three hydrogeomorphic types – drowned-river mouth, pelagic-protected, and littoral-protected. Drowned-river mouth embayments receive high watershed inputs and have short water residence times. Protected embayments have longer water residence times and vary in their hydrologic connections to their watershed and Lake Ontario. Pelagic-protected embayments have depths that exceed euphotic zone depth estimates for at least 10% of their area. Littoral-protected embayment depths do not exceed euphotic zone depth estimates.

For the second and third chapters, I focused on four of the eight embayments. I selected these embayments to represent ecosystems that differ in key external and internal features. Regarding external characteristics, the four embayments received watershed and Lake Ontario inputs to varying degrees. With respect to internal features, two embayments were dominated by pelagic habitat and two by littoral habitat. In Chapter 2, I explored energy and nutrient subsidies to and within embayment food webs. To infer the degree to which the base of the food web incorporates external subsidies from the watershed and Lake Ontario, I compared embayment pelagic primary producer (henceforth, seston) ^{13}C and ^{15}N stable isotope ratios with Lake Ontario seston stable isotope ratios. Stable isotope ratios of the dominant species in each fish community indicated the extent to which external

subsidies are transferred up the food web from primary producers. I also used these data to quantify the degree to which the fish communities incorporated internal subsidies from littoral and pelagic habitat. Hypotheses were based on previous findings reported in the literature regarding effects of water residence time, system productivity, and morphometry on energy flow through aquatic food webs.

Chapter 3 attempts to bridge Chapters 1 and 2 by addressing how structural and functional responses may interactively shape embayment fish communities. To do this, I focused on the population dynamics of yellow perch (*Perca flavescens*) in two pelagic-dominated and two littoral-dominated embayments. I tested the hypothesis that differences in prey availability (i.e., bottom up effects) between the two embayment types underlie relationships between yellow perch energy sources and population size structure. To test this hypothesis, I developed an energy budget model for yellow perch that estimated annual growth over their lifetime based on field estimates of prey composition and daily ration. I then compared model predictions of size at age and annual growth rate with corresponding otolith-based estimates of in situ growth. I assumed that agreement between model predictions and otolith-based estimates would imply that prey availability and thus bottom-up effects influenced population structure. Disagreement between predictions and estimates would suggest other factors, such as predation (i.e., top-down control), were important.

The results of all three chapters are synthesized in Chapter 4, in which I identified factors that control both structural and functional aspects of the fish community and assessed their importance for bottom-up versus top-down control among systems.

CHAPTER 1: Lake Ontario embayment fish community structure: the role of embayment physical and chemical features

Abstract

We explored how embayment watershed inputs, morphometry, and hydrology influence fish community structure among eight embayments located along the southeastern shoreline of Lake Ontario. Embayments differed in surface area and depth, varied in their connections to Lake Ontario and their watersheds, and drained watersheds representing a gradient of agricultural to forested land use. Most embayment fish communities were dominated numerically by yellow perch (*Perca flavescens*) and centrarchids. Biomass was dominated by piscivorous fishes including brown bullhead (*Ameiurus nebulosus*), bowfin (*Amia calva*), and northern pike (*Esox lucius*). We related various physicochemical factors, including total phosphorus load, embayment area, and vegetation, to fish community relative abundance, biomass, and size structure. Abundance differed among embayments and was positively related to percent vegetation within embayments. Fish relative biomass differed among embayments and was positively related to total phosphorus loading and embayment area. The relative influence of these two factors on biomass may differ among embayment hydrogeomorphic types. Fish community size structure, based on size spectra analysis, differed among embayments, with the frequency of smaller-bodied fishes positively related to percent vegetation. The importance of total phosphorus loading and vegetation in structuring fish communities has implications for anthropogenic impacts to embayment fish communities through activities such as farming and residential development, reduction of cultural eutrophication, and shoreline development and maintenance.

Introduction

Physicochemical features at multiple spatial scales (e.g., watershed, embayment, and habitat) can be important for fish community structure (Randall et al. 1996, Breneman et al. 2000, Höök et al. 2001). Variability in nutrient inputs, hydrology, and morphometry among and within aquatic ecosystems can shape fish communities (Rosenzweig and Abramsky 1993, Bachmann et al. 1996, Randall et al. 1996, Holmgren and Appelberg 2000). In turn, fish community structure influences ecosystem function, such as energy transfer and nutrient cycling (Polis et al. 1997, Vanni 2002, Vanni et al. 2005) via trophic interactions and, in some cases, habitat modification (Carpenter et al. 2001, Loughheed et al. 2004). Consequently, fish communities are an important component of aquatic ecosystems.

We were interested in how physicochemical features shaped fish communities in Lake Ontario embayments. Great Lakes embayments are relatively shallow, inshore habitats located between the shorelines of the lakes and their watersheds. Thus, embayments vary considerably in nutrient loading, hydrology, and morphometry. Additionally, embayments serve as conduits of nutrients and other materials from their watersheds (Jude and Pappas 1992, Uzarski et al. 2005), support high fish species diversity (Jude and Pappas 1992), provide spawning and nursery habitats for both nearshore and offshore Great Lakes fishes (Brazner and Beals 1997, Höök et al. 2001, Klumb et al. 2003), and are concentrated areas of human activities (Mackey and Goforth 2005). These characteristics make embayments ideal systems with which to address physicochemical effects on fish community structure in the context of ecosystem function.

Great Lakes embayments range in hydrogeomorphic type, including flooded river mouths, coastal wetlands, and large, deep enclosed bays (Keough et al. 1999, Hall et al. 2003, Klumb et al. 2003). Embayments are connected to their watersheds by tributary inflow, surface runoff, or groundwater flow (Trebitz et al. 2002). While some embayments lack direct, surface water connections to the main lake, most embayments have either man-made or natural connections that can be permanent, seasonal, or ephemeral (Trebitz et al. 2002). This combination of morphometric and hydrologic variability results in physicochemical habitat conditions that differ both among and within embayments (Mackey and Goforth 2005, Trebitz et al. 2005). For example, morphometry and water inflow from tributaries and the lake (via seiches) interact to influence water chemistry, submerged aquatic vegetation populations, and dissolved oxygen and temperature profiles (Trebitz et al. 2005).

For purposes of this research, we classified embayments into general hydrogeomorphic types, based on Keough et al. (1999): (1) drowned-river mouth embayments; (2) pelagic-protected embayments; and (3) littoral-protected embayments. Drowned-river mouth embayments receive high watershed inputs, have short water residence times, and have a surface water connection with Lake Ontario (Keough et al. 1999). Protected embayments have longer water residence times than drowned-river mouths, are separated from Lake Ontario by a sand barrier, and vary in their hydrologic connections to their watershed and Lake Ontario (Keough et al. 1999). Pelagic-protected embayments are defined as having depths that exceed euphotic zone depth estimates for at least 10% of their area. Littoral-protected embayment depths do not exceed euphotic zone depth estimates.

We posed the question: how do watershed inputs, hydrology, and embayment morphometry affect fish community structure in eight embayments located along the southeastern coast of Lake Ontario? We selected embayments to represent the three hydrogeomorphic types and to drain watersheds ranging from agricultural to forested land use. We also chose embayments with fish communities composed of similar species, allowing us to evaluate responses to environmental differences without confounding effects of radically different fish community compositions. We expected that physicochemical factors across spatial scales would influence multiple metrics of fish community structure, including diversity, relative abundance, biomass, and size structure.

At the watershed level, watershed size, discharge and land use affect productivity, which in turn, can influence fish community structure and dynamics. We hypothesized that high nutrient inputs to embayments, from either high watershed flows (i.e., short water residence time) or high nutrient concentrations due to land use, would positively affect fish abundance and biomass (Oglesby 1977, Ney 1996, Randall et al. 1996) and negatively affect species diversity (Rosenzweig and Abramsky 1993, Ludsine et al. 2001) (Table 1.1). At the system (i.e., embayment) level, greater surface area can increase habitat and resource heterogeneity, which positively impact fish abundance, biomass, and diversity (Eadie and Keast 1984, Holmgren and Appelberg 2000). For example, area can increase habitat heterogeneity via depth profiles that create multiple habitat types, and thus positively influence fish species diversity, abundance and biomass (Benson and Magnuson 1992). Within

Table 1.1. Hypothesized effects of different physicochemical factors on fish community structural characteristics, including species diversity, relative abundance, relative biomass, and size structure. Hypothesized effects are positive (+) or negative (–) and indicate the direction in which the structural characteristic responds to an increase in each physicochemical factor. A positive effect on size structure indicates a greater proportion of large-bodied fishes; a negative effect on size structure indicates a greater proportion of small-bodied fishes.

Structural characteristic	Physicochemical Factor		
	Nutrient inputs	Embayment area	Vegetation
Species diversity	–	+	+
Abundance	+	+	+
Biomass	+	+	+
Size-structure	n/a	+	–

systems, availability of vegetated, littoral habitat has similar effects on fish communities (Brazner and Beals 1997, Pierce and Tomcko 2005, Zambrano et al. 2006). As such, we predicted that embayments with higher habitat heterogeneity (e.g., large surface area and/or abundant, vegetated littoral habitat) would support more diverse and abundant fish communities than small or more homogeneous embayments (Table 1.1). Morphometry also impacts fish community size structure (Randall et al. 1996, Holmgren and Appelberg 2000). We hypothesized that a higher proportion of small-bodied than large-bodied fishes would occur in embayments dominated by vegetated habitat (Randall et al. 1996) (Table 1.1). In contrast, large embayments having deep, open habitat would provide support for large-bodied fishes (Holmgren and Appelberg 2000) (Table 1.1), resulting in a low proportion of small-bodied fishes due to predation (Carpenter et al. 2001, Olive et al. 2005).

Methods

Study sites

Study embayments were located in two clusters along the southeastern shoreline of Lake Ontario (Figure 1.1) and varied in several watershed and embayment characteristics (Table 1.2). Hydrogeomorphic classifications were: (1) drowned-river mouth: Sterling, Floodwood; (2) pelagic-protected: Blind Sodus, Little Sodus, South Sandy; and (3) littoral-protected: Juniper, North Sandy, and South Colwell.

Embayment-level characteristics

Morphometry. Morphometric measurements included watershed area, embayment area, maximum depth, and percent littoral habitat. Watershed boundaries for each of the embayment catchment areas were delineated using ESRI ArcHydro tools

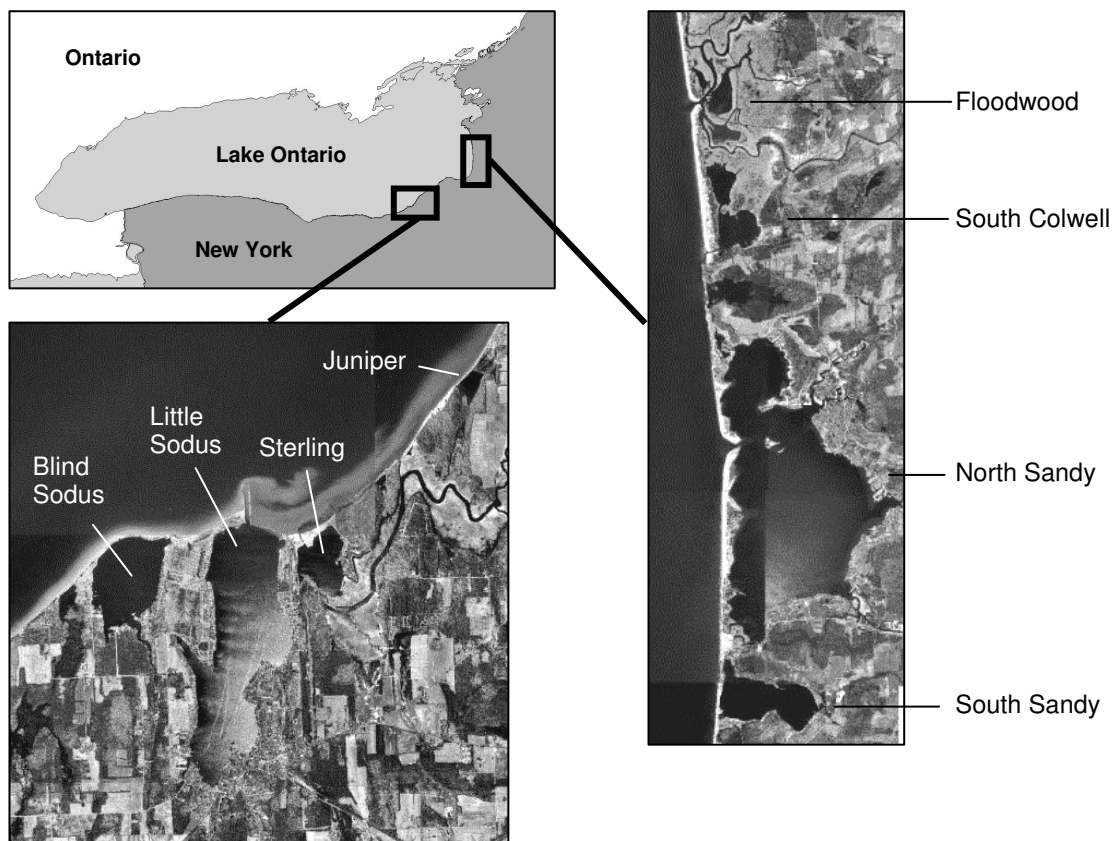


Figure 1.1. Location map and air photographs of the eight Lake Ontario study embayments. Air photographs were provided courtesy of the International Joint Commission.

Table 1.2. Morphometric, hydrologic, and land use characteristics of eight Lake Ontario embayments. Total phosphorus load and water residence time data were provided by X. Chen (unpublished data). Inter = intermittent; Perm = permanent; Ssnl = seasonal; Trib = tributary; Wet = wetland.

	Blind Sodus	Little Sodus	Sterling	Juniper
Watershed area (km ²)	35.2	8.56	210	0.60
% agricultural land use	36.7	17.4	41.1	40.3
Total phosphorus load (kg/yr)	596	31.9	4105	13.2
Embayment area (km ²)	0.97	2.96	0.38	0.05
Maximum depth (m)	7.3	11	3.0	2.7
Euphotic zone depth (m)	4.57	8.23	2.74	3.6
% euphotic zone area	0.49	0.57	1.00	1.00
Water residence time (d)	47	56	1.3	62
Connection				
Lake Ontario	Ssnl	Perm	Perm	None
Watershed	Trib	Inter Trib	Trib	None
	South Sandy	North Sandy	South Colwell	Flood- wood
Watershed area (km ²)	8.26	210	1.38	672
% agricultural land use	29.2	24.2	19.4	37.2
Total phosphorus load (kg/yr)	174	3043	10.2	17036
Embayment area (km ²)	1.23	9.73	0.42	0.08
Maximum depth (m)	6.4	5.2	3.0	5.2
Euphotic zone depth (m)	3.35	4.88	4.20	3.35
% euphotic zone area	0.54	0.99	1.00	0.97
Water residence time (d)	148	35	90	0.1
Connection				
Lake Ontario	Ind	Perm	Inter	Perm
Watershed	Wet/Trib	Trib	Wet	Trib

(Maidment 2002) in ArcGIS software. The area within the watershed boundary was summed to compute the watershed drainage area. Annual embayment area and maximum depth was calculated from bathymetric maps and annual averages of Lake Ontario water level (NOAA, Oswego, NY, station). Bathymetric maps were generated using depth measurements collected during 2001 for all embayments except North Sandy, which were collected in 2003. Elevations were calculated using depth measurements and, for reference over time, the 1985 Lake Ontario water level of 74.67 m (NOAA, Oswego, NY, station). Bathymetric data were converted first to points then to triangulated irregular networks (TINs) using geographic information systems (GIS) ArcInfo 8.1 software (ESRI 2001a). An Arc Macro Language program was used to calculate the area for each embayment from the TINs, given the lake level for the day in question.

Percent littoral habitat was calculated from bathymetric maps based on embayment-specific estimates of euphotic zone depth (EZD), i.e., the depth at which 1% incident light intensity occurs. Mean Secchi disk depth (z_{sd} ; m) for each embayment was calculated using data collected weekly from May through mid-October in 2001 and 2002, and biweekly from June through mid-October 2003 at sites located at approximately the center of each embayment. EZD was estimated from z_{sd} following

Cole (1994), where

$$EZD = 2.7 * z_{sd}$$

We acknowledge that using a single conversion factor across systems does not account

for differences in turbidity and water color among systems. Most embayments fall between clear and turbid; therefore, a value of 2.7 is reasonable, based on $EZD:z_{sd}$ estimates for clear (2.4) and turbid (3.3) lakes estimated by Koenings and Edmundson (1991). Additionally, estimates of EZD following Kalff (2002) yielded values within 0.01 of our calculations using Cole (1994). Depths less than or equal to the EZD in each embayment were defined as littoral; depths greater than EZD were defined as pelagic. Littoral and pelagic areas (km^2) in each embayment were estimated from bathymetric maps using Arcview GIS 3.x (ESRI 2001b). The actual depths used to estimate littoral and pelagic areas (Table 1.2) were limited to an accuracy of 0.3 m by the bathymetric map resolution. EZD estimates for Juniper and South Colwell exceeded maximum depths in these embayments; therefore, 100% of the habitat was considered littoral, which matches field conditions.

Water residence time and water chemistry. Water residence time and water chemistry were provided by X. Chen (Syracuse University, unpublished data). Water residence time was estimated by dividing stream inflow to each embayment by embayment volume (X. Chen, Syracuse University, personal communication). Total phosphorus loading to the embayments was calculated by multiplying stream discharge into the embayments by the input phosphorus concentration (X. Chen, Syracuse University, personal communication).

Site-level characteristics

Each embayment was sampled on one or two consecutive dates in July 2001, 2002, and 2003. Each year, between three and eight sites were sampled in each embayment,

based on embayment size. Sites were selected according to a random, stratified design using embayment bathymetric maps superimposed with a 30 x 30 m grid.

Embayments were divided into strata by dividing the embayment into thirds, fourths, sixths, or eighths, depending on embayment area. Grid intersection points at which the water column depth was ≤ 4 m were assigned a number. A single intersection point within each stratum was randomly selected using a random number generator, with different sites randomly selected each year. Embayment sample sites were located using Global Positioning System (GPS) UTM latitude and longitude coordinates, and marked with a buoy.

Habitat data were collected at all sites within each embayment between 0800 and 1800 hours. Bottom depth (m) and percent vegetation cover were measured along a circular transect of approximately 30 m radius from the buoy (hence, center). Bottom depth was measured to the nearest 0.1 m using a graduated Secchi disk line at four locations evenly spaced along the transect. Mean depth for each site was calculated as the average of all four measurements. Percent vegetation cover was visually assessed as the percent of sediment surface supporting macrophyte growth at 1 second intervals along the transect. Mean percent vegetation for each site was calculated as the average of all estimates taken along the transect. Secchi depth was measured to the nearest 0.1 m at the center of the site as follows: (1) a weighted Secchi disk was slowly dropped straight down the water column along the shaded side of the boat; (2) the depth at which the Secchi disk could no longer be seen was measured; (3) the disk was slowly raised until it was just visible, and the depth measured; (4) the mean of the two measured depths was recorded. Surface temperature to the nearest 0.1 °C was measured at the center using a thermometer.

Fish sampling

At each site, fish were collected using a 4.6 m boat equipped with a Smith-Root Type VI-A electrofishing unit and a 5000 watt generator. The transformer was set at 120 pulses per second DC, with either 125 or 250 volts and pulse width varying between 7-9 milliseconds. Fish were collected along 15 minute (min) circular transects starting at approximately a 30 m radius from the center of each site and gradually moving inward, if necessary. In 2001 and 2002, fish were sampled between 0800 and 1800 hours; in 2003, fish were sampled between 1300 and 2300 hours. In 2001 and 2002, fish were collected before the habitat data to reduce disturbance; in 2003, habitat data were collected either 3-6 hours earlier in the day than fish or the following morning. All fish captured were placed in aerated live wells and processed after transect sampling was complete. Fish were identified to species and total length was measured to the nearest 1.0 mm. In 2002 and 2003, the wet weight in grams (g) of all fish was measured using spring scales of various weight maxima and levels of precision (usually 0.1 – 0.5 g). Fish were not weighed in 2001.

Electrofishing was limited to habitats less than 4 m deep (i.e., primarily littoral habitat), and thus our conclusions are limited to littoral fish assemblages. However, gill net sampling conducted in littoral and pelagic habitats in Blind Sodus, Little Sodus, South Sandy, and North Sandy during late June – early July, 2002, yielded relatively few fish in pelagic habitat (89 fish, 3293 min total effort) compared with littoral habitat (215 fish, 3223 min total effort). Of fish captured in pelagic habitat, 18% were alewife (*Alosa pseudoharengus*) and 76% were yellow perch. These data suggest that the fish assemblages we sampled accurately represented the summer

resident fish communities in our study embayments and we likely undersampled only alewife by limiting sampling to bottom depths less than 4 m.

Data Analysis

For most analyses, fish data were separated into several taxonomic groups, based on how common they were to all embayments and to represent a range of trophic positions and feeding habits (e.g., planktivore, benthivore, piscivore). Eight focal species were identified that occur in relatively high numbers across all embayments: brown bullhead (*Ameiurus nebulosus*), bowfin (*Amia calva*), bluegill (*Lepomis macrochirus*), golden shiner (*Notemigonus crysoleucas*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), pumpkinseed (*Lepomis gibbosus*), and yellow perch (*Perca flavescens*). One species, walleye (*Sander vitreus*), was identified as a ninth focal species due to high densities in South Sandy. All other species were grouped as non-focal species.

Fish community structure. Fish species diversity was calculated from all fish species captured during 2001-2003. Diversity was estimated using Simpson's index (D^{-1}), because of its low sensitivity to sample size (Stiling 1999), which varied across embayments. We used ordinary least squares (OLS) linear regression to determine if species diversity was related to total phosphorus loading or to embayment area, which were log-transformed (\ln) to reduce heterogeneity of variances.

Length-weight regressions based on data collected in 2002 and 2003 or on length-weight relationships reported in the literature were used to estimate fish weights for all fish captured in 2001 (Appendix 1.1). When based on our own data, species-specific

length-weight regressions were generated either for each embayment or across all embayments, depending on the number of individuals per species captured within and across embayments. Annual catch per unit effort (number/min; CPUE) and biomass per unit effort (g/min; BPUE) were estimated for each taxonomic group in each embayment. Within an embayment-year combination, CPUE (BPUE) for each taxonomic group and all fish combined was calculated as the total number (biomass) of individuals caught in that group divided by total embayment sampling effort that year (min; summed across all sites).

Normalized size spectra (NSS) provide a quantitative way to evaluate the distribution of biomass within each embayment's fish community. The method identifies the size class that supports maximum biomass by sorting organisms (i.e., fish) into size classes and plotting total biomass in each size class versus size class. NSS were created for each embayment-year by transforming all fish weights by log base 2 (Duplisea and Castonguay 2006). The sum of transformed weights in each size class was plotted against the maximum transformed weight present in each size class (sensu Kimmel et al. 2006). If no data existed for a size class, then the maximum possible weight in that size class (e.g., $1-0.01=0.99$) was used. A quadratic equation was then fit to each curve, using OLS regression, where $y = c + b \cdot x + a \cdot x^2$. Quadratic equation values for the coefficients h and k correspond to the x and y coordinates, respectively, of the parabola vertex, where

$$h = \frac{-b}{2 \cdot a}$$

and

$$k = c + b \cdot h + a \cdot h^2.$$

Coefficient h approximates the weight class at which the majority of the fish community's biomass is concentrated. Coefficient k estimates total biomass at h and is correlated with total fish community biomass (Duplisea and Castonguay 2006).

Correlations between the coefficients (h and k) and between each coefficient and fish biomass were calculated. Coefficient h also was used as a response variable in the community response analyses (see below).

Fish community response to embayment and habitat characteristics.

Whole fish community analyses. We conducted mixed model analyses using PROC MIXED in SAS (Littell et al. 1996) both to identify differences in fish community descriptors (e.g., CPUE) among embayments and to relate descriptors to embayment abiotic and biotic features. We used a mixed model to account for the hierarchical structure of the data (sites within years within embayments) and for the use of both continuous and categorical variables. Community descriptors included: (1) CPUE of all fish combined; (2) BPUE of all fish combined; and (3) the vertex coordinate h of the NSS. CPUE and BPUE data for all fish species combined were square-root transformed to meet the assumption of normality; maximum biomass weight classes (NSS h coefficients) were normally distributed.

We considered the following physicochemical variables at both the embayment and site levels to include as predictors in our analyses: (1) embayment level: embayment:watershed area, embayment area (m^2), embayment volume (m^3), annual nutrient loading ($kg \cdot y^{-1}$), percent littoral habitat, and water residence time; (2) site level: water depth (m), Secchi depth (m), and percent vegetation. Variables included

in models were selected based on Pearson correlation coefficients to ensure that only uncorrelated variables were included in each model. Secchi depth measurements were not taken in South Colwell and Sterling in 2001. To prevent the loss of both years in the data analysis, we estimated Secchi depth as being equal to Secchi depth measurements from the center of each embayment collected within 3 days of fish sampling for a related project. Variables were transformed as follows: (1) natural log transformation: embayment:watershed area, embayment area, embayment volume, annual total phosphorus load, and site depth; (2) arcsine transformation: percent vegetation; and (3) reciprocal transformation: Secchi depth. Percent littoral habitat could not be transformed to a normal distribution and thus was converted to a binomial variable as either pelagic-dominated or littoral-dominated. Water residence time was normally distributed.

For the mixed model analyses of CPUE and BPUE, data were classified according to embayment, year, and site. Mixed model analysis of maximum biomass weight classes was conducted at the embayment level only, with data classified according to embayment and year. For all analyses, embayment was specified as a random effect, because we assumed the study embayments represent Lake Ontario embayments in general (Wagner et al. 2006). Year was categorized as a fixed effect, because of the unlikelihood that three consecutive years of data represent a random sample of years (Wagner et al. 2006). Uncorrelated physicochemical features at both the embayment and site level were included as fixed effects. Piscivorous fish BPUE (untransformed) was included as a fixed effect in the model of the maximum biomass weight classes. Piscivore BPUE included American eel (*Anguilla rostrata*), bowfin, chain pickerel (*Esox niger*), grass pickerel (*Esox americanus vermiculatus*), largemouth bass,

longnose gar (*Lepisosteus osseus*), northern pike, smallmouth bass (*Micropterus dolomieu*), walleye, and white perch (*Morone americana*). We included all largemouth bass, despite high catches of young-of-year bass, based on prey fish in diets of largemouth bass as small as 37 mm TL and on findings by Olive et al. (2005) that piscivory by high densities of small-bodied largemouth bass can structure fish communities. Degrees of freedom were adjusted using the Kenward-Rogers method.

To test the null hypothesis that variance in the responses among embayments equals zero, we calculated the likelihood ratio statistic for mixed models in which no fixed effects were included. For each response variable, two models were run. In the first model, embayment was specified as a random effect; in the second, no random effects were specified. The test statistic was calculated as the difference between the two models' log-likelihood values. It follows a χ^2 distribution, and its p-value is determined by dividing the probability of a greater χ^2 for one degree of freedom by two (Littell et al. 1996). We used analyses of the full mixed models to identify significant fixed effects for each response variable. Multiple models were compared, each including different combinations of predictors. The most parsimonious models which best explained the data were selected. The percent of the variation between location explained by each full mixed model was calculated as the difference in variance due to location between models with and without the physicochemical factors as predictor variables, expressed as a fraction of the variance due to location in the model without the physicochemical factors as predictor variables. Within embayment variation was calculated similarly, using the unexplained (i.e., residual) variance estimates for each model in place of variance due to location.

Focal species analyses. CPUE and BPUE data for focal fish species could not be transformed due to a high occurrence of zeroes. Instead, data were converted to the qualitative categories “none,” “some” and “many”. Within each site, a species was categorized as “some” if the CPUE or BPUE value fell within the first three quartiles for that species across all embayments; similarly, a species was categorized as “many” if the CPUE or BPUE value fell within the fourth quartile.

We conducted multinomial analyses (PROC GENMOD in SAS) to relate each focal species’ CPUE and BPUE to the following predictors: (1) the embayment physicochemical variables used in the whole fish community analyses; and (2) piscivorous fish BPUE for bluegill, golden shiner, pumpkinseed, and yellow perch only. Data were classified according to embayment and site. Annual data for each embayment were specified as correlated.

Results

Fish community structure

Across all embayments, we collected a total of 3475 fishes representing 42 different species and 16 families (Appendix 1.2). Simpson’s index estimates of species diversity ranged from 2.7 – 6.7 among embayments (Table 1.3), but were not related to total phosphorus loading, embayment area, or percent littoral area. In general, the sites clustered in the eastern section of our study area had greater species diversity than those clustered in the western section.

Relative abundance (CPUE) and biomass (BPUE) of all fish combined and of individual species varied among embayments and years (Figure 1.2). Fish

Table 1.3. Embayment characteristics, 2001 - 2003. Ranges (minimum and maximum) of values for mean site depth, percent vegetation, and secchi depth for each year. Species diversity (Simpson's diversity index) was calculated based on all individuals captured during July 2001-2003. Annual piscivore biomass (BPUE) was calculated for all piscivorous species. Size class at peak biomass (h) estimates from NSS analyses. Regression r^2 values are shown in parentheses.

Embayment	Year	# sites	Mean depth (m)	Percent Vegetation	Secchi depth (m)
Blind Sodus	2001	4	1.0 – 2.2	40 – 100	0.9 – 2.1
	2002	4	1.3 – 2.9	20 – 100	0.9 – 2.1
	2003	4	1.6 – 3.1	20 – 50	1.2 – 2.0
Little Sodus	2001	6	2.1 – 2.8	75 – 100	2.0 – 2.8
	2002	8	1.7 – 5.8	0 – 100	1.1 – 2.9
	2003	6	2.1 – 3.6	10 – 60	1.1 – 2.5
Sterling	2001	4	1.1 – 1.6	60 – 100	1.1
	2002	4	1.3 – 2.2	80 – 90	0.8 – 2.0
	2003	4	0.9 – 2.6	20 – 45	0.8 – 1.8
Juniper	2001	3	1.8 – 2.2	100	1.0
	2002	3	0.9 – 1.7	95 – 100	0.8 – 1.0
	2003	3	1.1 – 2.1	60 – 70	1.0 – 1.3
South Sandy	2001	4	1.2 – 2.5	–	0.9 – 1.0
	2002	5	1.3 – 3.1	0 – 50	1.0 – 1.2
	2003	4	1.3 – 3.5	0 – 10	0.7 – 0.9
North Sandy	2001	8	1.1 – 3.2	50 – 100	1.3 – 2.8
	2002	8	0.8 – 3.4	0 – 100	0.8 – 2.6
	2003	6	1.3 – 2.8	5 – 50	1.0 – 2.1
South Colwell	2001	4	1.5 – 2.0	100	1.8
	2002	4	1.6 – 1.8	50 – 100	1.1 – 1.2
	2003	5	1.1 – 2.1	40 – 50	0.9 – 1.9
Floodwood	2001	3	1.4 – 2.0	90 – 100	0.8
	2002	3	1.7 – 2.9	15 – 100	0.9 – 1.0
	2003	3	2.0 – 2.9	20 – 40	0.9 – 1.7

Table 1.3 (Continued).

Embayment	Year	Species Diversity	Piscivore BPUE	<i>h</i>
Blind Sodus	2001	2.77	178.3	6.15 (0.52)
	2002		283.8	6.57 (0.47)
	2003		162.2	6.00 (0.46)
Little Sodus	2001	2.64	229.9	5.62 (0.28)
	2002		111.4	5.64 (0.48)
	2003		27.4	6.07 (0.24)
Sterling	2001	3.32	163.3	5.12 (0.17)
	2002		260.7	5.09 (0.39)
	2003		485.5	5.86 (0.45)
Juniper	2001	4.62	0	3.77 (0.27)
	2002		0	3.82 (0.48)
	2003		0	4.66 (0.45)
South Sandy	2001	5.08	58.9	6.74 (0.45)
	2002		173.7	7.25 (0.40)
	2003		107.0	5.72 (0.40)
North Sandy	2001	3.43	98.6	5.12 (0.35)
	2002		62.6	5.16 (0.52)
	2003		268.3	7.10 (0.28)
South Colwell	2001	4.05	82.9	5.15 (0.30)
	2002		167.6	5.64 (0.46)
	2003		143.9	4.87 (0.40)
Floodwood	2001	6.72	175.0	6.47 (0.24)
	2002		191.0	7.75 (0.71)
	2003		169.6	5.94 (0.56)

communities were numerically dominated by yellow perch, pumpkinseed, bluegill, and largemouth bass (Figure 1.2a). With the exception of Floodwood and Juniper, yellow perch constituted between 20-60% (by number) of the fish community. In Floodwood, abundance was more evenly distributed across yellow perch and the centrarchid populations; in Juniper, golden shiner was the numerically dominant species (Figure 1.2a). Large piscivores accounted for the majority of the biomass in all embayments except Juniper, where large piscivores were not captured (Figure 1.2b). The most common non-focal species included alewife, common carp (*Cyprinus carpio carpio*), blacknose shiner (*Notropis heterolepis*), common shiner (*Luxilus cornutus*), banded killifish (*Fundulus diaphanus diaphanus*), black crappie (*Pomoxis nigromaculatus*), and smallmouth bass. Large common carp accounted for the high biomass of non-focal species in Blind Sodus, Little Sodus, South Sandy, and Floodwood.

Fish community size structure also varied among embayments and years. Standardized cumulative biomass plots show the annual distribution of biomass (BPUE) across lengths (Figure 1.3). Juniper consistently supported a small-bodied fish community, with all of the fish biomass concentrated in fishes less than 200 mm TL. Distribution of biomass across fish length varied across the remaining 7 embayments and among years within each embayment. In these, small-bodied fishes (< 200 mm TL) constituted between 10% and 25% of fish community biomass across all embayments. Fish biomass was distributed fairly evenly across fish lengths in Little Sodus, Sterling, North Sandy, and South Colwell. A greater proportion of medium- to large-sized fishes (200-500 mm TL) was observed in Blind Sodus, South Sandy, and Floodwood in most years.

Normalized size spectra quadratic models explained between 17-71% of the variation in total biomass per weight class for each embayment-year combination (Table 1.3). Vertex coordinates were much lower for Juniper than for the other embayments (Figure 1.4). Coordinates for all other embayments varied among embayment-year combinations, with peak biomass in Blind Sodus, South Sandy, and Floodwood occurring at larger weight classes than in the other embayments (Figure 1.4). These results concur with the cumulative biomass data that Juniper supported a small-bodied fish community, whereas Blind Sodus, South Sandy, and Floodwood fish communities contained a greater proportion of large-bodied fishes. Excluding Juniper, k was negatively correlated with h ($p = 0.002$); for all embayments, neither h nor k was correlated with total fish biomass.

Fish community response to embayment and habitat characteristics

Whole fish community. The following variables (Tables 1.2 and 1.3) were highly correlated at the watershed and embayment levels: total phosphorus loading and the ratio of watershed:embayment area ($p < 0.0001$); embayment area and volume ($p < 0.0001$); embayment area and depth ($p = 0.002$); and embayment volume and depth ($p < 0.0001$). Annual total phosphorus loading and water residence time also were moderately correlated ($p < 0.10$ for each year). At the site level, mean site depth was correlated with both Secchi depth ($p < 0.0001$) and percent vegetation ($p < 0.0001$). The correlation between site depth and Secchi depth likely was due to depth readings frequently limited by bottom depth or dense macrophyte beds. Therefore, we chose not to include Secchi depth in our analyses. Embayment percent vegetation was correlated with percent littoral habitat ($p = 0.055$).

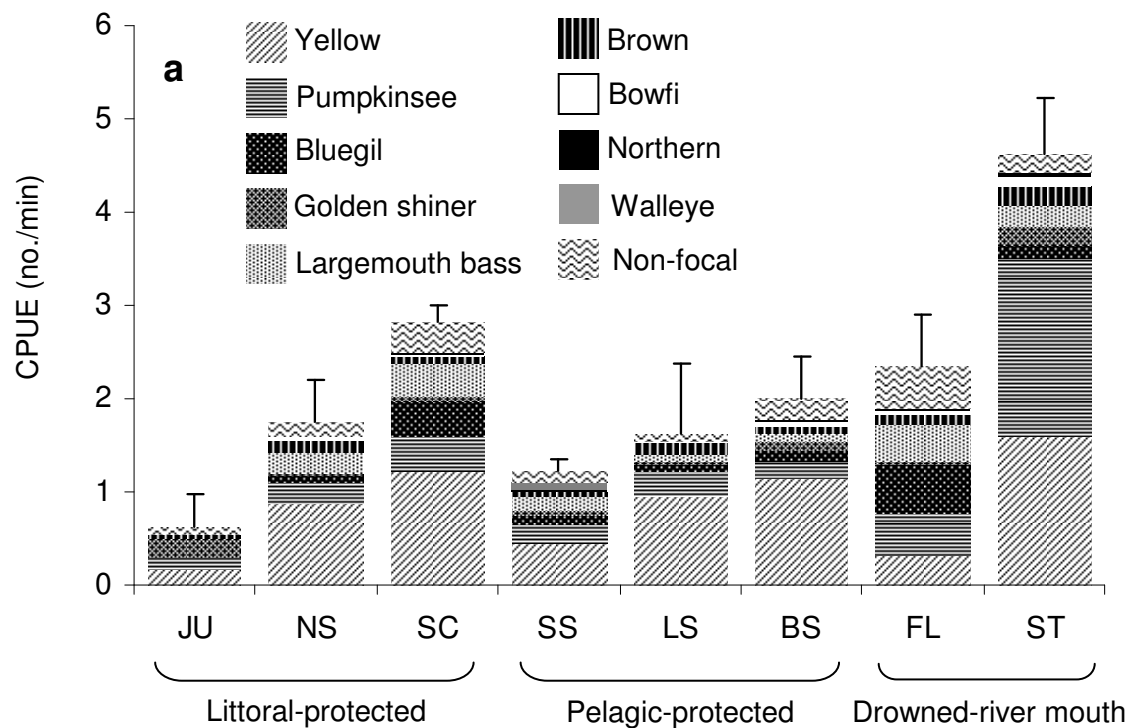
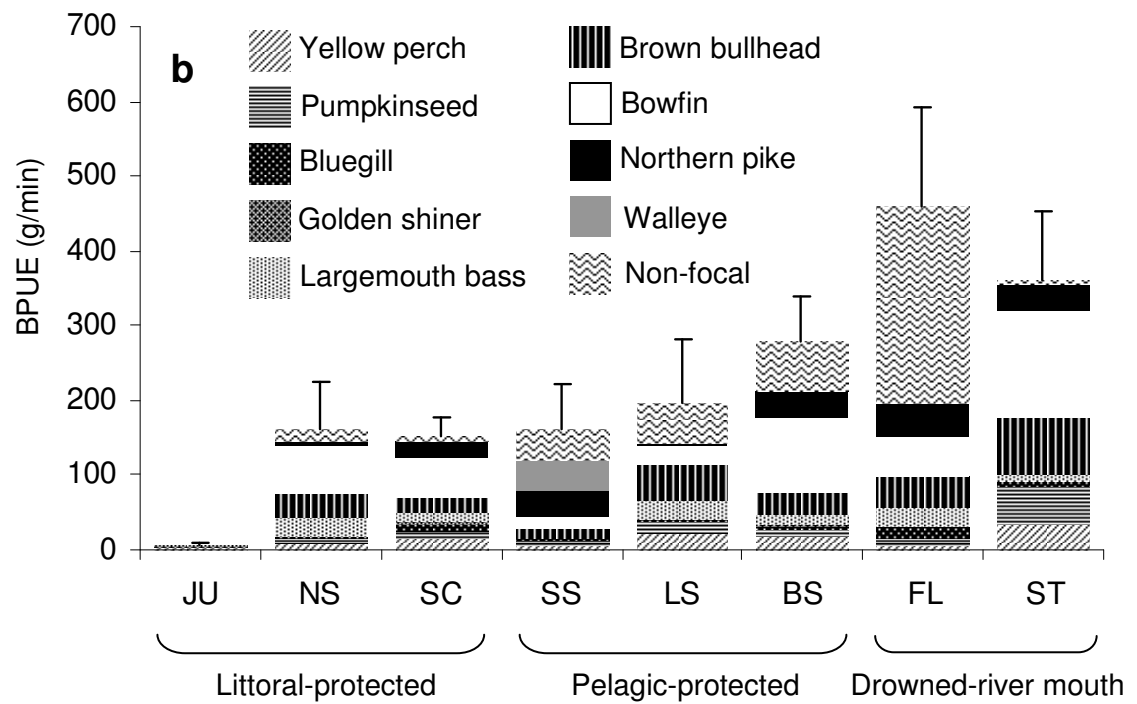


Figure 1.2. Relative (a) abundance and (b) biomass of embayment fish communities. Relative abundance was measured as total fish catch per unit effort (CPUE; mean #/min + standard error [SE] of all fish). Relative biomass was measured as total fish biomass per unit effort (BPUE; mean g/min + SE of all fish). Different patterns represent mean population abundance of focal fish species. Embayments are shown from left to right in order of increasing phosphorus loading, within each hydrogeomorphic type. Embayment codes are: SC, South Colwell; JU, Juniper; NS, North Sandy; LS, Little Sodus; SS, South Sandy; BS, Blind Sodus; ST, Sterling; and FL, Floodwood. High non-focal species biomass typically is due to the presence of common carp.

Figure 1.2 (Continued)



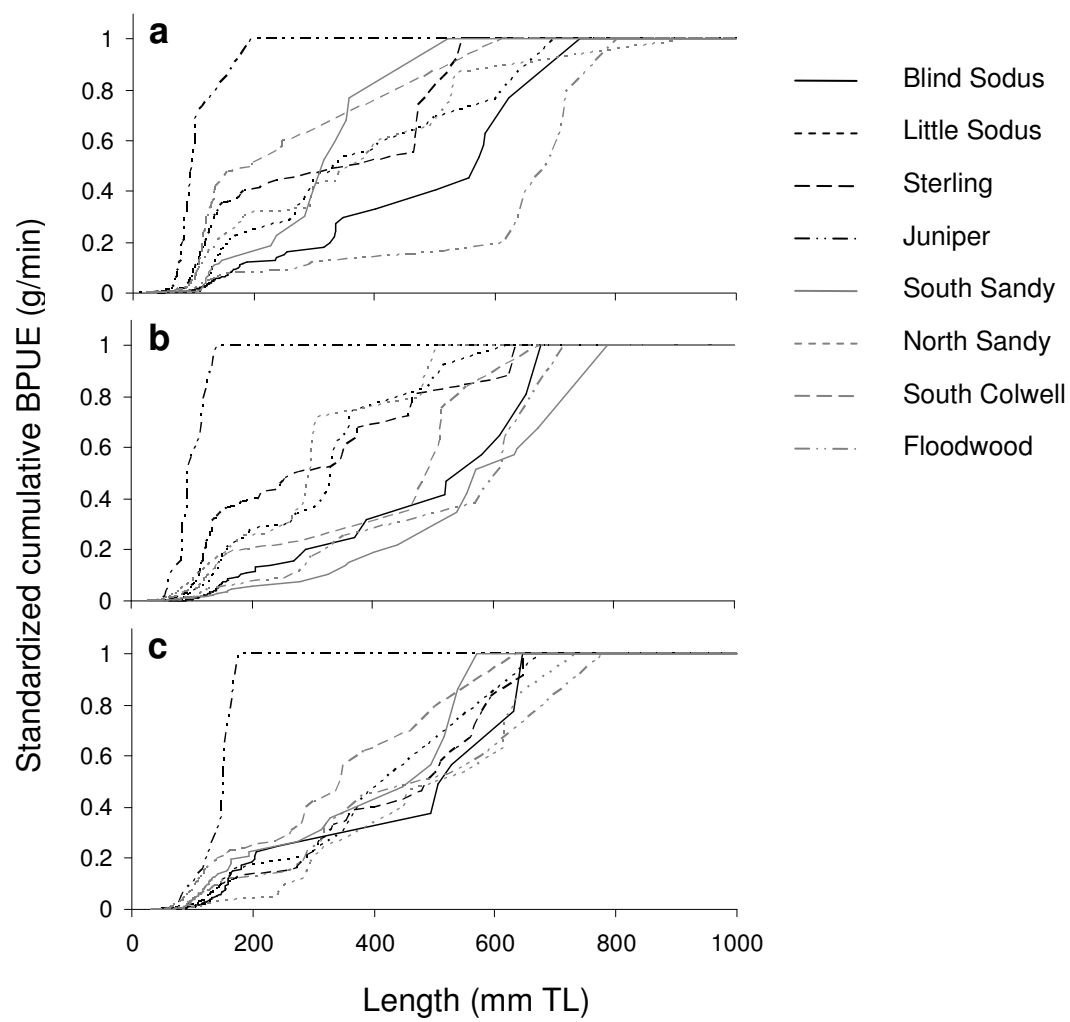


Figure 1.3. Standardized cumulative fish biomass (g/min) for each embayment in (a) 2001, (b) 2002, and (c) 2003.

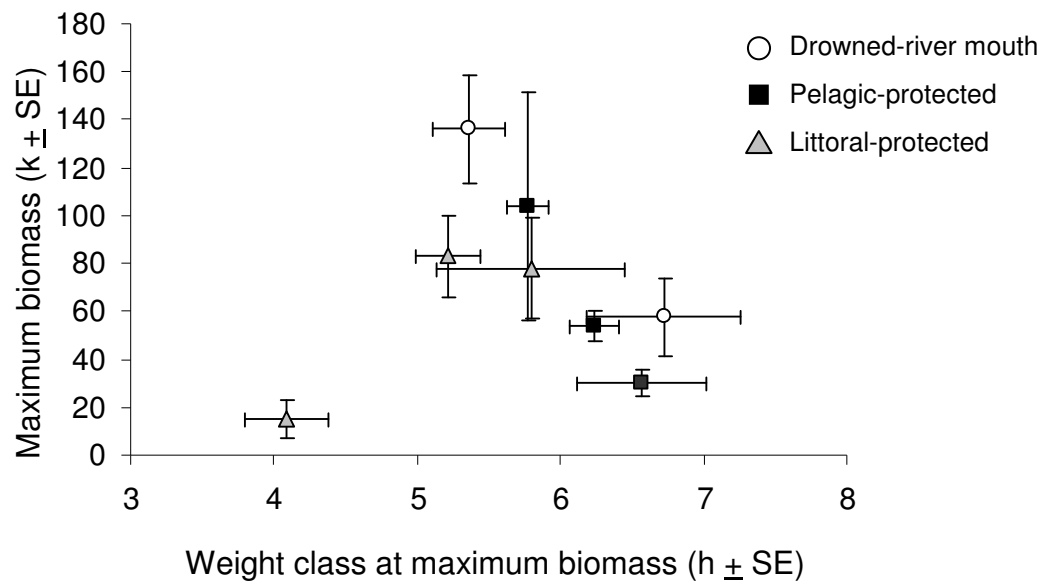


Figure 1.4. Maximum fish community biomass (k) versus weight class at maximum fish community biomass (h) for drowned-river mouth (open circles), pelagic-protected (black squares), and littoral-protected (grey triangles) embayments. Points represent 3-year means \pm SE.

We included the following variables in our analyses, either selecting one of two or more correlated variables, or testing correlated variables in separate model runs: year, water residence time, total phosphorus load, embayment area, site depth, percent vegetation, and percent littoral habitat. Year was retained in all models. We included embayment area, as opposed to volume or mean depth, in all of these models because it is known to structure fish communities (Eadie and Keast 1984, Holmgren and Appelberg 2000). We included total phosphorus loading rather than watershed:embayment area, because, as described above, phosphorus has been related to multiple fish community characteristics. For models with site depth included, we included percent littoral habitat, because they were not correlated with each other.

We selected those models that provided the best, most parsimonious fit to the data, based on model covariance estimates and number of parameters. Both CPUE and BPUE differed significantly among embayments, as indicated by the likelihood ratio test statistics ($p < 0.0025$ for both; Table 1.4). CPUE within embayments was positively related to percent vegetation ($p=0.02$; Table 1.4; Figure 1.5). BPUE among embayments was positively related to embayment area ($p = 0.04$) and total phosphorus load ($p = 0.02$; Table 1.4; Figure 1.6) and negatively related to the interaction between area and total phosphorus load ($p = 0.03$; Table 1.4). Maximum biomass weight class (the NSS coefficient h) also differed among embayments ($p=0.004$), and was negatively related to percent vegetation ($p = 0.005$; Table 1.4; Figure 1.7) between embayments.

Individual fish species. We viewed our analysis of individual species response as exploratory and did not correct for multiple tests. Results were not affected by

Table 1.4. “Variation embayment” indicates if variability for each response among embayments significantly differed from zero. Effects of total phosphorus load ($\text{kg} \cdot \text{y}^{-1}$), embayment area (m^2) and percent vegetation (% veg, below) on each characteristic are presented as slope estimates; ns indicates no significant effect of that factor; n/a indicates not applicable. P values are indicated in parentheses. The variation explained by each model (“Variation model”) is divided into variation between embayments (“Between”) and within embayments (“Within”). Between embayment variation is the difference in variance due to location between models with and without the physicochemical factors as predictor variables, expressed as a fraction of the variance due to location in the model without the physicochemical factors as predictor variables. Within embayment variation was calculated similarly, using the unexplained (i.e., residual) variance estimates for each model in place of variance due to location. Size structure was estimated as the weight class (g) at maximum biomass (h). A positive effect on size structure indicates a greater proportion of large-bodied fishes; a negative effect on size structure indicates a greater proportion of small-bodied fishes.

	Species diversity	CPUE ($\# \cdot \text{m}^{-2}$)	BPUE ($\text{g} \cdot \text{m}^{-2}$)	Size-structure (h)
Variation embayment	ns	$p < 0.0025$	$p < 0.0025$	$p = 0.04$
Physicochemical Factor				
TP load (0.88 – 4.34)	ns	ns	28 (0.02)	ns
Area (4.79 -- 7.05)	ns	ns	9.6 (0.04)	ns
TPload*Area	ns	ns	-4.3 (0.03)	ns
% vegetation (0 – 90)	ns	0.01 (0.02)	ns	-0.05 (0.005)
Variation model	n/a			
Between		-0.146	0.86	0.83
Within		0.132	0.005	-0.004

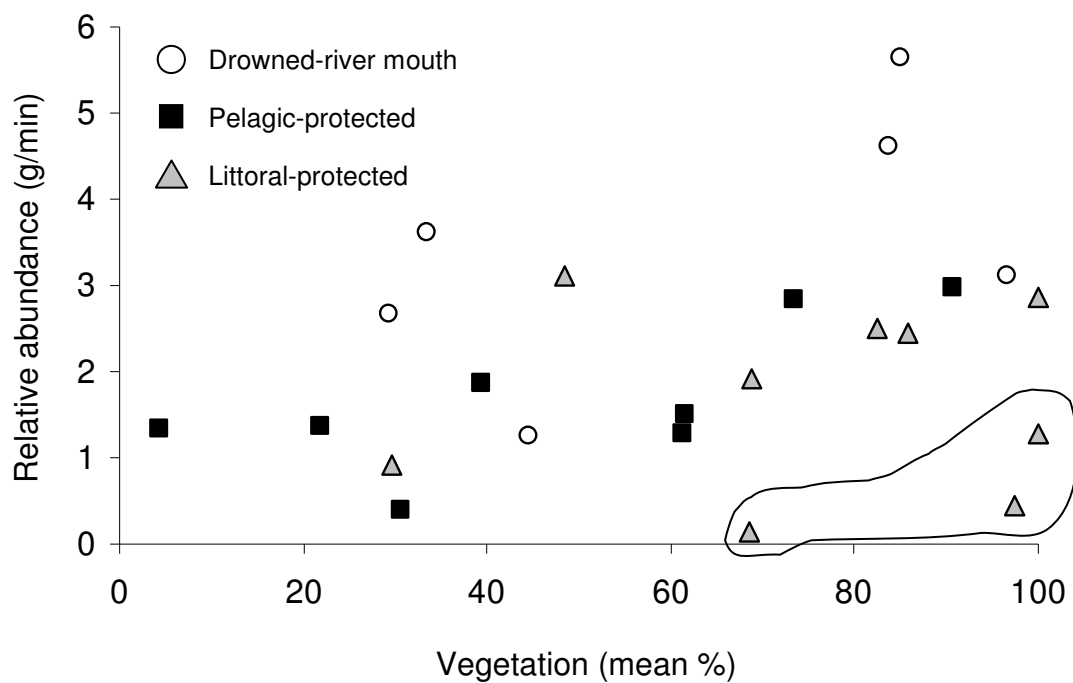


Figure 1.5. Annual total fish catch per unit effort (#/min) in July, 2001-2003 versus mean percent vegetation for drowned-river mouth (open circles), pelagic-protected (black squares), and littoral-protected (grey triangles) embayments. Circled data outliers represent a single embayment, in which relatively few fish were collected.

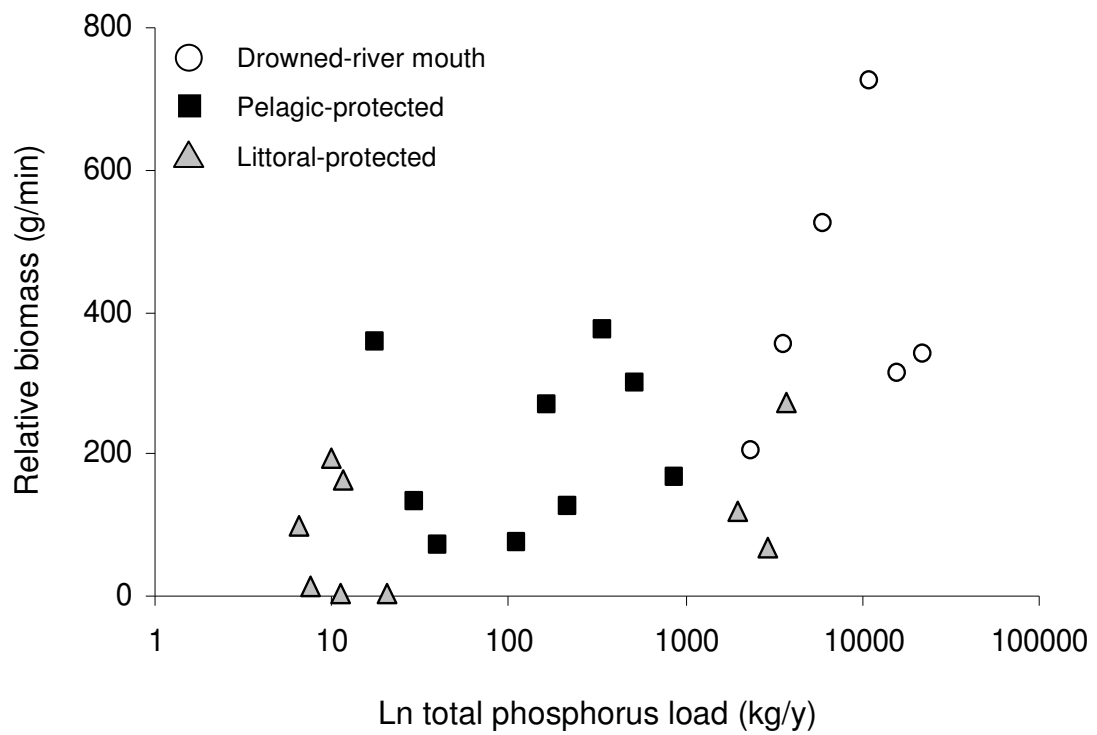


Figure 1.6. Annual total fish biomass per unit effort (g/min) in July, 2001-2003 versus the natural log of annual total phosphorus loading (kg/y) for drowned-river mouth (open circles), pelagic-protected (black squares), and littoral-protected (grey triangles) embayments.

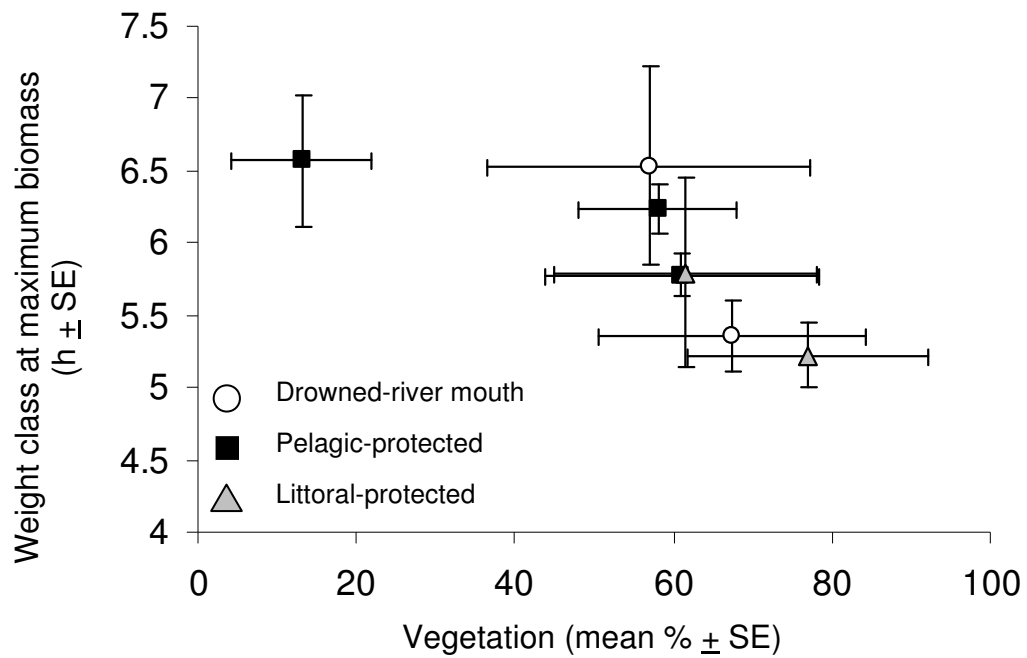


Figure 1.7. Weight class at maximum fish community biomass (h) versus percent vegetation for drowned-river mouth (open circles), pelagic-protected (black squares), and littoral-protected (grey triangles) embayments. Points are 3-year means \pm SE.

adjustment of p-values for multiple comparisons. Even at $\alpha = 0.05$, significant effects were detected only for largemouth bass CPUE and pumpkinseed and yellow perch CPUE and BPUE. Our inability to detect responses of individual species to physicochemical parameters likely is due to highly variable catch among sites, with many zero catches.

Discussion

Despite similar fish species composition and diversity among embayments, community relative abundance, biomass, and size structure differed among embayments in response to physicochemical attributes at the watershed and embayment levels. Greater fish biomass was supported by larger, deeper embayments and those receiving higher phosphorus loading. Vegetated embayments supported more fish, with biomass concentrated in small-bodied fishes. Water residence time did not influence fish community characteristics directly, but could inversely affect phosphorus loading by phosphorus dilution or reduced phosphorus retention at high flows.

Species diversity was unaffected by total phosphorus loading, despite a large range in loading. Our sites are located in eastern Lake Ontario, which is less impacted by urban and agricultural activity than western Lake Ontario and receives lower nutrient and sediment inputs from the watershed (Hall et al. 2003, Minns and Wichert 2005). Therefore, anthropogenic eutrophication may not be great enough in these systems to alter species composition noticeably. However, the effect of phosphorus loading on biomass suggests that impacts of nutrient enrichment on fish communities can be detected before changes in fish community composition are evident. Indeed, if the

entire range of phosphorus loading to Lake Ontario embayments had been included in our study, we would expect even greater variation among embayments in fish biomass, the relative abundance of individual fish species, and possibly species diversity. Unfortunately, detecting early response of individual species to physicochemical and biotic conditions is made difficult by high variability in fish catch among sampling sites.

As shown in other studies, fish biomass increased with total phosphorus loading (e.g., Oglesby 1977, Ney 1996, Randall et al. 1996) and embayment area (e.g., Eadie and Keast 1984, Holmgren and Appelberg 2000). In contrast, however, phosphorus inputs and area did not influence fish relative abundance or species diversity. Relative fish biomass may have been more sensitive to phosphorus loading because it more accurately represents the amount of energy needed to fuel the fish community than fish abundance. The positive effect of area was reduced as total phosphorus load increased, and vice versa. Differences among hydrogeomorphic types in the relative importance of area and phosphorus may explain this relationship. For example, fish biomass was largest in the drowned-river mouth embayments (Sterling and Floodwood), which receive the highest nutrient loading but are two of the smaller embayments. Area and productivity both appear to influence fish biomass in the pelagic-protected embayments (Little Sodus, South Sandy, and Blind Sodus). For example, South Sandy is intermediate to Little Sodus and Blind Sodus in size and productivity, and had the lowest biomass. Neither size nor productivity can easily be used to understand fish biomass in the littoral-protected embayments (Juniper, South Colwell, and North Sandy). Although North Sandy is the largest embayment and receives high phosphorus loading, it supports similar fish biomass to South Colwell, a

small embayment with little loading. Therefore, other factors, such as habitat availability within embayments, may be more important in structuring littoral-protected fish communities.

Indeed, studies of shallow, littoral-dominated systems have identified aquatic vegetation as an important factor in structuring fish communities (Randall et al. 1996, Zambrano et al. 2006). Randall et al. (1996) found that fish were more numerous and smaller sized in vegetated versus unvegetated littoral habitat in Lake Ontario and Lake Huron bays, but that fish biomass did not differ. Our results complement those findings, even when considering more pelagic-dominated systems. For example, the two drowned-river mouth systems, Sterling and Floodwood, supported similarly high fish biomass; however, numerous, small-bodied fishes dominated the fish community in Sterling, which supported dense macrophyte beds, whereas fewer but larger-bodied fishes occupied Floodwood, a less vegetated, somewhat deeper system. Furthermore, fish abundance and size structure appear to be related to vegetation itself, and not simply shallow habitat, because of the significance of percent vegetation as opposed to percent littoral habitat. Vegetation may be of greater benefit to small-bodied than large-bodied fishes, because it provides zoobenthivores, such as the numerically dominant yellow perch and pumpkinseed, with diverse, abundant prey and protection from predation (Randall et al. 1996, Zambrano et al. 2006). In embayments supporting a greater proportion of large-bodied fishes (e.g., Floodwood, Blind Sodus, and South Sandy), peak biomass is concentrated in fewer, but larger individuals with total biomass more evenly spread across weight classes. Neither embayment area nor piscivore biomass explained maximum biomass weight class, suggesting that medium-through large-bodied fishes benefited from larger surface area.

Different distributions of biomass across fish size classes among embayments could have implications for trophic interactions, such as the presence of trophic cascades (McQueen et al. 1986, Carpenter et al. 2001) and the susceptibility of some of these systems to shift from a macrophyte- to phytoplankton-dominated stable state (Scheffer 1990). For example, a more even distribution of biomass across size classes, with peak biomass occurring at larger size classes, may indicate a system controlled by top-down effects. Such systems may be less prone to eutrophication due to piscivory of planktivorous and benthivorous fishes (Carpenter et al. 2001). In contrast, a system such as Sterling, in which fish biomass is concentrated in smaller-bodied fishes may be more susceptible to eutrophication. In fact, zooplankton biovolume is low and phytoplankton biovolume is high in this embayment compared to the others (R. Doyle-Morin, Cornell University, personal communication). Additionally, a study of yellow perch growth and size structure in four Lake Ontario embayments suggests greater bottom-up control in shallow embayments, whereas predation may play a more important role in deep, less vegetated embayments (Chapter 3).

Our study contributes to general understanding of how fish communities respond to physicochemical features both at the watershed and lake levels. Our findings suggest that fish communities are structured by factors operating at multiple spatial scales and on multiple community characteristics. Additionally, the importance of these factors appears to differ with hydrogeomorphology. Therefore, the relative impacts of natural variability and anthropogenic activity on fish communities in wetlands are likely to differ somewhat from those in large, deep lakes. Influential factors of particular importance are those subject to human modification, such as percent vegetation and

total phosphorus loading. For example, as water clarity has improved in the Great Lakes, macrophyte densities have increased to the extent that they are now considered a nuisance to nearshore activities and are being controlled through mechanical harvesting. Shoreline development and modification of connections between embayments and the main lake impact the quality of littoral habitat, integrity of adjacent wetland habitat, and water residence time. Changing land use, such as the transformation of farmland to forested or urban land will continue to alter water discharge and nutrient and sediment loading. Identifying the actual mechanisms by which morphological and hydrological variables operate is challenging due to the degree to which many of these factors are correlated. However, developing a more explicit understanding of how these factors structure fish communities is important not only for coastal reclamation or restoration efforts along the Great Lakes coastline, but also for anticipating effects of future changes to inland, coastal, and offshore freshwater habitats and fish communities.

CHAPTER 2: Spatial energy and nutrient subsidies to fish communities: effects of hydrology, morphology, and land use

Abstract

Food web subsidies are nutrients, organic matter, and organisms that move from one ecosystem or habitat to another and are incorporated into the food web of the recipient ecosystem. Subsidies to aquatic ecosystems are common in both lotic and lentic systems and influence food web dynamics including trophic interactions, energy and nutrient cycling, and population stability. For example, headwater streams contribute carbon to downstream large river ecosystems and lakes. Within lentic environments, subsidies move between littoral and pelagic habitats. In this study, we explored the influence of physicochemical factors on subsidies to and within Lake Ontario coastal embayment food webs. These embayments are distinct ecosystems that vary in morphometry and watershed land use and are hydrologically connected to their watersheds and Lake Ontario to different degrees. Embayments support similar fish species, enabling us to evaluate effects of physicochemical factors on food web dynamics in the absence of large shifts in fish species composition. The stable isotope ratios of aquatic primary producers were used to identify basal resource subsidies to embayments. Embayment connectivity to Lake Ontario and the watershed and aquatic vegetation beds determined the extent to which subsidies from each adjacent habitat were incorporated into the base of embayment food webs. Fish muscle stable isotope ratios were used to identify littoral and pelagic subsidies to higher trophic levels within the embayments. Depth profile influenced fish reliance on littoral and pelagic subsidies, with fish communities in embayments dominated by pelagic habitat obtaining over 70% of their energy from pelagic resources; at most 50% of pelagic

energy was utilized by fish communities in embayments dominated by littoral habitat. Similarities in fish diets among embayments suggest that fish were not simply specializing on pelagic prey items in deeper systems, but rather that littoral habitat was subsidized by plankton production.

Introduction

Food web subsidies are nutrients, organic matter, and organisms that move from one ecosystem or habitat to another and are incorporated into the food web of the recipient ecosystem (Polis and Strong 1996, Polis et al. 1997). Aquatic ecosystems can receive allochthonous subsidies in the form of nutrients, energy (i.e., carbon), and organisms from adjacent aquatic and terrestrial ecosystems. Spatial heterogeneity within aquatic ecosystems creates multiple habitat types between which subsidies can move.

Subsidies among and within systems play an important role in aquatic food web dynamics by influencing trophic interactions, energy and nutrient cycling, and stability (Polis and Strong 1996, Huxel and McCann 1998, Vander Zanden and Vadeboncoeur 2002). The amount and type of subsidy entering a system are influenced by the extent of spatial coupling between ecosystems or habitats. Spatial coupling, in turn, depends upon various physicochemical characteristics of the system and the behavior and types of organisms present. Hydrology, land use effects on nutrient loading, and morphometry influence exchange rates and relative levels of productivity between systems and determine habitat availability within a system (Polis et al. 1997, Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002, Sierszen et al. 2006). Thus, they are important factors regulating subsidy flow between systems and habitats.

The goal of this study was to assess the influence of hydrology, morphometry, and

land use on spatial subsidies to food webs in Lake Ontario coastal embayments. We used stable isotope analysis of primary producers, primary consumers, and fish tissue to estimate the degree to which different types of spatial subsidies were incorporated into embayment food webs. The stable isotope ratio (δ) of a sample material is a measure of its isotopic composition relative to a standard material (Peterson and Fry 1987). Isotope ratios are expressed as parts per thousand (‰), which represent the difference between the isotopic composition of the sample and that of the standard (Peterson and Fry 1987). Isotope ratios are calculated as

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \cdot 1000 ,$$

where X is ^{15}N or ^{13}C and R_{sample} is the ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ of the sample (Peterson and Fry 1987). $R_{standard}$, the ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ of the standard, is based on atmospheric nitrogen and Pee Dee belemnite limestone, respectively (Vander Zanden et al. 1999b). Carbon isotope ratios are used by ecologists to track energy flow through food webs (Post 2002), because ratios differ among primary producers (e.g., phytoplankton and benthic algae) but are largely conserved as C is transferred up the food web (Peterson and Fry 1987). Nitrogen isotope ratios are used to estimate an organism's trophic position in a food web, because of enrichment in ^{15}N in the tissue of predators relative to their prey (Peterson and Fry 1987, Vander Zanden et al. 1999b).

Embayments are relatively shallow, inshore habitats along the shorelines of the Great Lakes that represent a gradient of lotic to lentic systems, ranging from freshwater

estuaries to protected, coastal wetlands (Keough et al. 1999, Brazner et al. 2001, Trebitz et al. 2002). Situated between the Great Lakes and their watersheds, most embayments are open to exchange of water, organisms, and other materials with both systems; however, the degree of connectivity is highly variable. As a result, embayment food webs likely play an important role in the transfer of materials between the Great Lakes and their watersheds. Diversity among embayments in morphometry, hydrology, and watershed characteristics provide an ideal setting in which to explore how these factors influence carbon and nutrient flow to and through the food web. Furthermore, embayments are exposed to multiple types of human activities, such as watershed land use, shoreline development, and water level management that can alter physicochemical conditions and subsequently subsidy dynamics (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). Furthering our understanding of the role of hydrology, land use, and lake morphometry on subsidy dynamics in aquatic food webs is of both basic and applied interest, as most aquatic systems experience high levels of natural variability and are vulnerable to current and future effects of human activities and climate change on these physicochemical characteristics.

The importance of spatial coupling is well understood in lotic systems, in which upstream or terrestrial carbon and nutrients support downstream consumer biomass (Vannote et al. 1980, Newbold et al. 1983, Howarth et al. 1992, Johnson et al. 1995). However, food webs in lentic habitats also can receive and utilize significant inputs of allochthonous materials from their watersheds and adjacent riparian habitats. Although the central role of nutrient subsidies in the cultural eutrophication of lakes is well studied (Schindler et al. 1973, Scheffer 1990, Carpenter et al. 2001), only

recently have aquatic ecologists begun to direct their attention to the importance of allochthonous carbon (C) subsidies to lentic food webs (Cole et al. 2006). For example, watershed derived carbon subsidies to North temperate lakes have recently been shown to regulate ecosystem processes and be incorporated into multiple levels of the food web (Carpenter et al. 2005, Cole et al. 2006). The importance of spatial subsidies within lentic aquatic systems also has received greater attention as the traditional focus on offshore (henceforth pelagic) processes has been replaced with the recognition that pelagic and nearshore (henceforth littoral) dynamics are linked via the movement of materials and organisms between these two habitats (Polis et al. 1997, Vadeboncoeur et al. 2002). Indeed, the pelagic component of many lake food webs is thought to rely on a significant amount of littoral energy subsidies (Polis et al. 1997, Vander Zanden and Vadeboncoeur 2002).

Energy and nutrient subsidies both to and within lake food webs are influenced by hydrology, land use, and lake morphometry. Hydrology determines water residence time and the rate of exchange between a water body and adjacent aquatic and terrestrial systems. Sierszen et al. (2006) found that phytoplankton C contributions to fish in Lake Superior coastal wetlands increased with water residence time. Watershed land use can establish productivity gradients between adjacent habitats, which also influence spatial coupling between and within aquatic ecosystems (Polis and Strong 1996, Polis et al. 1997). Less productive systems will incorporate inputs from more productive systems, such as when high levels of upland derived nutrients in tributaries subsidize phytoplankton growth in pelagic lake habitats. Within a system, high levels of nutrient loading can decrease the contribution of littoral C and benthic production to food webs by promoting phytoplankton growth and reducing littoral

primary production (Vadeboncoeur et al. 2002, Sierszen et al. 2006). At sufficiently high levels of eutrophication, settling phytoplankton can even subsidize littoral habitats (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). Morphometric measures such as lake size and the perimeter to area ratio regulate the incorporation of terrestrial and other watershed inputs, such as allochthonous C, into local food webs (Post 2002, Schindler and Scheuerell 2002). As lake size increases, coupling between littoral and pelagic habitat decreases, reducing the importance of littoral production (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002).

We studied four Lake Ontario embayments that differed in hydrology, land use, and lake morphometry and thus encompassed a range of watershed, Lake Ontario, littoral, and pelagic subsidies to identify the relative importance of these factors to embayment food web subsidy dynamics,. Two study embayments, Little Sodus and South Sandy, were relatively large, deep systems dominated by pelagic habitat (henceforth pelagic systems); two embayments, Sterling and South Colwell, were shallow, densely vegetated (henceforth littoral) systems. Water residence time and nutrient loading varied across all four embayments, such that each morphotype pair (pelagic versus littoral) included an embayment with one of the two shortest water residence times (Little Sodus and Sterling) and an embayment with one of the two highest total nutrient loads (South Sandy and Sterling). We considered both external subsidies to the base of the food web from the watershed and Lake Ontario and internal subsidies to the fish community from pelagic and littoral habitat.

We anticipated that hydrologic and land use differences among embayments would determine the relative strengths of each embayment's connection to its watershed and

Lake Ontario. Connection strength, in turn, should affect external spatial coupling between embayments and these adjacent ecosystems. Connection strength was determined based on the type of connection and rate of water exchange between the embayment and its two adjacent systems (Figure 2.1a). We presumed that an embayment that was not directly connected to Lake Ontario or that received high discharge from its watershed was more strongly connected to its watershed than to Lake Ontario (Figure 2.1b). Therefore, we hypothesized that external coupling with the watershed would be more important than external coupling with Lake Ontario in South Sandy and Sterling. South Sandy was not directly connected to Lake Ontario, whereas Sterling received high discharge and nutrient loading from its watershed. In contrast, we assumed embayments with large, permanent connections with Lake Ontario and receiving watershed inputs from ephemeral streams or via a wetland complex would be more strongly connected to Lake Ontario (Figure 2.1b). Subsequently, we predicted coupling with Lake Ontario would be more important to Little Sodus, which was more strongly connected to Lake Ontario and received watershed inputs through a small, ephemeral stream. South Colwell was situated within a wetland complex and had a natural connection to Lake Ontario that varied from open to closed depending on environmental factors. Therefore, we described South Colwell as weakly connected to both adjacent ecosystems (Figure 2.1b) and predicted its food web would be similarly coupled to both adjacent ecosystems.

We predicted that embayment morphometry would be the most important factor driving the degree to which embayment food webs, specifically the fish community, obtained their energy from planktonic versus benthic sources (Vadeboncoeur et al. 2002) (Figure 2.1a). We also considered water residence time and nutrient loading,

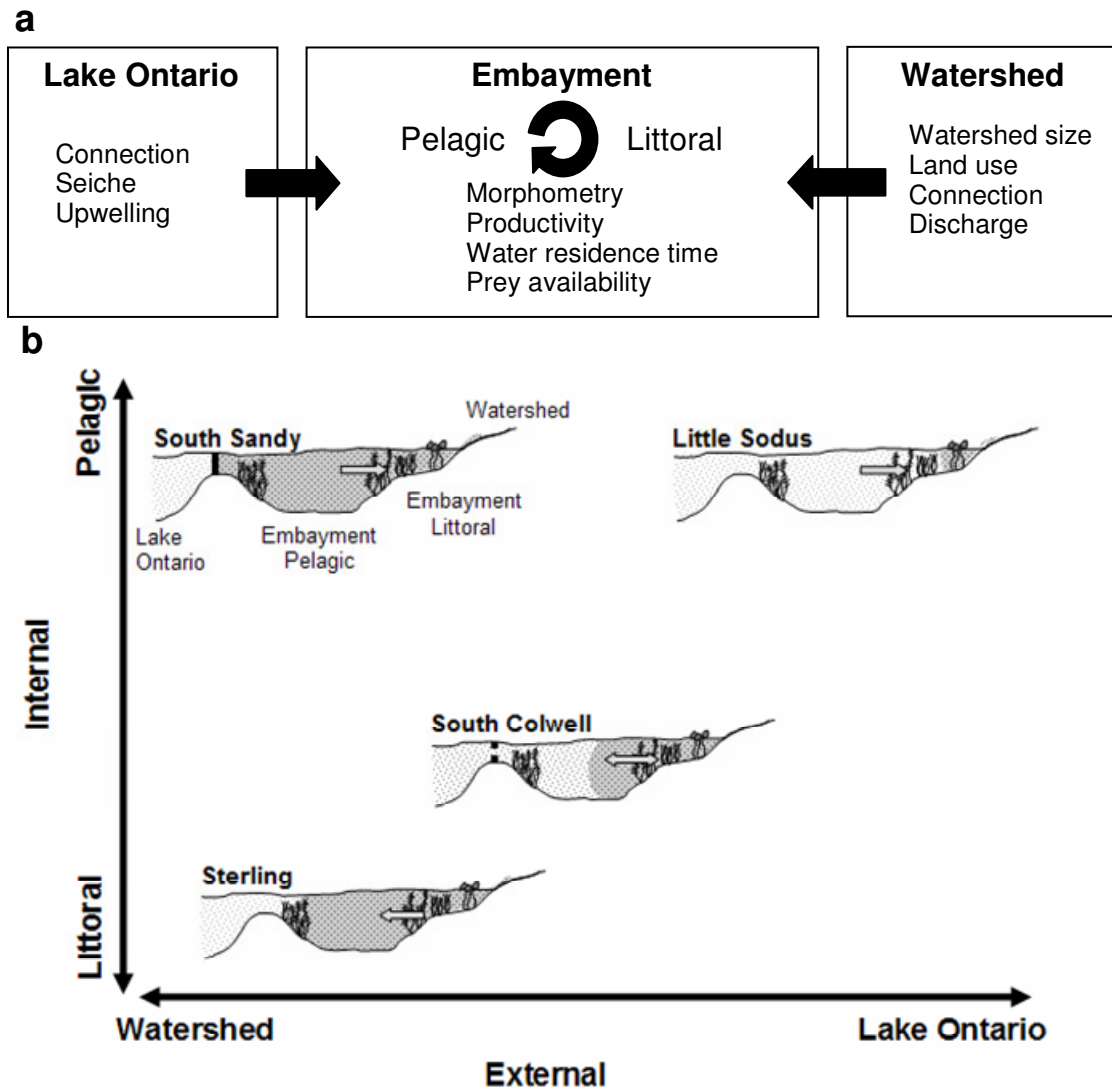


Figure 2.1. (a) Physicochemical factors that influence external spatial coupling between watersheds, embayments, and Lake Ontario, as well as internal spatial coupling (pelagic and littoral habitats). (b) Hypothesized relative importance of internal and external energy sources in four Lake Ontario embayments. External sources can come from Lake Ontario (stippled) or the watershed (cross hatched). The dominant color pattern indicates the dominant energy source in each embayment; if both patterns are equal, both external energy sources are hypothesized to be important. Internal sources originate in pelagic or littoral habitat. Grey arrows indicate if pelagic energy sources subsidize littoral habitats (arrow pointing to littoral), vice versa (arrow pointing to pelagic), or if energy from both habitats is utilized (double-headed arrow). Solid or dashed black lines indicate land barriers between ecosystems.

which were positively related to the proportion of plankton derived C in Lake Superior wetland fish communities (Sierszen et al. 2006). Based on morphometry, we hypothesized that fish communities in the pelagic embayments (Little Sodus and South Sandy) would rely primarily on pelagic energy (Figure 2.1b). In contrast, we expected that fish communities in the littoral embayments, Sterling and South Colwell, would rely primarily on littoral energy (Figure 2.1b). Between littoral embayments, we predicted that fishes in South Colwell would incorporate pelagic energy to a greater extent than in Sterling (Figure 2.1b), because of its longer water residence time (Sierszen et al. 2006).

Finally, we explored whether differences in embayment size or degree of omnivory within the fish communities (inferred from diet contents) were sufficient to affect maximum trophic position in embayment fish communities. In studies of North temperate lakes, both Vander Zanden and Rasmussen (1999) and Post et al. (2000) found a positive relationship between maximum trophic position and lake size, although Vander Zanden and Rasmussen (1999) were not able to distinguish effects of lake size from those of species richness and productive space. Post et al. (2000) suggested that lower levels of omnivory in large systems could underlie the positive relationship between lake size and maximum food chain length. We expected maximum food chain length in Little Sodus and South Sandy to be longer than in the other two embayments, because they are larger and deeper than the two littoral embayments and thus support fish communities that should consume primarily zooplankton and fish prey (Post et al. 2000). In contrast, we expected food webs in littoral embayments to be more reticulate, with shorter maximum food chain length, due to greater littoral macroinvertebrate prey availability to and consumption by fish

ranging in size and life history stage. We identified and enumerated fish diet contents to determine if fish altered their diets in pelagic- versus littoral-dominated systems, as has been demonstrated in some lakes (Vander Zanden and Vadeboncoeur 2002),.

Methods

Embayment physical and habitat characteristics

The four study embayments were located along the southeastern shoreline of Lake Ontario in Wayne, Cayuga, Oswego, and Jefferson Counties, New York (Figure 2.2). As described above, embayments differed in several hydrologic, morphometric, and chemical measures, including watershed area, watershed and riparian land use, nutrient loading, water residence time, embayment area, percent of littoral habitat, and connection to Lake Ontario and their watershed (Table 2.1). Data sources and methods for these measures are described in Chapter 1. We mapped vegetative cover (Figure 2.2) in June and July, 2004, along shore to shore transects driven by boat every 40 UTM across the entire embayment. Vegetation density was visually rated every 40 UTM along each transect as follows: 0 = no vegetation; 1 = sparse vegetation; 2 = moderate vegetation; 3 = dense vegetation; 4 = highly dense vegetation (with submerged macrophytes penetrating the water surface).

Sample Collection

Primary producer, primary consumer, and fish tissue were collected for stable isotope analysis in order to estimate the degree of external and internal spatial coupling. Primary producers included seston (phytoplankton and associated detritus), epilithon (benthic algae and associated detritus), and macrophytes. Primary consumers included dreissenid mussels and snails. Fish species sampled ranged from invertivores to

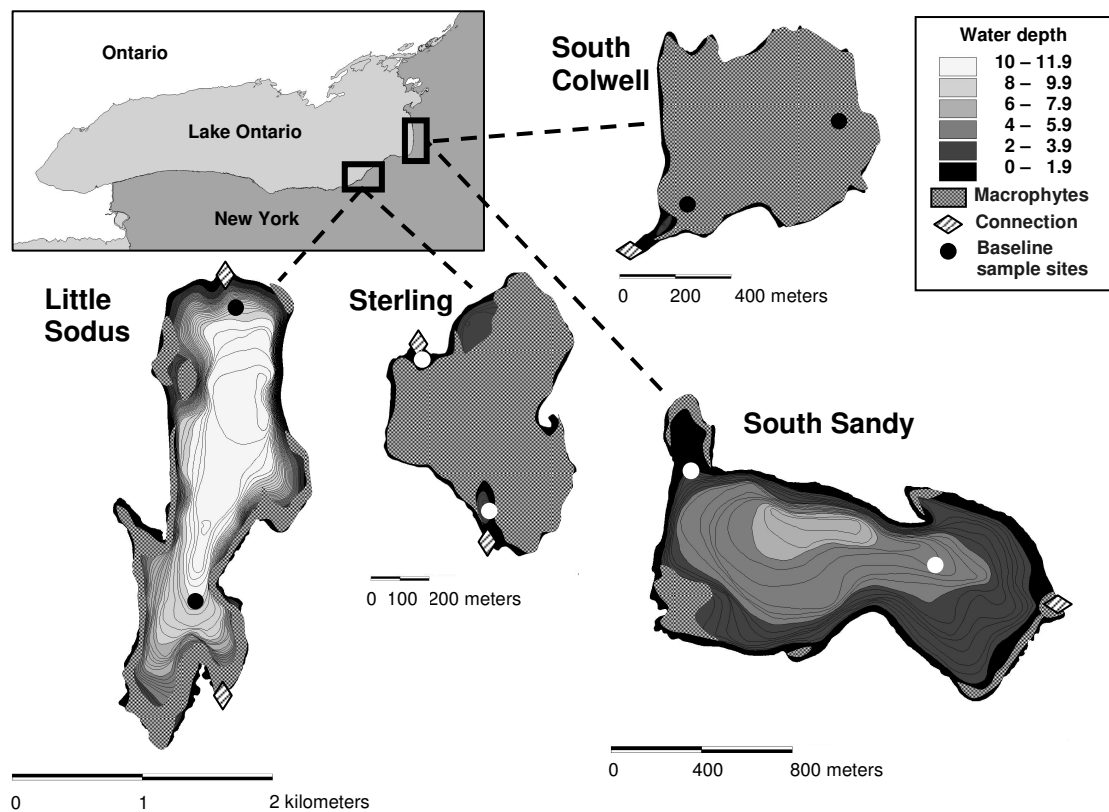


Figure 2.2. Maps of the four study embayments and their general location along the Lake Ontario shoreline. Bathymetric contours, vegetative cover, watershed and Lake Ontario connections, and sampling sites for stable isotope baselines are explained in the figure legend. South Sandy lacks a surface water connection to Lake Ontario; South Colwell lacks a direct tributary connection with its watershed.

Table 2.1. Morphometric, hydrologic, nutrient, and land use characteristics of the four Lake Ontario study embayments. DIC = dissolved inorganic carbon; Inter = intermittent; Perm = permanent; Ssnl = seasonal; Trib = tributary; Wet = wetland.

	Little Sodus	South Sandy	Sterling	South Colwell
Watershed area (km ²)	8.56	8.26	210	1.38
Watershed land use (%)				
Agricultural	17.4	29.2	41.1	19.4
Forested	46.6	51.8	51.3	50.6
Loading (kg/yr)				
Total phosphorus	31.9	174	4105	10.2
Total nitrogen (x 10 ³)	3.40	6.63	118	0.885
DIC (x 10 ⁴)	9.64	21.8	416	2.6
Water residence time (d)	56	148	1.3	90
Embayment area (km ²)	2.96	1.23	0.38	0.42
% littoral habitat	0.57	0.54	1.00	1.00
200 m riparian land cover (%)				
Residential/urban	53	< 1	2	n/a
Forested/mixed stand	2	99	94	86
Herbaceous wetland	< 1	< 1	< 1	3
Connection				
Lake Ontario	Perm	Ind	Perm	Inter
Watershed	Inter Trib	Wet/Trib	Trib	Wet

piscivores (see below).

Seston and epilithon. Seston and epilithon samples from each embayment and seston from Lake Ontario were collected every two weeks from late May through early September 2004. Within each embayment, we collected samples at two sites, one near the connection with Lake Ontario (hence referred to as “lake”) and the other near the connection to its tributary or, in South Colwell, the wetland complex (hence referred to as “stream”; Figure 2.2). Seston was collected in Lake Ontario at a site just offshore of Little Sodus and Sterling. We could not sample a Lake Ontario site near South Sandy and South Colwell due to boat and scheduling limitations. To collect seston, we deployed a tube sampler to a depth (m) of $1.5 \times \text{Secchi depth}$. Water from the tube sampler was poured through a $75\ \mu\text{m}$ mesh sieve to remove most zooplankton and large detritus and stored in 1 gallon jugs in a cooler on ice until processing in the lab.

Epilithon was collected at littoral lake and stream sites from less than 1 m depths as follows. The preferred method was to sample epilithon on bathroom tiles that had been deployed on the sediment, rough side up, in late May. If epilithon failed to develop on tiles, or if tiles could not be located (due to high macrophyte abundance or water level rise), we collected epilithon from rocks or, if unavailable, plants and woody debris. In all cases, epilithon was scraped with a toothbrush into 90 mL specimen cups containing deionized water. Cups were stored in a cooler on ice until processing in the lab. Toothbrushes were carefully rinsed with embayment water followed by deionized water between sample collections.

Upon returning to the lab, seston was again poured through a 75 µm mesh sieve into a vacuum filter and filtered onto Whatman GF/F 4.7 cm glass fiber filters. All filters were precombusted at 475 °C for 1 hour. To ensure enough sample was obtained for stable isotope analysis, we filtered each 1 gallon sample of water onto two separate filters until each filter was saturated or until no water remained. We poured epilithon samples through a 100 µm mesh sieve to remove large debris and filamentous algae. As with seston, each sample was filtered onto two glass fiber filters. Seston and epilithon filters were folded in half, placed in individual aluminum foil envelopes, and stored frozen until stable isotope analysis.

Macrophytes. We collected various species of macrophytes throughout the embayments in July 2004. Macrophyte species included Eurasian watermilfoil (*Myriophyllum spicatum*), shortspike milfoil (*M. sibiricum*), claspingleaf pondweed (*Potamogeton perfoliatus*), curly pondweed (*P. crispus*), flatstem pondweed (*P. zosteriformis*), Richardson's pondweed (*P. richardsonii*), Sago pondweed (*Stuckenia pectinata*), American eelgrass (*Vallisneria americana*), coon's tail (*Ceratophyllum demersum*), waterweed (*Elodea spp.*), and American white waterlily (*Nymphaea odorata*). Macrophytes were carefully rinsed with deionized water to remove epiphytic organisms and algae. Leaves and stems were placed in ziploc bags and stored on ice. At the lab, macrophytes were rinsed again with deionized water, placed in individual aluminum foil envelopes, and stored frozen for stable isotope analysis.

Invertebrates. Dreissenid mussels and various snail species were collected primarily by snorkeling near epilithon lake and stream sampling sites in July 2004. In some cases, e.g., Sterling and South Sandy, we could not find both mussels and snails at

these sites and thus collected samples from other littoral areas. Mussels and snails were placed in 90 mL specimen cups filled with deionized water for at least 3 hours to allow for gut evacuation. Upon returning to the lab, specimen cups were stored frozen until stable isotope analysis.

Fish. For stable isotope and diet analysis, we focused on seven fish species that were common to all embayments and represented a range of trophic positions. Focal fish species were golden shiner (*Notemigonus crysoleucas*), pumpkinseed (*Lepomis gibbosus*), yellow perch (*Perca flavescens*), brown bullhead (*Ameiurus nebulosus*), largemouth bass (*Micropterus salmoides*), bowfin (*Amia calva*), and northern pike (*Esox lucius*). In addition, we sampled walleye (*Sander vitreus*) in South Sandy because it is an important piscivore in the fish community. Fish were collected from 5 sites in Little Sodus and South Sandy and 4 sites in South Colwell and Sterling during June – August, 2003 and 2004, using an electrofishing boat. Sites were distributed fairly evenly throughout each embayment and were limited to water depths up to 4 m due to electrofishing efficiency. Complete sampling methods are described in Chapter 1. Each fish was identified to species, weighed to the nearest 0.1 - 0.5 g wet weight (depending on fish size and thus scale used) and measured to the nearest 1.0 mm total length (TL).

At each site, up to 5 individuals from each small- to medium-sizes species (< 200 mm TL; e.g., golden shiner, yellow perch, young-of-year largemouth bass) were placed in water in individual sealed bags, euthanized, and stored on dry ice. Once in the lab, fish were stored frozen until dissection of muscle tissue and stomachs for stable isotope and diet content analyses, respectively. Dorsal muscle tissue was dissected

from the left side of the fish, immediately anterior to and slightly below the dorsal fin. Scales and skin were removed previous to tissue removal. Each tissue plug was placed in a microcentrifuge tube and stored frozen until stable isotope analysis. Stomachs were dissected out of each fish and stored individually in 70% ethanol (EtOH).

Up to 5 individuals from each large-bodied species (> 200 mm TL; e.g., bowfin, northern pike) captured at each site were sampled for muscle tissue and stomach contents and then released. We used a Keyes dermal punch with either a 2 or 3 mm head to collect a dorsal tissue biopsy from the same location as for small-bodied fishes. We removed scales from the area before the biopsy was taken. The tissue plug was placed in a microcentrifuge tube and stored on dry ice in the field; tubes were stored frozen until stable isotope analysis. We removed stomach contents using gastric lavage (Seaburg 1957). A standard bilge pump was placed in a container of embayment water, with the pump intakes surrounded by a 75 μ m mesh net to exclude small invertebrates. The pump was fitted with clear, plastic tubing of appropriate length and diameter for the gape size of each fish. Stomach contents were captured in a container, filtered through a 75 μ m mesh sieve, transferred to a 90 mL sample cup, and preserved in 70% EtOH. A combination of denture glue and antibiotic were applied to the biopsy wound before releasing the fish.

Stable isotope analysis

To avoid any acidification effects on $\delta^{15}\text{N}$ (Bunn et al. 1995, Pinnegar and Polunin 1999), we analyzed both non-acidified and acidified subsamples of seston and epilithon filters for stable isotopes. In both cases, filters were dried at 60 °C for 48

hours. Eight subsamples were removed from each filter using a paper hole punch. For non-acidified samples, four hole punches were immediately placed in aluminum tins for isotope analysis. We acidified the other four hole punches by placing them in loosely capped glass vials and sealing the vials in a desiccator that contained a glass Petri dish filled with hydrochloric acid (HCl). Samples remained in the desiccator until a test sample no longer bubbled upon the addition of a droplet of HCl (Machas and Santos 1999). Acidified samples were then dried at 60 °C for 24 hours and placed in aluminum tins for isotope analysis. We also processed and ran the following filter blanks along with samples to ensure filters, deionized water, and acidification did not influence isotope signatures: (1) precombusted filter; (2) precombusted filters that had been rinsed with deionized water; (3) acidified precombusted filters. Due to unequal distribution of sample material on the filters, we did not include samples lacking sufficient material to produce a strong signal in our analysis (Table 2.2).

Macrophyte samples were dried at 60 °C for 48 hours and ground into a powder using mortar and pestle. We placed ground samples in glass vials and acidified them following the same methods as for seston and epilithon samples. Approximately 2 mg of sample were placed in aluminum tins for stable isotope analysis. We carefully removed invertebrates from their shells with forceps and examined them to ensure tissue was not contaminated with shell fragments. Between 2 and 10 individuals of mussels or snails of a single family were combined for analysis. For each embayment, we analyzed up to 30 individuals of each fish species for stable isotopes (Table 2.2). We dried invertebrate and fish tissue at 60 °C for 48 hours and ground tissue into a powder with mortar and pestle. Lipids were extracted from dried invertebrate and fish tissue by submerging up to 20 mg of tissue in 1.0 mL of a 2:1 chloroform-methanol

Table 2.2. Sample sizes and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope ratio means and standard errors (in parentheses) for organisms collected in Little Sodus and South Sandy.

Taxon group	Little Sodus			South Sandy		
	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Seston – Lake	7,6	7.05 (0.22)	-24.0 (0.86)	7,6	3.04 (0.80)	-26.9 (0.52)
Seston – Stream	7,5	7.61 (0.24)	-21.3 (1.3)	7,5	3.00 (0.54)	-26.8 (0.39)
Epilithon – Lake	6,6	7.24 (0.62)	-19.0 (2.4)	6,7	3.58 (0.38)	-22.8 (0.76)
Epilithon – Stream	6,5	6.81 (1.1)	-18.4 (1.9)	6,7	2.89 (0.58)	-24.3 (0.31)
Macrophytes	14	6.97 (0.64)	-13.6 (0.69)	8	1.88 (0.72)	-13.6 (0.47)
American white waterlily	1	5.26 (-)	-25.5 (-)	2	0.839 (0.82)	-24.3 (0.61)
Dreissenid mussels	7	8.40 (0.37)	-23.3 (1.7)	3	5.80 (0.26)	-25.4 (0.28)
Snails	8	8.67 (0.43)	-22.0 (1.6)	4	6.32 (0.15)	-25.9 (2.0)
Golden shiner	19	13.8 (0.12)	-21.9 (0.18)	19	11.1 (0.14)	-25.5 (0.14)
Brown bullhead < 300 mm	3	14.1 (0.86)	-21.2 (0.44)	5	11.4 (0.33)	-25.6 (0.62)
Pumpkinseed	20	14.1 (0.16)	-20.0 (0.30)	23	11.8 (0.15)	-24.8 (0.27)
Yellow perch	20	14.5 (0.16)	-20.3 (0.41)	27	11.7 (0.15)	-25.9 (0.20)
Largemouth bass < 100 mm	4	14.8 (0.36)	-20.4 (0.12)	7	12.3 (0.24)	-26.4 (0.20)
Brown bullhead \geq 300 mm	7	14.3 (0.17)	-20.1 (0.33)	4	12.5 (0.71)	-23.8 (0.58)
Northern pike	1	16.5 (-)	-20.5 (-)	6	13.4 (0.32)	-23.7 (0.46)
Walleye	-	-	-	14	13.6 (0.19)	-24.5 (0.27)
Largemouth bass \geq 100 mm	13	16.1 (0.23)	-20.3 (0.26)	6	14.3 (0.61)	-23.6 (0.77)
Bowfin	10	16.5 (0.37)	-21.0 (0.68)	2	14.5 (0.08)	-24.4 (0.01)

Table 2.2 (Continued). Sample sizes and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope ratio means and standard errors (in parentheses) for organisms collected in Sterling, and South Colwell.

Taxon group	Sterling			South Colwell		
	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Seston – Lake	5,5	5.43 (0.50)	-28.5 (0.48)	7,5	5.65 (0.31)	-22.8 (1.2)
Seston – Stream	5,5	6.46 (0.77)	-34.0 (1.6)	7,5	3.49 (0.43)	-24.7 (0.76)
Epilithon – Lake	7,5	5.41 (0.27)	-27.3 (0.15)	6,6	5.71 (0.26)	-20.9 (1.4)
Epilithon – Stream	7,5	5.36 (0.17)	-29.2 (0.27)	2,2	1.57 (0.42)	-27.6 (0.78)
Macrophytes	9	2.67 (0.77)	-22.0 (0.89)	4	3.95 (0.64)	-14.3 (1.4)
American white waterlily	2	0.116 (1.5)	-25.6 (0.23)	1	-0.196 (-)	-24.8 (-)
Dreissenid mussels	7	7.74 (0.25)	-20.7 (1.4)	3	7.03 (0.59)	-22.7 (1.4)
Snails	5	7.63 (0.22)	-20.0 (2.7)	4	6.84 (0.51)	-24.3 (1.6)
Golden shiner	23	10.9 (0.16)	-28.3 (0.31)	19	13.8 (0.12)	-21.9 (0.18)
Brown bullhead < 300 mm	5	11.3 (0.50)	-28.6 (0.71)	12	11.5 (0.43)	-23.5 (0.57)
Pumpkinseed	27	12.2 (0.15)	-28.1 (0.46)	20	11.3 (0.24)	-23.1 (0.60)
Yellow perch	23	12.8 (0.14)	-28.7 (0.41)	21	11.8 (0.22)	-23.0 (0.44)
Largemouth bass < 100 mm	16	12.3 (0.22)	-31.1 (0.46)	4	10.4 (0.43)	-19.8 (3.0)
Brown bullhead \geq 300 mm	14	13.4 (0.32)	-22.3 (0.76)	3	13.2 (1.0)	-20.1 (1.0)
Northern pike	12	13.6 (0.25)	-25.6 (0.42)	2	13.7 (0.44)	-21.0 (0.88)
Walleye	-	-	-	-	-	-
Largemouth bass \geq 100 mm	5	14.4 (0.57)	-26.3 (0.83)	13	13.8 (0.28)	-22.5 (0.61)
Bowfin	19	14.3 (0.34)	-26.7 (0.33)	9	14.0 (0.39)	-23.3 (0.42)

solution (Post 2002). The solution-tissue mixture was shaken periodically to ensure all tissue was exposed to the solution. After 60 minutes, the solution was poured off of the tissue and the tissue was re-dried at 60 °C for 24 hours. Approximately 1 mg of tissue was placed in aluminum tins for stable isotope analysis.

Stable isotope analysis was conducted at the Cornell University Stable Isotope Laboratory (COIL) on a Finnegan MAT Delta Plus isotope ratio mass spectrometer interfaced to a Carlo Erba NC2500 elemental analyzer through a Conflo II open split interface (A. Kasson, COIL, personal communication). Mean error for all sample runs was 0.11 ‰ for $\delta^{15}\text{N}$ and 0.10 ‰ for $\delta^{13}\text{C}$, based on either a cabbage or brown trout in-house standard. The large number of fish tissue samples analyzed required that we run multiple analyses over several months. To identify any variability in machine accuracy among runs, we ran a verification analysis that contained about 5-7 fish tissue samples from each previous analysis. We selected samples to represent the range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of each analysis. Two of the previous analyses produced consistently high $\delta^{15}\text{N}$ values; therefore, $\delta^{15}\text{N}$ values for all samples run on those two dates were adjusted based on the mean difference in $\delta^{15}\text{N}$ values between the original and verification run.

We calculated mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for seston and epilithon using $\delta^{15}\text{N}$ data from non-acidified samples and $\delta^{13}\text{C}$ data from acidified samples. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were calculated for submerged macrophytes pooled, American white waterlily, dreissenid mussels, all snails pooled, and individual fish species. We divided largemouth bass into two size groups, individuals less than 100 mm TL and individuals greater than or equal to 100 mm TL, based on ontogenetic changes in

feeding with growth for largemouth bass (Ludsin and DeVries 1997, Post 2003).

Brown bullhead also were split into two size groups, individuals less than 300 mm TL and individuals greater than or equal to 300 mm TL, based on changes in N and C stable isotope ratios with size. Brown bullhead changes with size likely are due to differences in foraging behavior or habitat preference among adults of different sizes, but such differences have not been well-documented to our knowledge.

External spatial coupling. Without a watershed stable isotope signal, we could not quantitatively analyze the relative importance of the watershed versus Lake Ontario as external sources of materials to the embayments. Instead, we inferred relative contributions from each water source by comparing mean seston $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values at lake and stream sites in each embayment with mean seston $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in Lake Ontario. Water chemistry and land use data also were used to inform inferences. Studies of Lake Superior wetlands have shown that wetland food web energy sources are isotopically distinct from energy sources of the nearshore lake food web, because they include dissolved inorganic carbon (DIC) derived from the watershed or from the decomposition of embayment aquatic vegetation (Keough et al. 1996, Sierszen et al. 2004). We assumed Lake Ontario embayment energy sources, similarly, would have distinct isotopic signatures from the lake, and that relative differences between embayment seston isotopic signatures and those of Lake Ontario would reflect the degree to which embayment food webs are connected to and subsequently incorporate subsidies from their watersheds and Lake Ontario (Table 2.1). Finally, we expected that subsidies from watersheds with high levels of human activities – either agricultural or residential land use – could be identified by enriched $\delta^{15}\text{N}$ values due to fertilizer use and human or animal waste (Peterson and Fry 1987). In contrast

subsidies from primarily forested watersheds would be evident from relatively unenriched $\delta^{15}\text{N}$ values.

Internal spatial coupling. We used seston and epilithon mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values as baselines to estimate the incorporation of pelagic (seston) versus littoral (epilithon) energy by fishes. Although primary consumers can be used as baselines (Post 2002), we could not use mussels and snails because of high variability and overlap of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (see Results). A two source mixing model would not account for spatial differences in seston and epilithon values between lake and stream sites; therefore, we used the IsoSource Visual Basic program to produce a distribution of plausible percent contributions by multiple sources based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ means (Phillips and Gregg 2003). IsoSource identifies all possible combinations of source contributions that achieve isotope ratios within a set range (hence “mass balance tolerance”) around a focal organism’s isotope ratios, for example the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of a particular fish species (Phillips and Gregg 2003). Source values are adjusted by the expected fractionation that would occur as the source moves up the food web to the trophic position occupied by the focal organism (Phillips and Gregg 2003). IsoSource tests source contributions iteratively, by increasing each source’s percent contribution by a set amount (hence “source increment”) (Phillips and Gregg 2003). Contributions cannot be estimated when focal isotope ratios fall outside of the area bounded by adjusted source values on an isotope biplot (Phillips and Gregg 2003).

We used IsoSource to estimate possible contributions of lake and stream site seston and epilithon to individual fish species (Appendix 2.1). This produced a large number

of results (9 species groups*4 embayments*4 sources); therefore, we grouped fish species as either omnivore or piscivore to facilitate the evaluation of energy flow to the fish community. Omnivores include brown bullhead less than 300 mm TL, golden shiner, largemouth bass less than 100 mm TL, pumpkinseed, and yellow perch. Piscivores include brown bullhead at least 300 mm TL, bowfin, largemouth bass at least 100 mm TL, northern pike, and walleye. Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each group were calculated from individual fish measurements. Keough et al. (1996) estimated fractionation of source ^{13}C isotope ratios with each increase in trophic position to be between 1-2‰ in Lake Superior coastal wetlands. Other studies show less enrichment, with values ranging 0-1‰ (Peterson and Fry 1987, Post 2002). Because our systems are similar to Lake Superior wetlands, we assumed ^{13}C to be enriched 1‰ with each trophic step. We assumed 3.4‰ enrichment in $\delta^{15}\text{N}$ (Vander Zanden and Rasmussen 2001, Post 2002). Mass balance tolerance was set to 0.05 ‰ and the source increment to 1 ‰ for all calculations.

Trophic structure. In each embayment, we calculated individual fish trophic positions using the following equation from Post (2002), using seston and epilithon as baseline organisms for the calculations.

$$\text{Trophic position} = \lambda + \frac{\delta^{15}\text{N}_{fish} - [\alpha \cdot \delta^{15}\text{N}_{seston} + (1 - \alpha) \cdot \delta^{15}\text{N}_{epilithon}]}{3.4}$$

$$\text{where } \alpha = \frac{\delta^{13}\text{C}_{fish} - \delta^{13}\text{C}_{epilithon}}{\delta^{13}\text{C}_{seston} - \delta^{13}\text{C}_{epilithon}}$$

and $\lambda = 1$, the trophic position of primary producers. $\delta^{13}\text{C}_{fish}$ and $\delta^{15}\text{N}_{fish}$ are values

for each individual fish; $\delta^{13}C_{seston}$ and $\delta^{15}N_{seston}$ and $\delta^{13}C_{epilithon}$ and $\delta^{15}N_{epilithon}$ are means for seston and epilithon, respectively, from stream and lake sites pooled. The denominator in the equation, 3.4, is the fractionation (‰) of $\delta^{15}N$ with each increase in trophic level (Vander Zanden and Rasmussen 2001, Post 2002). The term α is a two end-member mixing model that estimates the proportion of C derived from seston food sources. Alpha ranges from 0 to 1, with $\alpha = 1$ indicating the fish derives 100% of its energy from seston and $\alpha = 0$ indicating the fish derives 100% of its energy from epilithon. The proportion of C derived from epilithon food sources is estimated by $1 - \alpha$. The trophic position equation assumes the proportions of N derived from each food source are the same as the C proportions (Post 2002). We compared omnivore and piscivore trophic positions among embayments using one-way ANOVA in Minitab. Differences among embayments were determined from pairwise comparisons based on Tukey's 95% simultaneous confidence intervals.

Diet content analysis

We identified and enumerated the stomach contents of the fish that were used for stable isotope analysis (collected June – August 2003 and 2004) to validate and better understand stable isotope results. We identified prey items to the lowest practical taxonomic classification depending on the state of the prey item and dissecting scope limitations. For prey items that were torn apart, we only counted the number of heads present in the stomach. We identified most amphipods, isopods, zooplankton, and fish to family or genus; aquatic insects and mollusks typically to order or family; mites as Hydrachnidia; and crayfish as Decapoda. Algae and vascular plants present in the stomach were recorded as percent of the total volume of stomach contents. Prey items were aggregated into the following groups: zooplankton, amphipod/isopod, insect,

mollusk, other, fish, and plant. “Other” included Hydrachnidia, oligochaetes, eggs, unidentified crustaceans, and any other unidentifiable stomach items. Plant included both algae and vascular plants. We calculated the proportion of each group in an individual fish’s stomach based on the percent of stomach content volume remaining after subtracting the percent volume occupied by plants. We then calculated mean percentages of each diet group for omnivorous and piscivorous fishes.

Results

External spatial coupling

Little Sodus lake seston was slightly enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compared to Lake Ontario seston (Figure 2.3). Enrichment most likely was due to septic inputs, as 53% of land use in the 200 m riparian zone around Little Sodus was residential (Table 2.1). In contrast, South Sandy seston $\delta^{15}\text{N}$ and, to a lesser extent, $\delta^{13}\text{C}$ were much lower than that of Lake Ontario (Figure 2.3), probably because South Sandy received the majority of its water from a predominantly forested watershed (Peterson and Fry 1987) (Table 2.1). South Sandy seston were similar in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at both sites, suggesting that South Sandy inputs come exclusively from its watershed and mix evenly throughout the embayment.

Seston $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in both Sterling and South Colwell differed between sites, with lake site seston values more similar to those of Lake Ontario than stream site values (Figure 2.3). For example, Sterling seston was less enriched in ^{13}C at both sites, but most notably at the stream site (Figure 2.3). Dense vegetation in both systems may have prevented water from mixing throughout the embayments, such that lake subsidies were restricted to areas close to the channels while watershed subsidies were

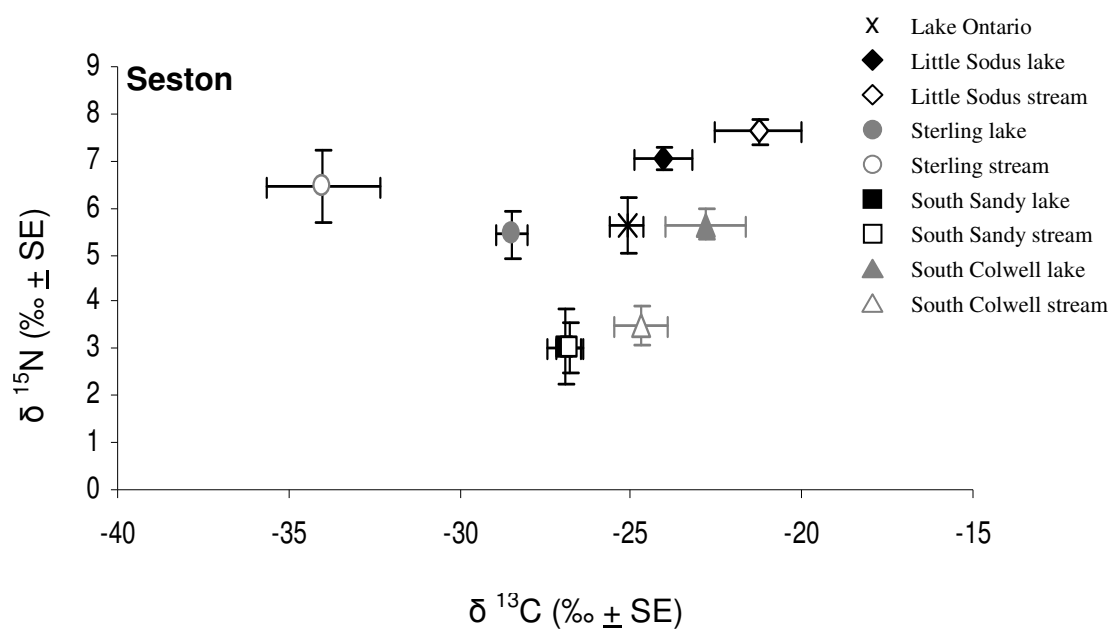


Figure 2.3. Stable isotope ratios for seston in Lake Ontario and embayment lake and stream sample sites. Data points represent mean parts per thousand \pm standard error (SE). Black symbols represent pelagic-dominated systems; grey symbols represent littoral-dominated systems.

retained closer to the tributary and wetland inflows. Similar to South Sandy, spatial coupling between South Colwell and its forested watershed was reflected by the light isotope ratios of seston at the stream site (Figure 2.3).

Internal spatial coupling

Energy source baselines. Possible baselines for identifying pelagic versus littoral energy flow to the fish community included primary producers (seston, epilithon, and macrophytes) and primary consumers (dreissenid mussels and snails). Among primary producers, epilithon was more enriched in ^{13}C than seston for a given site within each embayment (Table 2.2; Figures 2.4a-d), with the exception of the South Colwell stream site (Table 2.2; Figure 2.4d). Spatial differences in $\delta^{13}\text{C}$ among sites in Sterling and South Colwell caused seston and epilithon baseline signals to overlap each other (Table 2.2; Figures 2.4c,d). With the exception of waterlily, macrophytes were more enriched in $\delta^{13}\text{C}$ than all other baselines. Across embayments, waterlily $\delta^{13}\text{C}$ values were less enriched than other macrophytes and ranged from less to more enriched than seston and epilithon (Table 2.2; Figures 2.4a-d). Seston and epilithon $\delta^{15}\text{N}$ values were similar within embayments, except in South Colwell where seston and epilithon at the stream site were less enriched in ^{15}N than at the lake site.

Dreissenid mussels and snails within each embayment were highly variable in $\delta^{13}\text{C}$ such that ranges overlapped and thus did not reflect separate pelagic and benthic energy pathways (Table 2.2; Figures 2.4a-d). For example, in Little Sodus and South Sandy, both mussel and snail mean $\delta^{13}\text{C}$ values were more similar to seston $\delta^{13}\text{C}$ values than to epilithon $\delta^{13}\text{C}$ values (Table 2.2; Figure 2.4a,b). Additionally, mussel and snail isotope ratios in Sterling were more enriched in $\delta^{13}\text{C}$ than expected based on

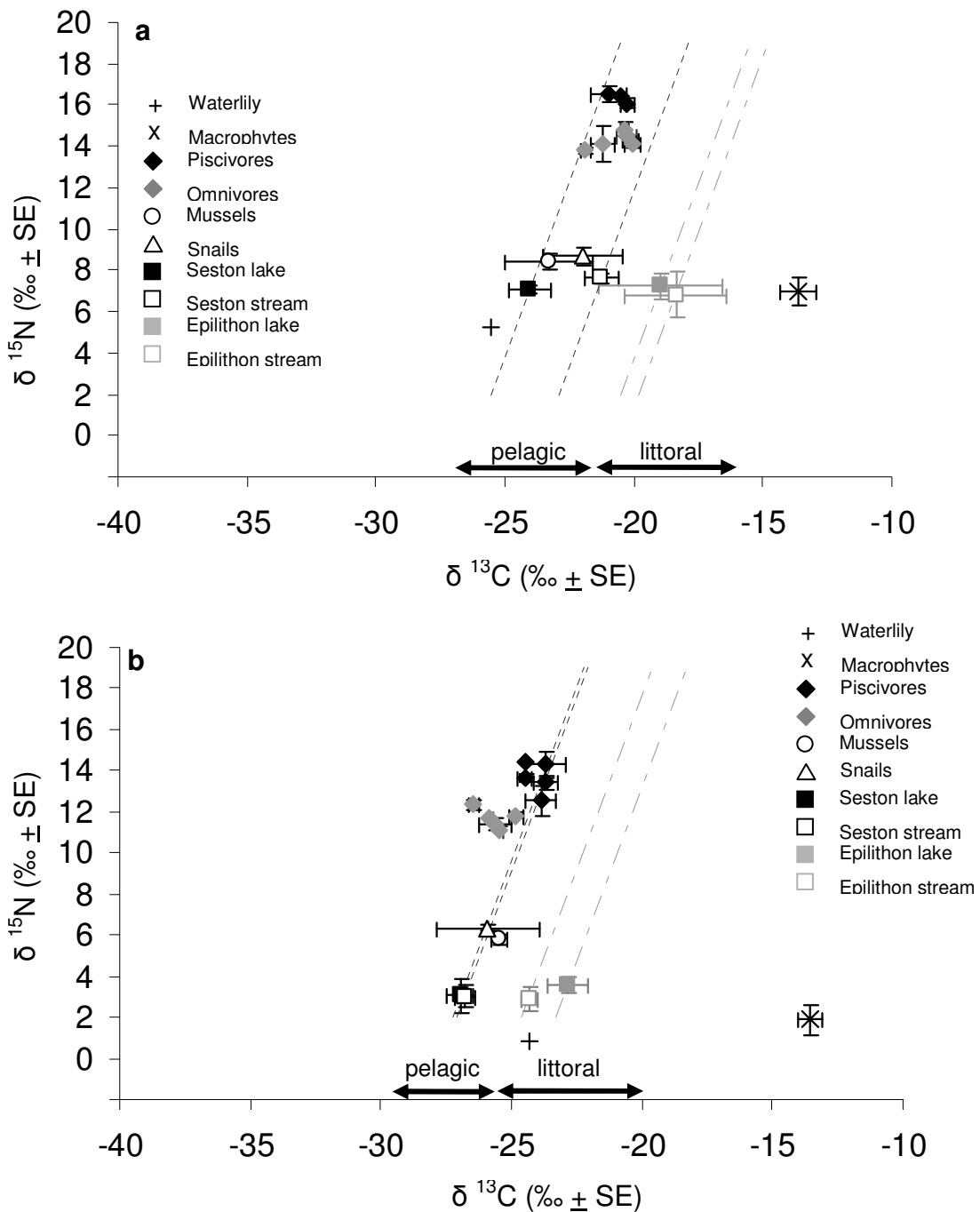
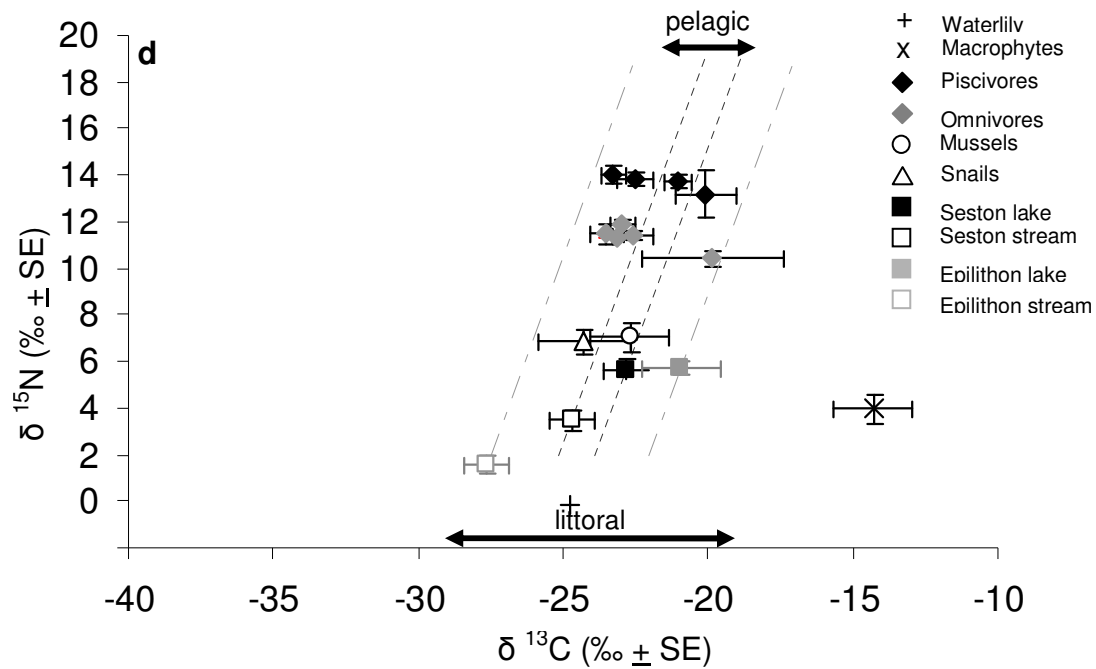
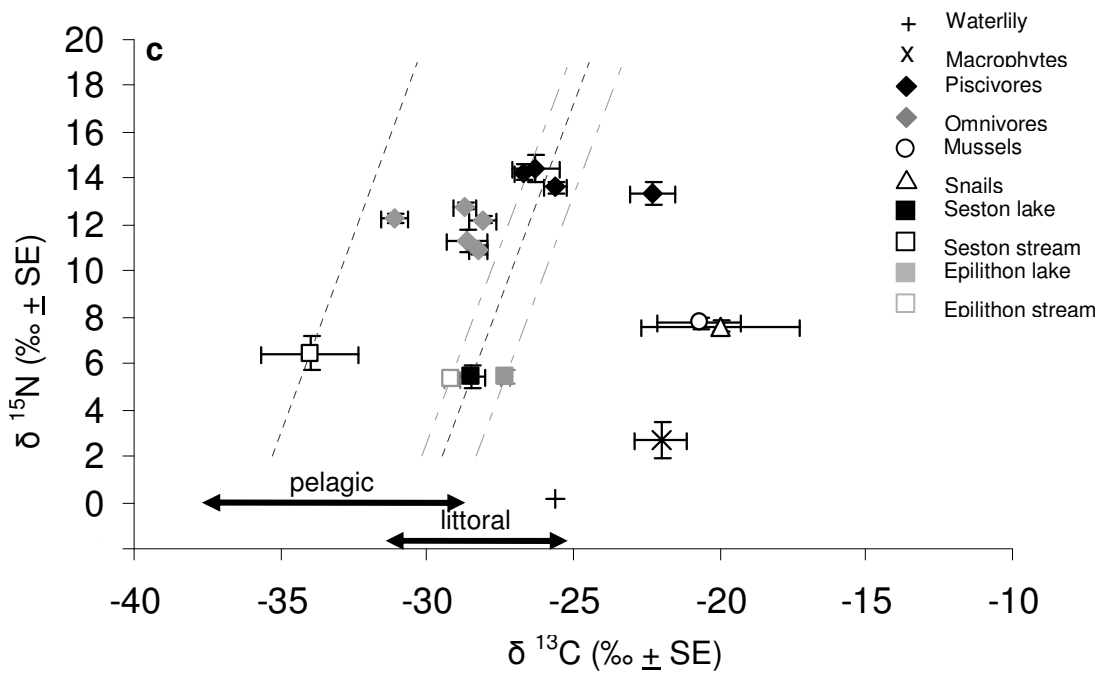


Figure 2.4. Stable isotope ratios for pelagic embayments, (a) Little Sodus and (b) South Sandy, and for littoral embayments, (c) Sterling and (d) South Colwell. Data points are mean parts per thousand \pm SE. Dashed lines represent expected enrichment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as it moves up the food web, based on estimated enrichment of 1‰ ^{13}C and 3.4‰ ^{15}N with each increase in trophic level.

Figure 2.4 (Continued)



seston and epilithon ratios (Table 2.2, Figure 2.4c). As such, mussels and snails could not be used as baselines for determining littoral versus pelagic energy source contributions to fish communities.

Energy source contributions to the fish community. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for individual fish species within each embayment are presented in Table 2.2. For ease in the interpretation of results, isotope biplots (Figure 2.4a-d) show individual fish species mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with species identified as being either an omnivore or a piscivore. Dashed lines depict expected fractionation in baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as assimilated carbon and nitrogen moves up the food web, showing energy source contributions to the fish community in these figures. Energy source distributions (medians, interquartile ranges [IQR], quartiles $\pm 1.5 \times \text{IQR}$, and outliers) for omnivorous and piscivorous fishes, estimated using IsoSource, are shown in Figure 2.5a and 2.5b, respectively.

All fish species in the pelagic embayments, Little Sodus and South Sandy, fell within the range of seston $\delta^{13}\text{C}$ values (Figure 2.4a), suggesting primary incorporation of pelagic energy. Based on IsoSource distributions for both the omnivore and piscivore groups in Little Sodus, lake site seston contributed between 60-80% of fish energy, with stream site seston contributing another 5-25% (Figure 2.5a,b). In South Sandy, light $\delta^{13}\text{C}$ means for omnivores and piscivores fell outside of (i.e., were isotopically lighter than) the expected range of mean seston and epilithon isotope signatures. Stream site snails also were less enriched in ^{13}C , suggesting an additional energy source or temporal isotopic variation not captured by the seston summer means (see Discussion). Therefore, we ran the IsoSource program with stream site snails added as

a fifth source in addition to the site-specific seston and epilithon signatures. The stream snail source was the dominant energy source to both omnivorous (55-65%) and piscivorous (30-45%) fishes (Figure 2.5a,b). Piscivorous fishes also derived between 10-35% from each seston source (Figure 2.5b).

Mean $\delta^{13}\text{C}$ signatures in the littoral-dominated embayments, Sterling and South Colwell, varied among species to a greater extent than in Little Sodus or South Sandy (Table 2.2; Figure 2.4c,d). The wider range of fish $\delta^{13}\text{C}$ signatures was most noticeable in Sterling, with omnivorous fish species being generally less enriched in ^{13}C than piscivorous fishes (Figure 2.4c). Fish species in Sterling and South Colwell obtained energy from a combination of seston and epilithon sources, although overlap among sources makes interpretation difficult. IsoSource results suggest omnivorous fishes in Sterling obtained energy from all sources fairly equally. Between 35-40% of energy was derived from stream seston and 10-30% from each of the other three sources (Figure 2.5a). In contrast, lake epilithon contributed from 75-85% of energy to piscivorous fishes (Figure 2.5b). Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for large brown bullhead in Sterling fell outside of the range of sources (Table 2.2; Figure 2.4c) and was not included in the piscivorous fish mean. In South Colwell, the majority of both omnivorous and piscivorous energy derived from stream epilithon (35-50% and 45-55%, respectively) and stream seston (10-40% and 10-35%, respectively; Figure 2.5a,b); however, overlap among baselines question the reliability of these estimates.

Trophic structure. Fish species trophic positions varied among embayments, but the relative order of species was similar (Table 2.3). Golden shiner occupied the lowest trophic position except in South Colwell, in which young-of-year largemouth bass

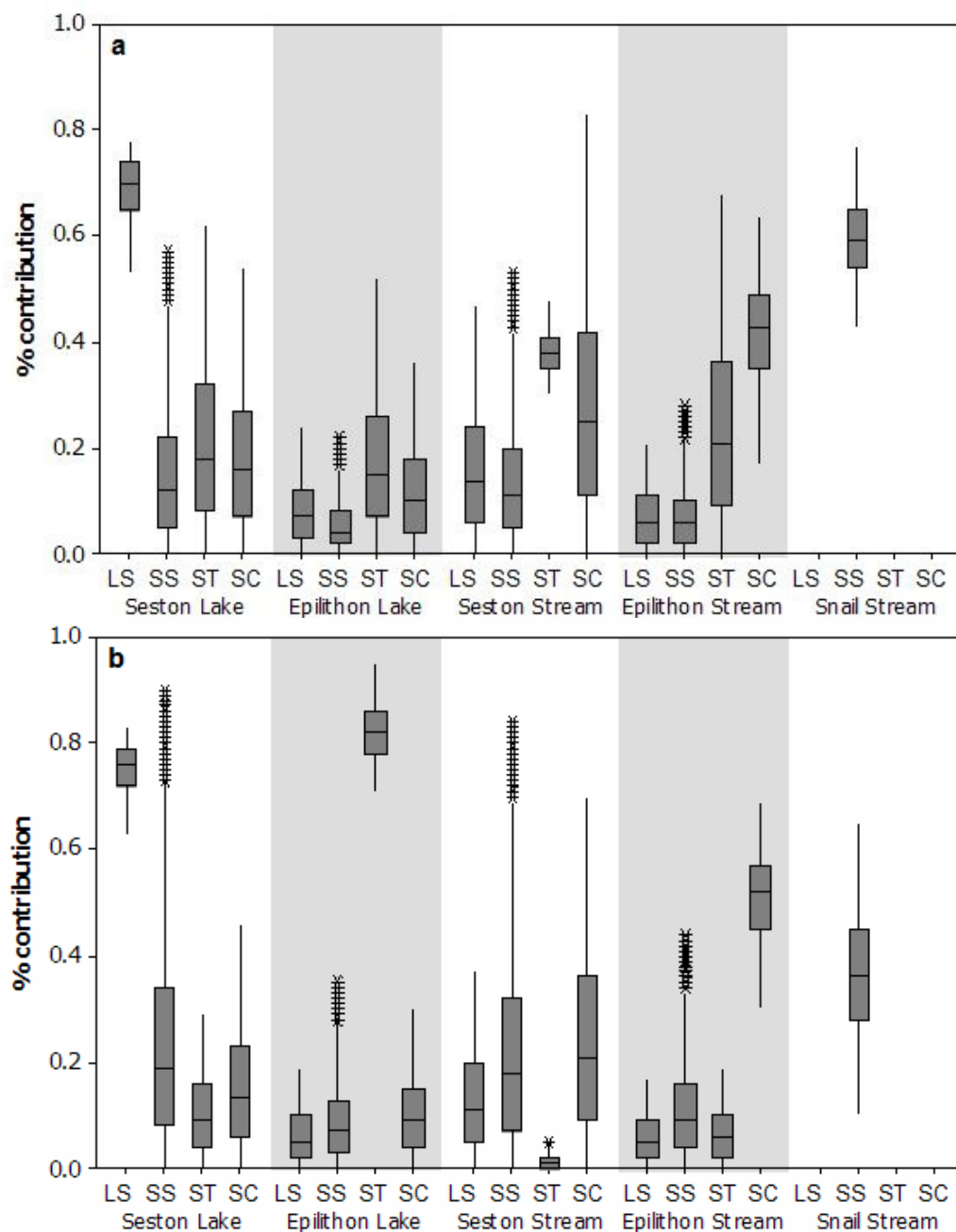


Figure 2.5. Distribution of percent contribution of energy sources to (a) omnivorous and (b) piscivorous fish stable isotope ratios generated using IsoSource in Little Sodus (LS), South Sandy (SS), Sterling (ST), and South Colwell (SC). Lines are median values; boxes are interquartile ranges (IQR); whiskers are the third quartile value+1.5*IQR and the first quartile value-1.5*IQR; asterisks are outliers (asterisks occur in a line immediately above the whiskers).

were lowest. Bowfin always occupied the highest trophic position, followed by adult largemouth bass and Northern pike. Young-of-year largemouth bass trophic position varied the most among embayments, ranging from 2.6 to 3.7. The trophic positions of omnivorous and piscivorous fish groups differed among embayments ($p < 0.001$ for both omnivore and piscivore ANOVAs). Trophic positions of both omnivores and piscivores in South Sandy were significantly higher than those of their counterparts in the other embayments (Figure 2.6). Omnivores in Little Sodus occupied significantly higher trophic positions than in Sterling (Figure 2.6).

Diet contents

The percentages of prey items found in fish diets are based on counts as opposed to prey biomass. Therefore, results do not reflect the actual energetic importance of prey items to the fish. Across embayments, omnivorous fishes ate a greater proportion of zooplankton, amphipods and isopods, and aquatic insects than other prey items (Figure 2.7a). No clear differences were evident between pelagic-dominated and littoral-dominated embayments, although a greater proportion of benthic invertebrates (i.e., amphipods, isopods, and aquatic insects) were consumed in the littoral embayments, Sterling and South Colwell. Among the omnivores, prey fish were consumed primarily by young-of-year largemouth bass and yellow perch, with South Sandy omnivorous fish diets containing the highest percent of prey fish.

In general, zooplankton, prey fish, plants and items categorized as “other” (see Methods) were most common in piscivore diets (Figure 2.7b). Plants primarily occurred as filamentous algae in brown bullhead diets. Consumption of filamentous algae by brown bullhead has been observed in other systems (Kline and Wood 1996).

Table 2.3. Fish species mean trophic positions in each embayment. Data are means with standard errors in parentheses.

Species	Little Sodus	South Sandy	Sterling	South Colwell
Golden shiner	2.9 (0.04)	3.4 (0.04)	2.6 (0.05)	3.0 (0.07)
Brown bullhead < 300 mm	3.0 (0.25)	3.4 (0.10)	2.7 (0.13)	3.0 (0.12)
Pumpkinseed	3.0 (0.04)	3.5 (0.04)	3.0 (0.06)	3.0 (0.07)
Yellow perch	3.2 (0.05)	3.5 (0.04)	3.1 (0.05)	3.1 (0.06)
Largemouth bass < 100 mm	3.2 (0.11)	3.7 (0.07)	2.9 (0.06)	2.6 (0.13)
Brown bullhead \geq 300 mm	3.1 (0.05)	3.7 (0.22)	3.6 (0.13)	3.4 (0.27)
Northern pike	3.7 (-)	4.0 (0.08)	3.6 (0.09)	3.6 (0.15)
Walleye	-	4.1 (0.05)	-	-
Largemouth bass \geq 100 mm	3.6 (0.07)	4.2 (0.17)	3.7 (0.21)	3.7 (0.08)
Bowfin	3.7 (0.12)	4.3 (0.02)	3.7 (0.10)	3.8 (0.10)

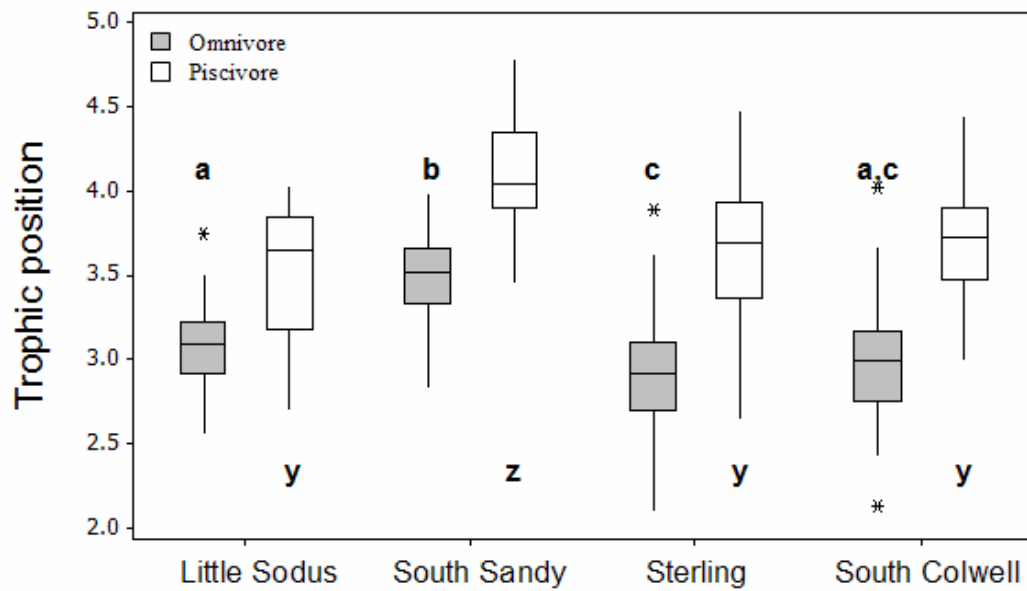


Figure 2.6. Omnivorous and piscivorous fish trophic position distribution in each embayment. Lines are medians; boxes are IQR; whiskers are third quartile value +1.5*IQR and first quartile value -1.5*IQR; asterisks are outliers. Significant differences between omnivorous fish trophic positions are indicated with letters a-c; significant differences between piscivorous fish trophic positions are indicated with letters y and z.

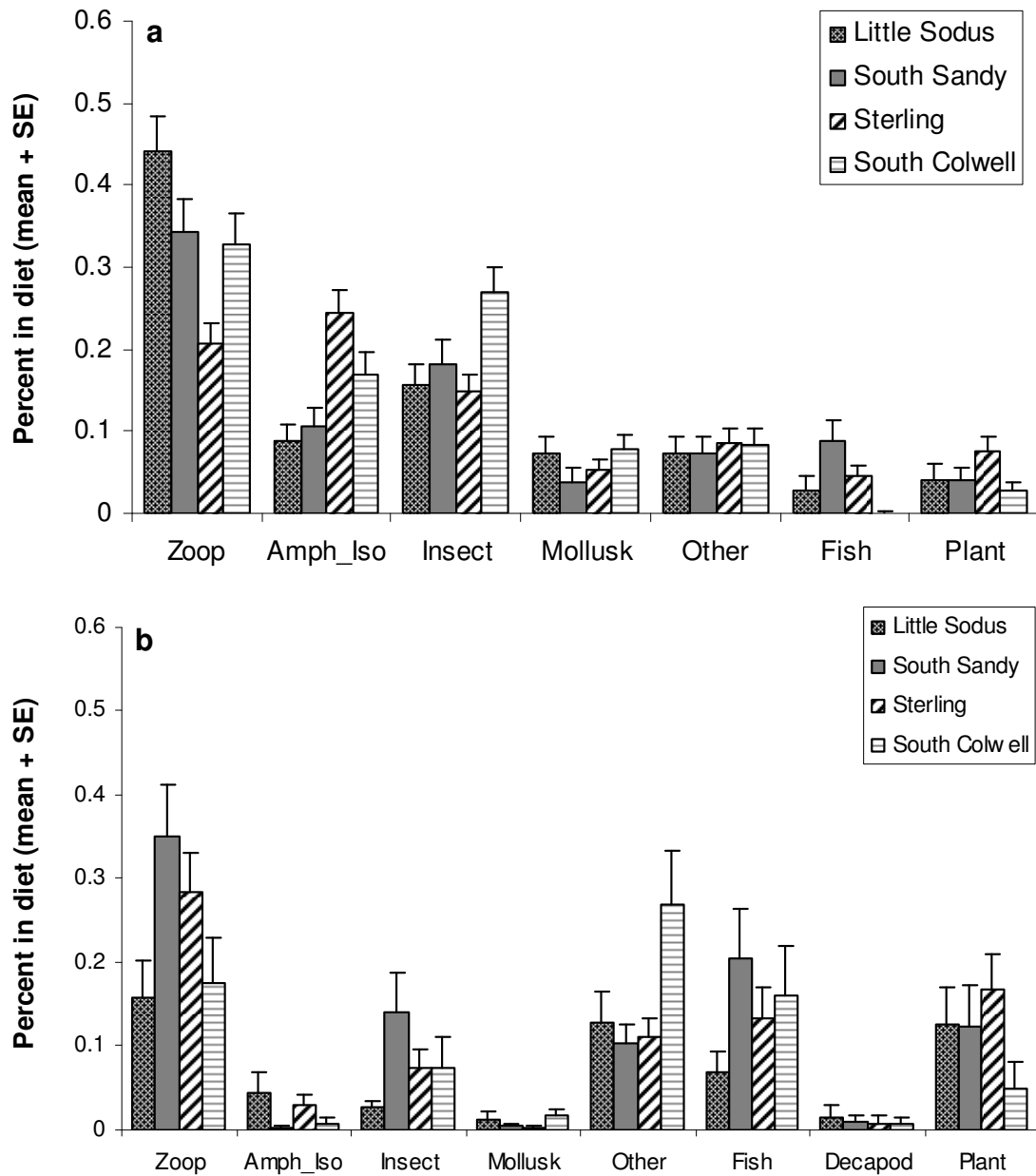


Figure 2.7. Percent of diet items in (a) omnivorous and (b) piscivorous fish stomachs (mean + SE). Percent plants are percent stomach volume; percent of all other diet items are based on numbers in diet of the remaining percent volume. "Other" includes Hydrachnidia, oligochaetes, unidentifiable invertebrates, and organic materials such as eggs; "plant" includes vascular plant, algal, and detrital materials.

Both zooplankton and vascular plant pieces found in the stomachs of piscivores may have been captured incidentally while preying on invertebrates or fish. Some zooplankton could have come from prey fish stomachs; however, care was taken during processing to insure that prey fish stomachs were kept intact. Similar to omnivores, no patterns in piscivore diet contents existed between pelagic and littoral embayments. For example, piscivores in South Sandy consumed the highest percentage of fish among embayments, whereas Little Sodus piscivores consumed the lowest proportion (Figure 2.7b).

Discussion

We found that embayment food webs differed in both the extent of external spatial coupling with their watersheds and Lake Ontario and the extent of internal spatial coupling between littoral and pelagic habitats. Hydrologic connectivity to adjacent ecosystems determined food web uptake of external subsidies in general, while macrophyte density and distribution, as determined by morphometry, resulted in spatial heterogeneity in uptake of external subsidies. Fish community reliance on pelagic and littoral subsidies primarily was a function of depth profile (i.e., morphometry).

We relied on both seston $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to identify relative contributions of watershed and Lake Ontario subsidies to embayment food webs. In the absence of a watershed stable isotope signal, knowledge of watershed land use aided in our interpretation of these data. We predicted that the isotope ratios of seston incorporating N and C from forested watershed inputs would be less enriched in ^{15}N and, to a lesser extent, ^{13}C than those of seston incorporating inputs from more human-

impacted watersheds. As predicted, seston were less enriched in South Sandy and South Colwell, both embayments draining watersheds with predominantly forested land use.

The degree to which the base of an embayment's food web incorporated subsidies from each system influenced the nature of its connection with its watershed and Lake Ontario. We had predicted South Sandy and Sterling seston would primarily incorporate watershed subsidies, Little Sodus seston would incorporate Lake Ontario subsidies, and South Colwell seston would rely on inputs from both adjacent systems fairly equally. As predicted, South Sandy incorporated subsidies almost exclusively from its watershed. In contrast, the other three embayments incorporated inputs from both their watersheds and Lake Ontario. Seston uptake of both types of external subsidies was most surprising in Little Sodus. Hydrodynamics indicate that Lake Ontario is the primary source of water to Little Sodus, due to negligible water flow from its watershed (Rueda and Cowen 2005). However, we were able to detect the incorporation by seston of subsidies from the residential, riparian zone. Presumably, riparian inputs have higher nutrient concentrations than Little Sodus and Lake Ontario water, which may have increased their importance to primary producers (Polis et al. 1997).

Additional evidence for the incorporation of both watershed and Lake Ontario energy sources was provided by spatial heterogeneity in seston stable isotope ratios in all embayments except South Sandy. In general, stream site seston incorporated watershed subsidies to a greater extent than lake site seston; similarly, lake site seston incorporated Lake Ontario subsidies to a greater extent than stream site seston. We

expected to see spatial heterogeneity in South Colwell, but not in Sterling where we predicted high discharge and levels of nutrient and energy inputs from the watershed would result in greater seston uptake of watershed subsidies than Lake Ontario subsidies at both sites within the embayment. Sterling seston was depleted in ^{13}C overall, but particularly at the stream site. Greater algal uptake at the stream site of DIC derived from watershed sources, such as decomposed terrestrial plant material (Cole et al. 2006), could explain this result. Alternate possibilities are spatial differences in seston utilization of autochthonous DIC from decomposed vascular plant material in the embayment (Keough et al. 1996, Post 2002, Sierszen et al. 2004) or biogenic methane (Sierszen et al. 2004, Hershey et al. 2006).

Spatial differences in seston isotope ratios provide additional insight into how hydrology and morphometry can interactively influence embayment openness and the degree to which embayment food webs receive external subsidies. For example, embayment morphometry determines habitat availability to macrophytes, and dense macrophyte beds in Sterling and South Colwell appeared to prevent incoming Lake Ontario and watershed water from mixing evenly throughout the embayments. As a result, differences in stable isotope ratios were fairly pronounced between lake and stream sites. In pelagic Little Sodus, spatial differences between stream and lake site seston could arise from slow or incomplete mixing of water throughout the embayment due to its large size and dependence on seiche-induced Lake Ontario water inputs.

Internal spatial coupling between littoral and pelagic habitats also differed among embayments. As hypothesized, fish communities in the two pelagic systems, Little

Sodus and South Sandy, relied almost exclusively on pelagic energy sources. We estimated that over 70% of fish energy derived from lake and stream seston. In contrast to the pelagic embayments, the fish community in Sterling, a littoral embayment, obtained energy from a combination of pelagic and littoral pathways, with about 60% of its energy attributed to pelagic sources. We were unable to accurately quantify the percent energy contribution from each habitat in the other littoral embayment, South Colwell, due to overlap of pelagic and littoral $\delta^{13}\text{C}$ values. However, fish diets in South Colwell showed that fishes consumed a combination of pelagic and littoral prey.

In South Sandy, seston stable isotope ratios were more enriched than those of some of the fish tissue, potentially because our seston time series did not capture the entire range of temporal variability in carbon stable isotope ratios (Post 2002). As a result, we needed to include the stream snail isotope values as a possible energy source (i.e., baseline) in South Sandy to estimate percent contributions of pelagic versus littoral energy to the fish community using the Isosource program (despite not being able to use snail and zebra mussel isotope ratios as our pelagic and littoral baselines). Although snail tissue typically reflects littoral energy sources, stable isotope ratios for all snails in South Sandy were most closely aligned with seston values, suggesting reliance on pelagic energy. Therefore, we assumed the large amount of energy attributed to the stream snail signal reflected pelagic energy to the fish community.

Our assumption that stream snail energy contributions to the fish community equate to pelagic energy contributions could be misleading for two reasons. First, as opposed to reflecting pelagic subsidies to littoral habitat, less enriched stream site snail C stable

isotope ratios could have resulted from snails directly consuming particulate detrital C inputs from the watershed. The similar C stable isotope values observed in phytoplankton would be explained by uptake of dissolved watershed inputs (Cole et al. 2006). However, if this were the case, we would have expected similar epilithon C stable isotope values as well, because epilithon included both benthic algae and detritus. Second, depleted ^{13}C values of fish tissue compared to ^{13}C values of seston could reflect fish consumption of profundal prey (e.g., deep-dwelling chironomids), which tend to be less enriched in ^{13}C (Vander Zanden and Rasmussen 1999). We think this alternate explanation is less likely, because fishes in Little Sodus, which also has substantial profundal habitat, were not similarly depleted in ^{13}C .

Greater reliance by the fish community on pelagic energy in the relatively large, deep study embayments suggests that fish community incorporation of pelagic and littoral subsidies primarily was a function of depth profile (i.e., morphometry). This differs from Sierszen et al. (2006), who found that fish reliance on planktonic C in Lake Superior coastal wetlands was best explained by water residence time and, to a lesser extent, nutrient loading. Possibly, water residence time and nutrient loading influence fish community reliance on internal energy subsidies within the constraints of morphometry. However, omnivorous fishes in Sterling incorporated pelagic energy to a greater degree than predicted, based on Sierszen et al.'s (2006) findings that fish reliance on pelagic C increases with water residence time.

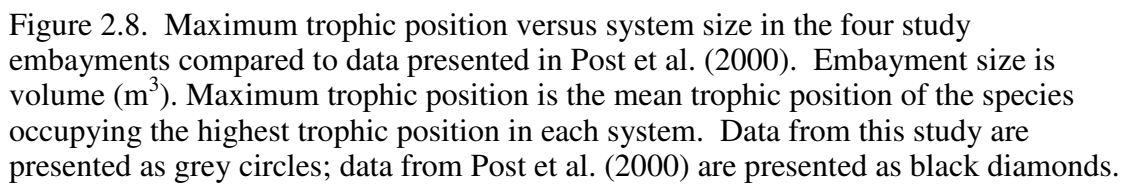
Fish movement between embayments and Lake Ontario also complicates our interpretation of energy flow to the fish community. In Sterling, energy source contributions differed for omnivores and piscivores, with piscivores estimated to have

acquired almost 80% of their energy from lake epilithon. Piscivore estimates may be compromised by fish migration between Sterling and Lake Ontario. Sterling seston and epilithon were much less enriched in ^{13}C than those of Lake Ontario and the other embayments. Consequently, adult piscivore tissue enriched in ^{13}C could indicate that these fishes spent time in nearshore Lake Ontario or neighboring embayments, where their prey would be more enriched in ^{13}C . Fish movement between Lake Superior and coastal wetlands was detected with stable isotopes by Keough et al. (1996) and Sierszen et al. (2006). Additionally, yellow perch captured during September 2003 for a separate study were enriched in ^{13}C (-25.7 to -17.5 ‰), suggesting they had recently immigrated to Sterling (K. Arend, unpublished data). Fish immigration probably occurred to varying degrees in the other embayments as well, but could not be detected due to similarities in seston and epilithon C stable isotope values among embayments and Lake Ontario.

Interestingly, energy source contributions to individual fish species appeared to be more variable in the littoral embayments than in the pelagic systems, based on C stable isotope ratios. In Sterling, this could be due to fish immigration, as described above. In both Sterling and South Colwell, variability among fish energy sources could stem from littoral habitat being more structurally complex and thus able to support a greater diversity of prey than pelagic habitat (Brazner and Beals 1997). Individual fish species may have been able to occupy separate niches or forage on more preferred prey; however, diet data do not indicate large differences in prey consumption among embayments, and we do not have sufficient data to estimate fish species' feeding electivities.

Similar fish diets among embayments suggest that fish were not limited to or did not specialize on pelagic prey items in Little Sodus and South Sandy. Instead, most organisms in Little Sodus and South Sandy food webs, including mussels and snails, may rely on carbon fixed by phytoplankton. These results support our predictions of greater reliance on pelagic energy with increased lake depth and settling of phytoplankton in littoral habitats (Vadeboncoeur et al. 2002). Similarity in fish diets among embayments also reduces the likelihood that fish in the littoral embayments were more omnivorous than in the pelagic systems. Therefore, any differences in maximum trophic position among embayments are unlikely to be related to the degree of omnivory in the fish community.

With the exception of South Sandy, embayment maximum trophic positions fell within the range presented by Post et al. (2000) for systems of their size (Figure 2.8). Maximum trophic position in South Sandy was slightly higher than what was observed for similar-sized systems by Post et al. (2000). Each fish species in South Sandy had higher trophic positions than its counterpart in the other embayments. South Sandy has the largest populations of predatory zooplankton, including *Leptodora kindtii*, which may add an additional trophic level to the food web. Alternatively, South Sandy fish would appear to occupy higher trophic positions if they consumed prey more enriched in ^{15}N than predicted based on seston and epilithon N stable isotope ratios. For example, fish in South Sandy may have consumed profundal prey (e.g., *Chaoborus* spp. or deeper-dwelling Dipteran fly larvae), which tend to be enriched in ^{15}N (Vander Zanden and Rasmussen 1999, Lepak et al. 2006). Additionally, if fish spent time in Lake Ontario, where seston and epilithon are enriched in ^{15}N compared to South Sandy, trophic position would appear higher. We think the first explanation



is most likely, because both juvenile and adult fish occupied higher trophic positions. Furthermore, fishes in Little Sodus, which also has substantial profundal habitat, are not similarly enriched in ^{15}N . We cannot rule out fish immigration to South Sandy, because it is connected to an adjacent embayment with a direct connection to Lake Ontario. However, all species and size classes were enriched in ^{15}N , suggesting even juvenile and older fish residents in South Sandy occupied higher trophic levels.

This study adds to the growing body of evidence that hydrology, morphometry, and watershed land use operate at multiple spatial scales and interactively impact energy flow to and within aquatic ecosystems. Characterizing external and internal energy and nutrient subsidies to and subsequently through embayment food webs is important for several reasons. As freshwater estuarine systems, embayments influence the transfer of materials from watersheds to the Great Lakes, while also providing valuable habitat for resident, spawning, and juvenile fishes. As physicochemically diverse systems containing similar species composition, embayments provide a good setting for investigating how hydrology, land use, and morphometry influence aquatic food web dynamics. Finally, as systems subject to both anthropogenic and natural environmental change, embayments provide insight into how impacts on spatial coupling within and among aquatic systems affect food web dynamics such as energy flow and food web structure.

CHAPTER 3: Factors influencing yellow perch (*Perca flavescens*) population structure

Abstract

Yellow perch populations in Lake Ontario embayments differ in relative abundance, size structure, and the degree to which they rely on pelagic versus littoral energy sources. We hypothesized that differences in yellow perch size structure between embayments dominated by pelagic habitat versus littoral habitat are driven by differences in prey availability. To test this hypothesis, we developed an energy budget model to predict yellow perch growth in two pelagic-dominated and two littoral-dominated embayments, based on the biomass, composition, and energetic quality of prey consumed by yellow perch. Model predictions of size at age and annual growth rates were compared with otolith-based estimates for each population. Yellow perch in all embayments grew slowly, suggesting prey limitation across populations. Model predictions matched growth and size at age in the littoral embayments, supporting our hypothesis. In contrast, the model predictions underestimated growth and size at age in the pelagic embayments. More rapid growth and larger size at age than predicted in pelagic embayments compared to littoral embayments could be due to size selective mortality from higher predation pressure on yellow perch. Despite relying on different energy sources (pelagic versus littoral), yellow perch in both types of embayments consumed a combination of pelagic (zooplankton) and littoral (benthic invertebrate) prey. As opposed to altering prey availability, embayment type possibly influenced yellow perch growth and population size structure via effects on the abundance of predators, such as walleye, and thus the relative influence of bottom-up and top-down processes.

Introduction

Fish community structure (abundance, biomass, size structure) and function (trophic interactions, energy and nutrient flow) are determined by habitat and resource availability and predator-prey interactions. In turn, habitat and resource availability are influenced by ecosystem features including watershed land use, connectivity to adjacent ecosystems, morphometry, and habitat complexity. While effects of nutrient loading and cultural eutrophication on fish community structure and function have long been recognized, a more recent body of work has begun to explore the general importance of both nutrient and energy subsidies to fish communities. Subsidies include energy and nutrients of allochthonous origin (Carpenter et al. 2005, Cole et al. 2006) as well as energy and nutrients transported between habitats within a system (Vander Zanden and Vadeboncoeur 2002, Sierszen et al. 2006). Both external and internal (inter-habitat) subsidies have been hypothesized to influence food web dynamics by altering predator-prey interactions (Polis and Strong 1996, Vander Zanden and Vadeboncoeur 2002), with effects likely dependent on food web structure, the amount of subsidies, and the trophic levels at which subsidies are incorporated into the food web (Carpenter et al. 2001, Huxel et al. 2002, Cole et al. 2006).

One of the most common examples of internal subsidization occurs between littoral (i.e., shallow benthic) and pelagic habitat, henceforth referred to as littoral-pelagic coupling. The degree to which littoral-pelagic coupling occurs depends on environmental factors, such as nutrient loading, water residence time, and morphometry (Polis et al. 1997, Vadeboncoeur et al. 2002, Sierszen et al. 2006), and biological factors, including prey availability in each habitat, ontogenetic changes in

fish species feeding and habitat preferences, and how flexible fish are regarding habitat and feeding preferences (Polis et al. 1997, Vander Zanden and Vadeboncoeur 2002). Effects of habitat coupling have been explored both at the community and population levels. At the community level, the focus typically is to better understand factors underlying the relative incorporation of alternate sources of energy (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). At the population level, mechanisms driving habitat coupling and the effects of differences in habitat coupling on fish growth and trophic position have been explored (e.g., Vander Zanden et al. 1999a, Lepak et al. 2006). Effects on population growth and trophic position not only impact population size structure, but also may alter size-structured trophic interactions within the food web and, subsequently, fish community structure. We posit that understanding interactions between environmental factors, habitat coupling, and fish population structure offers mechanistic insight into broader effects of habitat coupling on fish communities.

To test the idea that differences in habitat coupling underlie differences in population size structure and trophic interactions, we focused on yellow perch (*Perca flavescens*) populations in two littoral-dominated and two pelagic-dominated Lake Ontario embayments. Fish communities and populations in the two pelagic-dominated systems obtained the majority (over 70%) of their energy from planktonic sources, whereas communities in the two littoral-dominated communities obtained energy from both planktonic and benthic sources (Chapter 2). Although fish species composition in all four embayments was similar, relative abundance, biomass, and size structure of the entire fish community and of individual species populations, including yellow perch, differed (Chapter 1). We anticipated that differences in littoral-pelagic

coupling among embayments would underlie differences in yellow perch population structure and trophic interactions and, possibly, reflect effects of coupling on overall fish community structure.

Yellow perch are numerically dominant in these systems and, as flexible omnivores that undergo ontogenetic shifts in habitat and diet, play a role in the transfer of energy and nutrients between pelagic and littoral habitats. Yellow perch are located in the middle or near the top of the food web, depending on whether they occur in systems that support larger-bodied piscivorous fishes. As such, yellow perch population dynamics are sensitive to both bottom-up (prey availability) and top-down (predation pressure) controls, with implications for fish community trophic interactions and food web dynamics in Lake Ontario embayments. Wide variation in size structure among yellow perch populations has been attributed to physicochemical factors, including temperature and nutrient loading, density-dependent intraspecific competition, and abundance or detectability of benthic invertebrates (Diana and Salz 1990, Heath and Roff 1996, Schaeffer et al. 2000). For example, decreased growth rates in young-of-year (YOY) yellow perch have been observed with early shifts to benthic prey, mostly in response to large declines in large cladoceran zooplankton abundance (Mills and Forney 1981, Prout et al. 1990), but also because of stratification (Wu and Culver 1992). However, slow growth also has been linked to the inability of older YOY yellow perch to shift to benthic prey (Post et al. 1997) and poor detection of benthic prey (Heath and Roff 1996). Slow yellow perch growth rates and development of stunted (i.e., small-bodied, early maturing) populations (Persson 1983, Heath and Roff 1996) could expose yellow perch to greater predation pressure and size-selective mortality (Wu and Culver 1992, Campbell 1998, Schaeffer et al. 2000). Nielsen

(1980) attributed young yellow perch (ages 1 and 2 years) mortality in Oneida Lake, NY, to walleye predation, and found predation rates were influenced partly by yellow perch length.

We expected that variation in adult (age 1 year and older) yellow perch population size structure among embayments was mainly due to effects of habitat and prey availability (i.e., bottom-up effects) on growth. Specifically, we hypothesized yellow perch in the two littoral-dominated systems would grow faster because of the availability of both pelagic (zooplankton) and littoral (benthic invertebrate) energy. In both pelagic-dominated systems, we expected growth to be slow due to low availability of littoral prey. In one of the pelagic-dominated systems (South Sandy, see below), we expected top-down effects to be important, because, unlike the other embayments, it supported a large walleye population. Walleye have been shown to consume between 28 and 90 % of YOY yellow perch (Hartman and Margraf 1993), so we hypothesized that dominance of YOY perch followed by a sharp decline in relative abundance reflected high mortality from predation in this embayment. To test these hypotheses, we compared otolith-based estimates of yellow perch age and growth with growth predictions from an energy budget model based on field observations of yellow perch prey ration and composition.

Methods

Study sites

The four study embayments are located along the southeastern shore of Lake Ontario in New York State (Figure 3.1). Little Sodus and South Sandy are both fairly large and deep embayments, with little vegetative cover; Sterling and South Colwell are

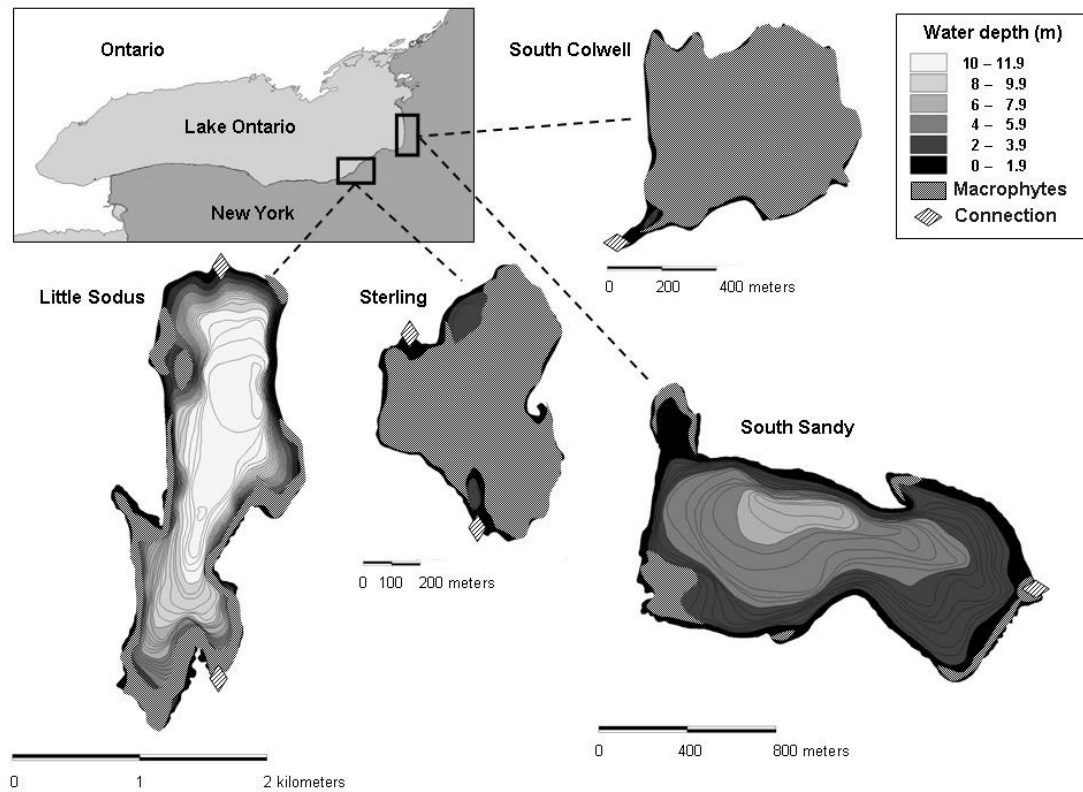


Figure 3.1. Location map and bathymetric maps of study sites. Depth contour lines are in meters. Macrophyte beds are shown as hatched, grey areas. Diamonds indicate where embayments are connected to Lake Ontario and their watersheds. South Sandy does not have a direct, surface-water connection with Lake Ontario. South Colwell lacks a single connection to its watershed because it drains a wetland complex.

Table 3.1. Embayment morphometric and biological characteristics. YP = yellow perch; Pred:YP is the ratio of predator CPUE to YP CPUE.

Embayment	Little Sodus	South Sandy	Sterling	South Colwell
Surface area (km ²)	4.06	1.88	0.92	0.57
Volume (m ³ ·10 ⁵)	193	38.7	7.79	7.15
Maximum depth (m)	11	6.4	3.0	3.0
% littoral area	0.29	0.65	1.00	1.00
YP CPUE (#/min)	0.96	0.45	1.6	1.2
YP BPUE (g/min)	23.0	5.47	35.3	16.9
YP trophic position	3.17	3.53	3.14	3.12
Proportion of pelagic energy to YP	70	85	60	35
Proportion of littoral energy to YP	20	10	35	60
Ratio of predator to YP CPUE				
< 90 mm TL	13.4	1.24	3.64	2.56
90-119 mm TL	0.208	1.41	0.264	0.113
≥ 120 mm TL	0.094	0.960	0.212	0.289
Frequency of prey fishes and YP				
< 90 mm TL	0.043, 0.048	0.304, 0.252	0.255, 0.084	0.333, 0.129
90-119 mm TL	0.041, 0.222	0.129, 0.077	0.224, 0.136	0.095, 0.257
≥ 120 mm TL	0.231, 0.414	0.124, 0.113	0.136, 0.163	0.093, 0.093

small, shallow, and dominated by dense macrophyte beds (Table 3.1). All embayments are open to exchange with Lake Ontario either directly or indirectly (Figure 3.1). Both Little Sodus and Sterling have man-made channels connecting them to Lake Ontario, while South Colwell has a natural channel that can be open or closed. South Sandy is indirectly connected to Lake Ontario through an adjacent embayment.

Our previous work indicates that yellow perch relative abundance, biomass, and size structure differ among the four embayments. Relative abundance and biomass is highest in Sterling and lowest in South Sandy (Table 3.1). The South Sandy population is dominated by small, YOY yellow perch, whereas fish are more normally distributed across size classes in Little Sodus, Sterling, and South Colwell (Figure 3.2). Little Sodus supports the greatest proportion of large-bodied yellow perch (Figure 3.2). Prey availability also differs among embayments, with Little Sodus supporting over twice as much benthic invertebrate biomass as the other embayments (K. Arend, unpublished data). Mean zooplankton biomass estimates for May through October 2002 suggest standing biomass of zooplankton in Sterling is much lower than in the other three embayments (R. Doyle-Morin, Cornell University, unpublished data). Stable isotope analysis showed yellow perch derived the majority of their energy from pelagic sources in Little Sodus and South Sandy, but from a combination of sources in Sterling and South Colwell (Table 3.1; Chapter 2). Additionally, yellow perch mean trophic position is higher in South Sandy than the other embayments (Table 3.1).

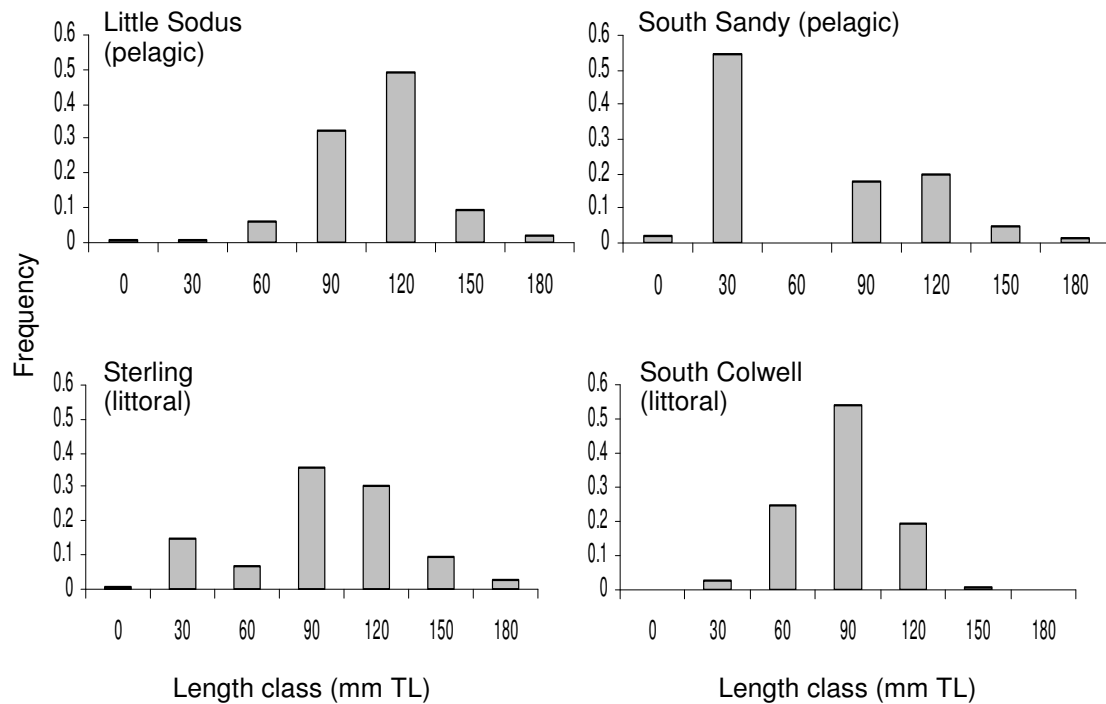


Figure 3.2. Length frequency distributions of yellow perch across 30 mm TL length classes. Yellow perch were collected using a stratified random design during July 2001-2003 as part of a related study (see Chapter 1).

Prey ration and composition

Field estimates of yellow perch mean prey ration ($\text{g wet} \cdot \text{g wet}^{-1} \cdot \text{d}^{-1}$) across embayments and prey composition within each embayment were used to estimate biomass consumed ($\text{g wet} \cdot \text{g wet}^{-1} \cdot \text{d}^{-1}$) by yellow perch as a function of yellow perch weight. We collected 20-40 individuals in each embayment during the summers of 2003 and 2004 using boat-mounted electrofishing equipment (methods described in Chapter 1). Yellow perch are diurnal foragers, typically with peak stomach fullness occurring around dusk (Nakashima and Leggett 1978, Persson 1983, Grant and Kott 1999). To maximize the likelihood of capturing fish with fairly full stomachs, the majority of fish were collected between 16:00 and 22:00 hours. Prey items present in the stomach only were identified to the lowest practical taxon, counted, and measured (body length, head length, head width, or telson width) to the nearest 0.01 mm using an ocular micrometer. Benthic invertebrate prey size was converted to biomass (mg dry weight) using equations from Benke et al. (1999) (Appendix 3.1). Zooplankton biomass estimates ($\mu\text{g wet weight}$) were based on equations in Bottrell (1976) (Appendix 3.2). *Leptodora kindtii* and mite biomasses were assumed to be 0.027 mg wet weight (R. Doyle-Morin, Cornell University, personal communication) and 0.20 mg dry weight (S. Miehl, Great Lakes Fishery Commission, personal communication), respectively. For benthic invertebrates and mites, dry weight was converted to g wet weight using % water (dry:wet mass) values (Cummins and Wuycheck 1971, Hanson et al. 1997) (Appendix 3.3).

Daily ration (C_{24} ; $\text{g wet} \cdot \text{g wet}^{-1} \cdot \text{d}^{-1}$) was estimated as follows (Eggers 1977):

$$C_{24} = 24 \cdot R \cdot S_{\text{mean}} \quad (1)$$

where R is the evacuation rate per hour of prey from the stomach and S_{mean} (g wet·g wet⁻¹·d⁻¹) is the mean biomass of stomach contents throughout the day. R was estimated according to Persson (1979) as:

$$R = a \cdot e^{b \cdot T}$$

where $a=0.02$, $b=0.14$ (for *P. fluviatilis*), and T =embayment temperature (°C) on the capture date.

Based on yellow perch foraging behavior, we assumed: (1) perch stomachs were full at the time of capture; (2) perch consuming invertebrate prey have full stomachs for 10 hours each day and half-full stomachs the remaining 14 hours (i.e., period of prey digestion), which simplifies to full stomachs for 17 hours per day; (3) perch consuming fish prey feed only once per day, digesting the prey over 24 hours. Therefore, for non-fish prey we estimated S_{mean} as:

$$S_{mean} = \frac{17 \cdot W_{totprey}}{24 \cdot W_{fish}},$$

where $W_{totprey}$ is the total weight of prey in the stomach; $W_{totprey}$ has units g·d⁻¹; and W_{fish} is the weight (g) of the fish. For fish prey, $S_{mean} = W_{totprey} / 24 \cdot W_{fish}$.

The water temperature (T) on the date each fish was collected was calculated using embayment-specific temperature curves. Temperature curves for each embayment were determined by fitting a curve to embayment surface water temperatures collected

weekly from May through October 2001 and 2002 and biweekly from May through October 2004 (Bain 2007) (Appendix 3.4).

We calculated daily ration (C_{24}) for each fish and estimated the relationship between fish biomass and daily ration for all embayments combined. We used nonlinear least squares (NLS) regression to fit the following power function to the data and estimate coefficient means and upper and lower 95% confidence intervals.

$$\text{Ration} = aW_{fish}^b,$$

where Ration is the NLS estimate of C_{24} at a given yellow perch biomass. Ration was converted to its energetic equivalent in yellow perch biomass (B_{cons} ; g wet·g wet⁻¹·d⁻¹), accounting for embayment-specific prey composition in yellow perch diets, as follows.

$$B_{cons} = \frac{E_{cons}}{4186}, \quad (2)$$

where 4186 is the energy density of yellow perch J·g wet⁻¹; Hanson et al. 1997), and E_{cons} is the mean energy consumed (J·g wet⁻¹·d⁻¹) by a yellow perch in each embayment. We estimated E_{cons} from captured yellow perch stomach content data. We divided prey items into 7 categories and calculated the mean proportion of each prey category eaten in each embayment. We calculated embayment E_{cons} as:

$$E_{cons} = \text{Ration} \cdot \sum_i^7 (PP_i \cdot ED_i),$$

where PP_i is the mean proportion of prey i consumed by yellow perch in a particular embayment and ED_i is the energy density ($J \cdot g \text{ wet}^{-1}$) of prey i (Table 3.2).

Age and growth

Yellow perch were collected from all four embayments during April and September 2005. Fish selected to span a range of length classes were measured and weighed in the field, stored on ice in individually marked bags, and returned to the lab where they were frozen until further processing. In the lab, a subset of fish was dissected to remove the fish's sagittal otoliths and identified as male, female, or juvenile. One otolith from each fish was embedded in epoxy and cross sectioned using a double-blade Isomet saw. We then glued each cross section to a slide and polished it in preparation for age and growth estimates. The number of annuli on each otolith was counted by two experienced readers to determine fish ages. A third reader was used when ages from the first two readers disagreed (5% of all otoliths). We estimated fish size at age and annual growth rates by using the Q Capture Pro image analysis system (version 5.0.1.26; QImaging) to measure the distances from the focus to each annuli along two axes of the otolith: (1) from the focus to the dorsal tip, along the distal edge; and (2) from the focus to the proximal edge, along the dorsal ridge of the sulcus. Size at age (L_a ; mm total length [TL]) was back-calculated according to Campana (1990) as follows:

$$L_a = L_c + (O_a - O_c) * (L_c - L_o) * (O_c - O_o)^{-1},$$

where L_a is the back-calculated length at age a ; O_a is the length of the otolith (focus to annulus) at age a ; L_c and O_c are the length of the fish and otolith (focus to edge),

Table 3.2. Proportion and energy density ($\text{J}\cdot\text{g}^{-1}$) of prey categories consumed by yellow perch in each embayment. All values for energy density are from Hanson et al. (1997), except for mollusks and mites, which are from Cummins and Wuycheck (1971). The value for mites is a mean value of two terrestrial arachnids.

Prey category	Little Sodus	South Sandy	Sterling	South Colwell	Energy density
Amphipod/Isopod	0.30	0.15	0.56	0.36	4429
Zooplankton	0.16	0.33	0.07	0.11	2500
Diptera	0.24	0.17	0.06	0.19	1700
Other Insect	0.15	0.08	0.06	0.22	4600
Fish	0.06	0.25	0.20	0.02	2512
Mollusk	0.03	0.00	0.00	0.07	2010
Mite	0.05	0.03	0.05	0.04	5025

respectively, at capture; and L_o and O_o are the length of the fish and otolith at the biological intercept. The biological intercept for each embayment was determined as the smallest age 0+ yellow perch captured.

Lengths were converted to weights (g) using embayment-specific length-weight relationships (Appendix 1.1). Annual growth rates ($\text{g}\cdot\text{d}^{-1}$) were calculated from the size at age data for each embayment. We assumed larval fish begin feeding on 15 May based on spawning dates and time to hatch and yolk-sac absorption in Rose et al. (1999) and Post and McQueen (1988). For age 0+ fish captured during the fall of their first year, age in days was estimated by subtracting the Julian date of first feeding from the Julian date of capture. For age 0+ fish collected during the spring of their second year, age in days was estimated by subtracting the Julian date of first feeding from the sum of 365 and Julian capture date of year. This method also was used to estimate the fish age in days at age 1 for all fish age 1 and older. Growth rate to age 0+ or 1 was then calculated by subtracting size at hatch from size at age 0+ or 1 and then dividing by the fish's age in days. Growth rates to all other ages were calculated by subtracting the size at age $n-1$ from the size at n and dividing by 365. Finally, we generated age distributions for yellow perch captured during July in 2001 through 2003 for a related study (Chapter 1). An age-length key was generated from otolith length at age estimates. The fish data were grouped into length classes (mm TL) and assigned probabilities for being in each length class accordingly. Probabilities for each age class were summed for all fish and divided by the number of fish.

Model

We developed an energy budget model (Appendix 3.5) to generate growth curves for

adult yellow perch feeding on prey compositions unique to each embayment (Figure 3.3). We modified the basic yellow perch bioenergetics model (Kitchell et al. 1977, Hanson et al. 1997) to include increasing active metabolic costs with greater daily food consumption, metabolic losses to winter metabolism, and energetic losses to gonadal production. We also added dynamically varying allocations of production to somatic growth, energy storage (lipids), and reproduction (gonads) based on the empirically observed allocation patterns. The model equations and parameter values are based on yellow perch bioenergetics models (Kitchell et al. 1977, Boisclair and Leggett 1989, Hanson et al. 1997) and empirical estimates of energy allocation to lipid mass (Hayes and Taylor 1994) and gonadal growth (Hayes and Taylor 1994, Henderson et al. 2000). Yellow perch ration, yellow perch prey composition, and embayment temperature profiles are from data collected from the study embayments. Separate models were built for male and female yellow perch, to account for differences in metabolic costs and energy allocation to gonadal growth.

The basic form of the bioenergetics model developed by Kitchell et al. (1977) is:

$$C = G + W + M$$

where C is the energetic equivalent of prey biomass consumed, G is energy used for somatic and gonadal growth, W includes energetic losses to egestion and excretion, and M includes metabolic costs for maintenance and food ingestion. These terms are all expressed as specific rates ($\text{g wet} \cdot \text{g wet}^{-1} \cdot \text{d}^{-1}$). In the model presented here, G is allocated to three compartments as opposed to two; somatic growth, lipid storage, and gonadal growth. We include 5 state variables in the model: fish biomass, lipid weight,

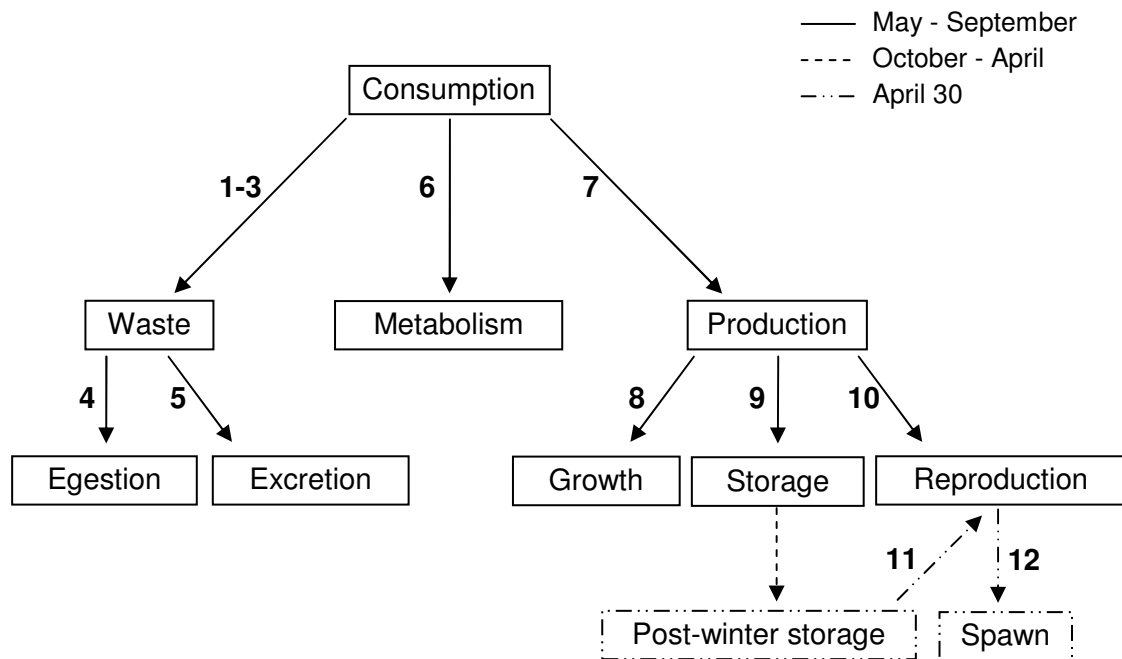


Figure 3.3. Conceptual diagram of the energy budget model used to predict yellow perch growth in each embayment. Numbers correspond with equations described in the text and in Appendix 3.5.

and gonad weight, and the proportions of assimilated energy shunted to lipid and gonad growth. The model is a system of ordinary differential equations that was solved in R (R Core Development Team 2006) using the *lsoda* function in the *odesolve* package (Setzer 2006). The proportions of energy allocated to lipid storage and gonadal growth are determined by requiring that lipid weight equal 15% of somatic weight (Hayes and Taylor 1994) and gonad weight equal 20% of somatic weight for females (Hayes and Taylor 1994, Henderson et al. 2000) and 13% of somatic weight for males (Hayes and Taylor 1994). The proportion of energy allocated to somatic growth is the proportion of G remaining after allocation to lipids and gonads.

Simulations for individual fish were run for 7 years, starting with age 0+ fish. We chose 7 years because otolith data indicate yellow perch reach a maximum age of 7 years in these embayments. Initial perch biomass was based on age 0+ yellow perch weights for each embayment. Mean age 0+ length (mm TL) was calculated for all age 0+ fish based on otolith analysis. Lengths were converted to weights (g) using embayment-specific length-weight regressions (Appendix 1.1). We assumed lipid mass was equal to 4% of body weight at the beginning of the simulation and that gonad development had not yet begun. Within each year, the model was solved from 1 May through 30 September, when the majority of food consumption occurs (Persson 1983). We varied ration each year by assigning a value of coefficient a in the power function using a random number generator with mean equal to the point estimate of coefficient a (described above) and standard deviation equal to 0.01. We randomly varied ration values to reflect that fish daily ration varies under natural conditions (Nakashima and Leggett 1978, Persson 1983), which leads to variability in growth

rates among individual fish. Immediately prior to spawning, a certain proportion of lipids were lost to metabolic demands for overwinter survival and another proportion was shunted to gonad biomass. Spawning is the final time step of each year, at which time fish gonad biomass drops to 2% of body biomass and lipid biomass to 4% of body biomass (Hayes and Taylor 1994). To account for slower observed growth rates of males compared with females, males were assumed to have higher activity rates than females. We ran 100 simulations for each embayment, to produce a “population” of fish. Population simulations were run separately for 100 female and 100 male fish.

Predation pressure

We used the ratio of predators to yellow perch in three yellow perch length classes as an index of predation pressure. Predators included adult yellow perch, bowfin (*Amia calva*), grass pickerel (*Esox americanus vermiculatus*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreum*). Catch per unit effort (CPUE, #/min) and total length data from surveys conducted in July 2001-2003 (Chapter 1) were used to calculate the CPUE of predators in each embayment capable of consuming yellow perch between 20-89 mm TL (i.e., YOY), 90-120 mm TL, and at least 120 mm TL. Yellow perch vulnerability to predation was calculated as the maximum yellow perch length a predator could consume (Table 3.3). Maximum lengths of yellow perch vulnerable to predation by adult yellow perch, walleye, largemouth bass, and northern pike were based on the literature (Table 3.3). We assumed smallmouth bass were able to consume prey of similar size proportion as largemouth bass, and bowfin and grass pickerel were able to consume prey of similar size proportion as walleye greater than 200 mm TL. We calculated the ratio of predators to prey by summing the CPUE of

Table 3.3. Yellow perch maximum size of vulnerability to predation by several piscivore species. Abbreviations are as follows: TL, mm total length; yellow perch, YP; walleye, WE; largemouth bass, LMB; smallmouth bass, SMB; northern pike, NP; bowfin, BF; and grass pickerel, GP.

Predator	Predator length class (mm TL)	Vulnerable YP maximum length (mm TL)	Source
Adult YP	> 90	$0.2 * L_{\text{adultYP}}$	Rose et al. 1999. Ecol. Mon. 69:127-154
WE	< 200	$0.6 * L_{\text{WE}}$	Rose et al. 1999
WE	≥ 200	$0.4 * L_{\text{WE}}$	Rose et al. 1999
LMB	< 100	$0.3 * L_{\text{LMB}}$	Olson. 1996. Ecology 1:179-190
LMB	≥ 100	$0.5 * L_{\text{LMB}}$	Katano et al. 2002. Ich. Res. 49:392-396
SMB	< 100	$0.3 * L_{\text{SMB}}$	n/a
SMB	≥ 100	$0.4 * L_{\text{SMB}}$	Fritz and Pearsons. 2006. TAFS 135:853-860
NP	n/a	$0.5 * L_{\text{NP}}$	Nilsson and Brönmark. 2000. Oikos 3:539-546
BF	n/a	$0.4 * L_{\text{BF}}$	n/a
GP	n/a	$0.4 * L_{\text{GP}}$	n/a

predators capable of eating each length class of yellow perch with the CPUE of predators capable of eating any smaller length classes and dividing by the total CPUE of yellow perch in each vulnerable length class. To assess the relative availability of non-yellow perch prey fishes (hence prey fishes) versus yellow perch to predators, we calculated the frequencies of prey fishes and yellow perch in each of the three length classes using catch data from surveys conducted in July 2001-2003 (Chapter 1). Prey fishes included all non-piscivorous fishes.

Results

Prey ration and composition

Ration ranged from 0 to $0.48 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$, with a mean equal to $0.016 (\pm 0.003 \text{ standard error})$ and median equal to 0.008. Ration was negatively correlated with fish size (Figure 3.4). Power coefficient a had an estimated value of 0.04, with lower and upper 95% confidence intervals equal to 0.03 and 0.06, respectively. The estimated value of coefficient b was -0.39, and lower and upper 95% confidence intervals were equal to -0.57 and -0.20, respectively. Mean prey composition across fish sizes varied among embayments, with zooplankton, amphipods, Dipterans, and fish prey occurring most frequently (Table 3.2). The proportion of amphipods in pelagic-dominated South Sandy yellow perch stomachs was lower than in the other embayments. Fish prey were prevalent in South Sandy and littoral-dominated Sterling yellow perch. In littoral-dominated South Colwell, yellow perch relied most heavily on benthic invertebrates (amphipods and aquatic insects).

Growth

We obtained otoliths from 67, 72, 73, and 69 fish in Little Sodus, South Sandy,

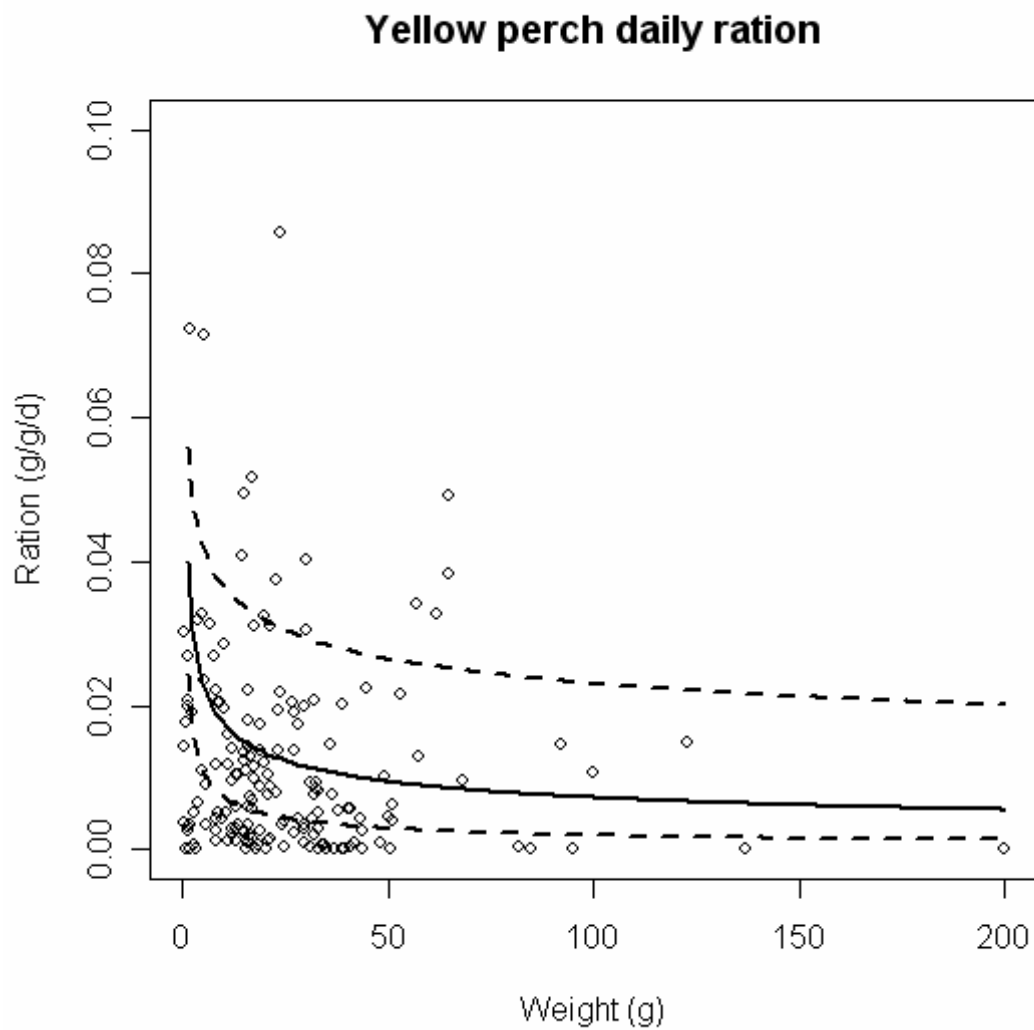


Figure 3.4. Daily ration ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) estimates of yellow perch collected in all embayments during June and July 2003-2004 (circles). A power function was fit to the data to estimate mean ration across lengths (solid line) and the upper and lower 95% confidence intervals (dashed lines).

Sterling, and South Colwell, respectively. Otolith-based estimates of size (g) at age (hence referred to simply as weight or size at age) differed among embayments. Male yellow perch were smaller than female yellow perch in pelagic-dominated Little Sodus and Sterling (Figure 3.5). Female yellow perch were largest across ages in Sterling, followed by Little Sodus; females were smallest in South Colwell (Figure 3.5). Male weights were largest in Little Sodus, followed by South Sandy, Sterling, and South Colwell (Figure 3.5). These growth profiles corresponded with maximum mean lengths (mm TL) of 205, 150, 220, and 165 for females and 170, 135, 145, and 120 for males in Little Sodus, South Sandy, Sterling, and South Colwell, respectively. The energy budget model predicted that yellow perch in Sterling and South Colwell, the littoral embayments, would be larger at a given age than fish in Little Sodus and South Sandy, the pelagic embayments (Figure 3.5). Model predictions were driven by differences in embayment prey composition and energy consumed. Amphipods and non-Dipteran insects have two of the highest prey energy densities (Table 3.2) and accounted for about 60% of diet contents in Sterling and South Colwell. In contrast, South Sandy yellow perch primarily consumed zooplankton, Dipterans, and fish, all of which have low energy densities (Table 3.2). In Little Sodus, prey composition was more evenly distributed across taxonomic groups, which explains intermediate estimates of size at age. Difference in predicted weights between males and females were most noticeable starting at age 2, and increased with age (Figure 3.5).

Female yellow perch growth rates calculated from otoliths were at least two times faster for age 2 fish (i.e., growth during their second year of life) than for age 1 fish (i.e., growth during their first year of life; Figure 3.6). Females age 2 and older grew at similar rates in Little Sodus ($0.034 - 0.050 \text{ g} \cdot \text{d}^{-1}$), South Sandy ($0.031 - 0.043 \text{ g} \cdot \text{d}^{-1}$)

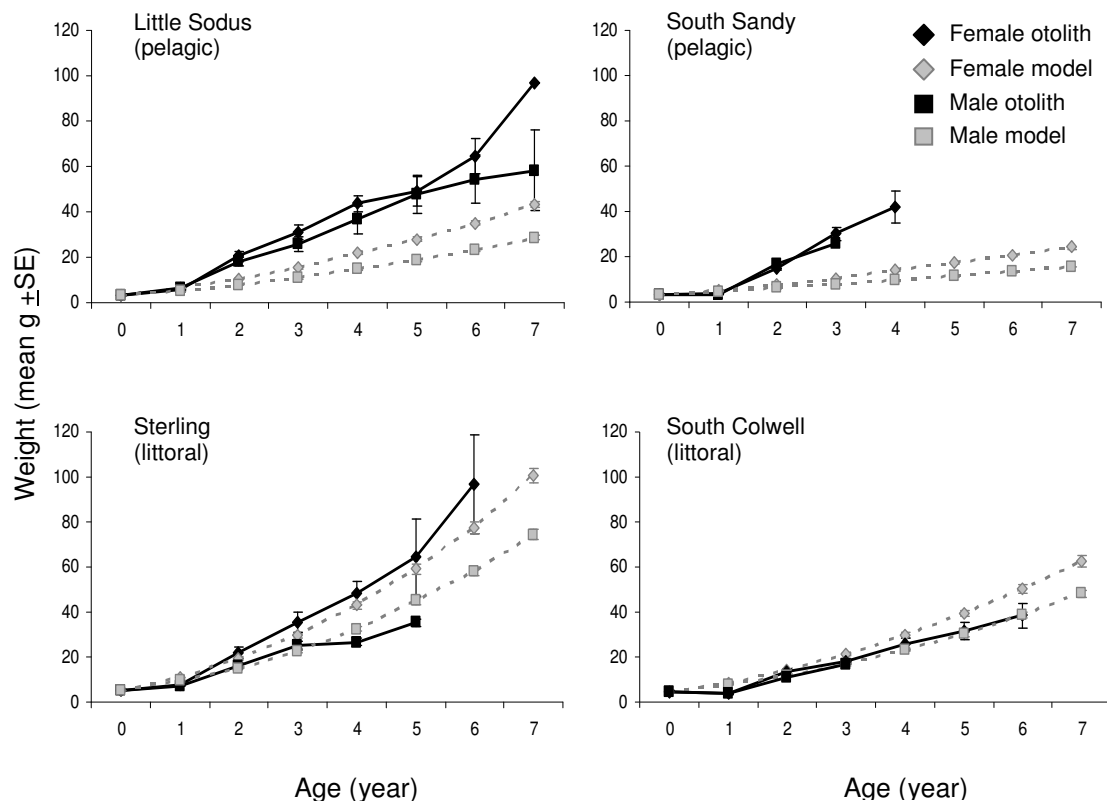


Figure 3.5. Female (diamonds) and male (squares) yellow perch mean weight (g \pm standard error [SE]) at age. Black symbols connected by solid lines represent observed weight at age estimated from otolith microstructure. Grey symbols connected by dashed lines represent weight at age predicted by the model.

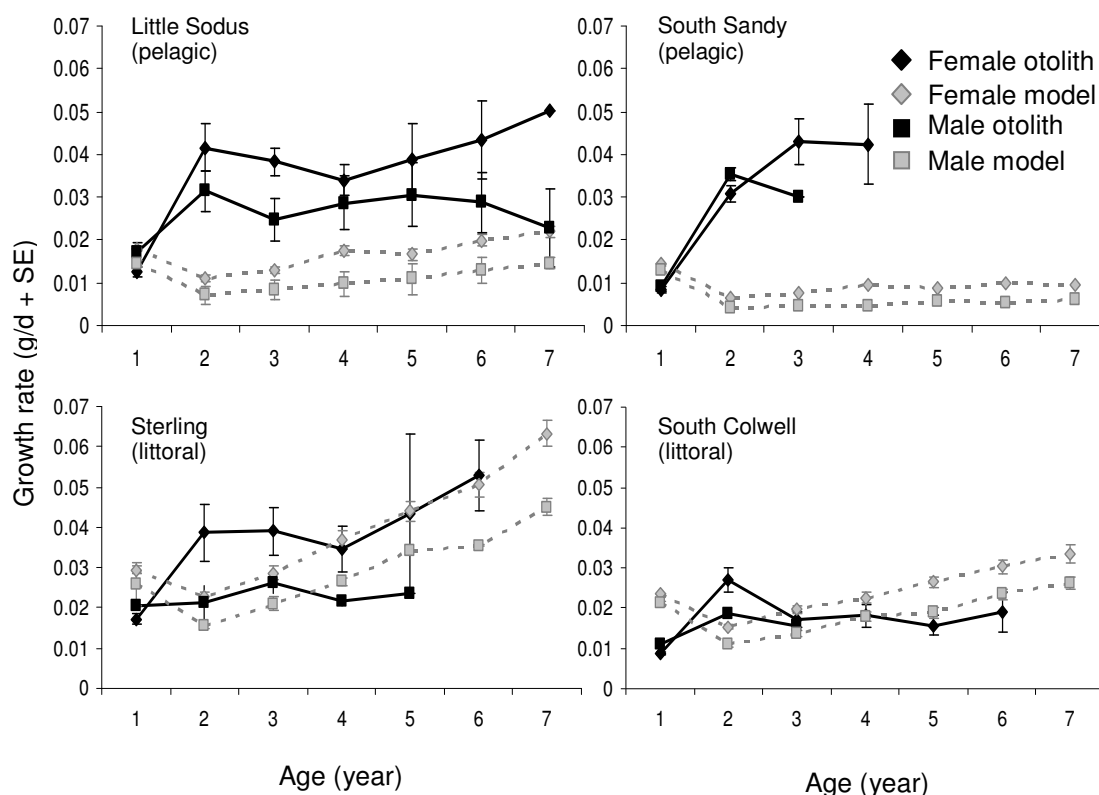


Figure 3.6. Mean annual growth rates ($\text{g} \cdot \text{d}^{-1} \pm \text{SE}$) for female (diamonds) and male (squares) yellow perch. Black symbols connected by solid lines represent observed growth rates estimated from otolith microstructure. Grey symbols connected by dashed lines represent predicted growth rates using the energy budget model.

¹), and Sterling ($0.034 - 0.053 \text{ g}\cdot\text{d}^{-1}$), but grew much more slowly in South Colwell ($0.016 - 0.027 \text{ g}\cdot\text{d}^{-1}$). Male yellow perch growth rates were similar for age 1 and age 2 fish in the littoral embayments, Sterling and South Colwell, and were 1.5 and 2 times slower for age 1 than age 2 fish in Little Sodus and South Sandy, respectively (Figure 3.6). Males age 2 and older grew fastest in South Sandy ($0.030 - 0.035 \text{ g}\cdot\text{d}^{-1}$), followed by moderate growth in Little Sodus ($0.023 - 0.031 \text{ g}\cdot\text{d}^{-1}$) and Sterling ($0.021 - 0.026 \text{ g}\cdot\text{d}^{-1}$). As for females, growth was slowest in South Colwell ($0.016 - 0.019 \text{ g}\cdot\text{d}^{-1}$). Both male and female yellow perch grew fastest between their first and second years or their second and third years, except in Little Sodus, where females grew fastest during their seventh year of life and in Sterling where females grew fastest during their sixth year of life.

Whereas observed growth rates were variable across sizes and generally higher in younger fish, modeled female and male yellow perch growth rates increased with age by about 1.5 to 3 times across embayments. Predicted maximum rates for both females and males were highest in the two littoral embayments, Sterling (0.063 and $0.045 \text{ g}\cdot\text{d}^{-1}$, respectively) and South Colwell (0.033 and $0.026 \text{ g}\cdot\text{d}^{-1}$), followed by the pelagic embayments, Little Sodus (0.022 and $0.014 \text{ g}\cdot\text{d}^{-1}$) and South Sandy (0.010 and $0.006 \text{ g}\cdot\text{d}^{-1}$; Figure 3.6). Compared with otolith estimates, model predictions underestimated female and male growth to age 2 in all embayments and underestimated female and male growth across ages in pelagic-dominated Little Sodus and South Sandy (Figure 3.6).

We compared yellow perch size at age in the study embayments with mean, minimum, and maximum size at age reported in the literature for populations from lakes and bays

of different sizes throughout the northeastern United States and the Great Lakes region of the United States and Canada (Jobes 1952, Keast 1977, Diana and Salz 1990, Hayes and Taylor 1994, Rose et al. 1999, Schaeffer et al. 2000). Yellow perch growth in all of our study embayments fell between the mean and minimum of size at age data reported in the literature (Figure 3.7).

Age Distribution

The maximum age of female and male yellow perch captured for otolith analysis differed among embayments. Females and males up to seven years old were captured in Little Sodus. The maximum ages of female and male yellow perch were 4 and 3 years old, respectively, in South Sandy, 6 and 5 years old in Sterling, and 6 and 3 years old in South Colwell (Figure 3.5). Age distributions of yellow perch collected during July in 2001 through 2003 suggest age 1 fish were most numerous in all embayments except South Sandy, where age 0+ fish were captured most frequently (Figure 3.8). Yellow perch age distribution in South Sandy also differed from the other embayments by showing a more gradual decline in frequency with increased age (Figure 3.8). Little Sodus had more age 6 fish than would be expected and Sterling had more age 3 fish than would be expected, given declines in occurrence with age.

Predation pressure

Predator pressure on all three yellow perch size classes varied at least 12-fold among embayments (Table 3.1). Predation pressure on YOY (< 90 mm TL) yellow perch was highest in pelagic-dominated Little Sodus (13.4 predator:yellow perch CPUE) and lowest in littoral-dominated South Colwell (1.24 predator:yellow perch CPUE). Predator pressures on yellow perch between 90 - 120 mm TL and greater than 120 mm

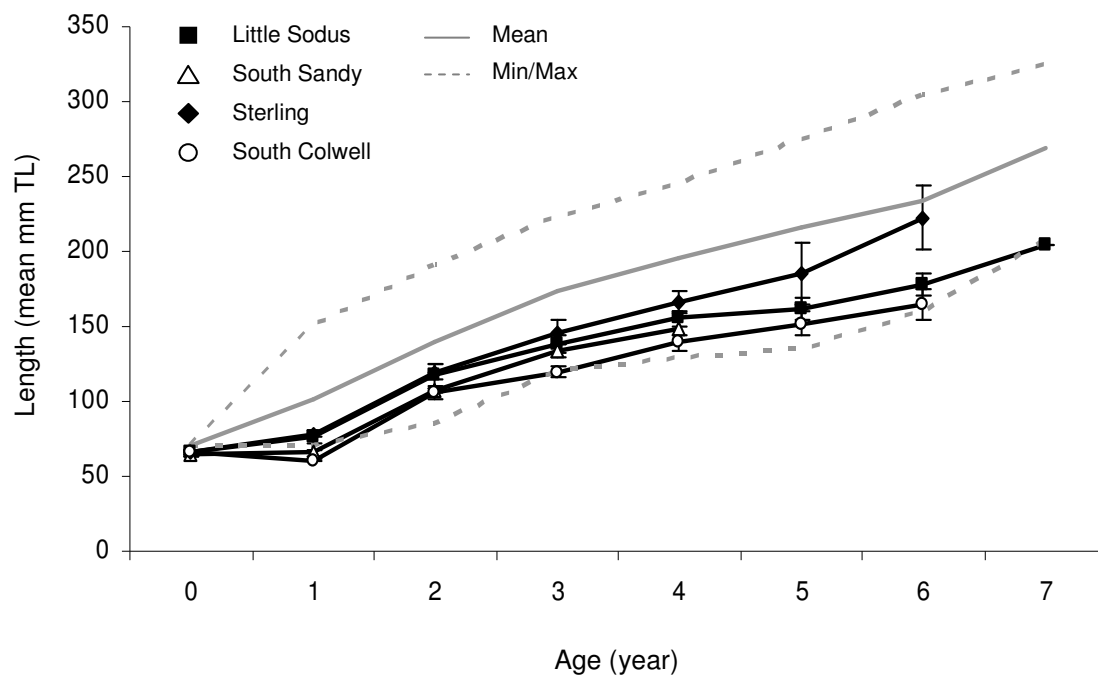


Figure 3.7. Comparison of embayment observed mean length at age (mm TL \pm SE; black lines) with mean (solid grey line), minimum (dashed grey line), and maximum (dashed grey line) length at age reported in the literature.

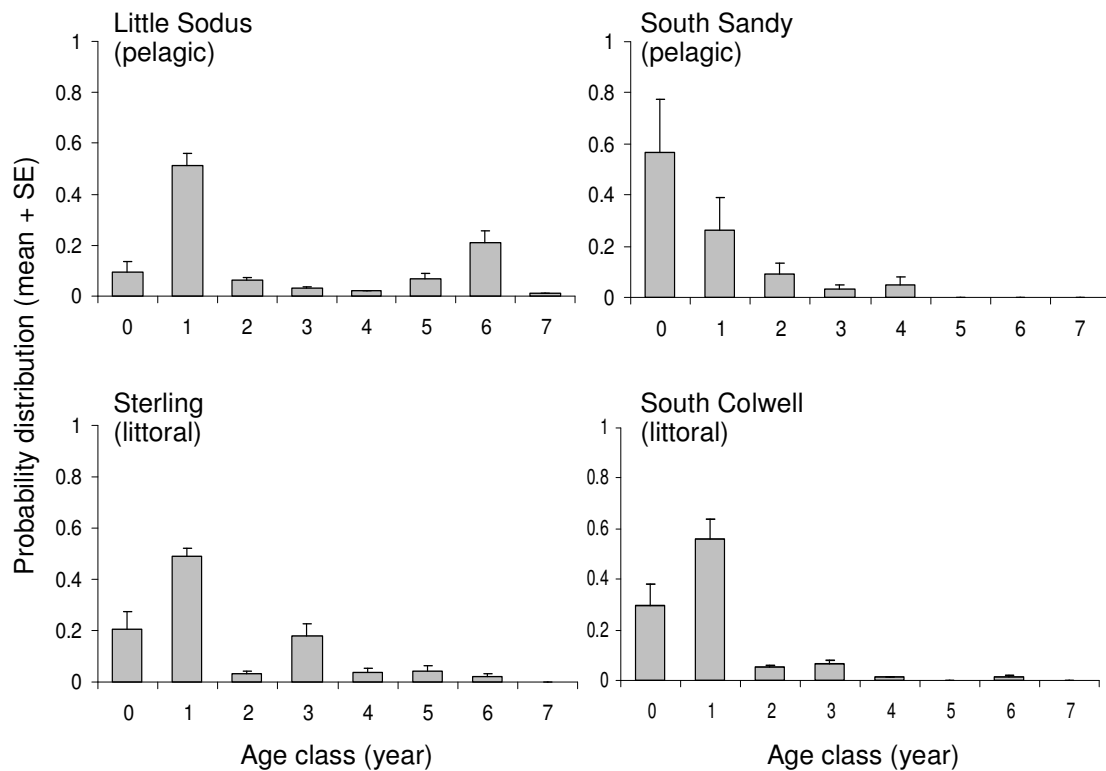


Figure 3.8. Age frequency distributions (mean \pm SE) of yellow perch in each embayment. Data are based on lengths and catch per unit effort of yellow perch collected during July 2001-2003.

TL were highest in pelagic-dominated South Sandy, with predator:yellow perch CPUE equal to 1.41 and 0.96, respectively (Table 3.1). Relative frequencies of prey fishes versus yellow perch varied among embayments and size classes (Table 3.1). Yellow perch frequencies were greater than prey fish frequencies across size classes in Little Sodus. In contrast, yellow perch frequencies were less than those of prey fishes for the 0-89 mm TL size class in South Sandy, Sterling, and South Colwell (Table 3.1). Similarly, yellow perch 90-119 mm TL occurred less frequently than prey fishes in South Sandy and Sterling; however yellow perch frequencies were greater in South Colwell (Table 3.1).

Discussion

Yellow perch size at age, growth rates, and age distributions differed among embayment populations. In the two littoral embayments, Sterling and South Colwell, the energy budget model predicted actual size at age and growth rates fairly well. In contrast, observed size at age and growth rates were greater than model predictions in the two pelagic embayments, Little Sodus and South Sandy. Discrepancies between observations and model predictions may be due to differences in the relative influences of prey consumption and composition (bottom-up effects) and predation pressure (top-down effects) on yellow perch population size structure in pelagic- versus littoral-dominated embayments. If bottom-up effects alone determine yellow perch growth, we would expect yellow perch growth to reflect prey availability and the energetic quality of prey consumed. If top-down effects are important in shaping yellow perch populations, then we would expect model predictions to underestimate yellow perch growth, based on the level of predation pressure and assuming predators selectively consume smaller, slower growing perch (Post and Prankevicius 1987).

Yellow perch growth in all four embayments may be limited by prey availability. Yellow perch size-at-age and growth rates across all four study embayments fall within the lower range of those reported in the literature. Ration estimates from yellow perch stomach contents are similarly low, as ration levels up to $0.65 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ have been reported for YOY (Post 1990) and $0.08 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for adult yellow perch (Hayward et al. 1991). Prey availability also could contribute to differences between observed and predicted growth rates in the embayments. We hypothesized more rapid growth in the littoral-dominated systems, Sterling and South Colwell, due to bottom-up effects of greater habitat and prey availability to multiple life history stages. In contrast, actual size-at-age and growth rates were highest in Sterling (littoral) and Little Sodus (pelagic) for females and Little Sodus and South Sandy (pelagic) for males. High growth rates in Little Sodus could be due to high benthic prey densities compared to the other three embayments. Unlike in South Sandy, yellow perch in Little Sodus consumed high proportions of amphipods and aquatic insects. Thus, dominance of pelagic habitat in Little Sodus did not appear to reduce yellow perch consumption of littoral prey.

In Sterling and South Colwell, low prey availability and high densities of yellow perch and other invertivorous fishes (e.g., pumpkinseed and bluegill; Chapter 1) could result in reduced growth due to insufficient prey or competition for prey or habitat (Hayes and Taylor 1994, Schaeffer et al. 2000). Despite having access to littoral and pelagic prey in close proximity and consuming a greater proportion of energy-rich prey, yellow perch may have expended greater energy (i.e., had higher activity rates) searching for food and thus suffered reduced growth rates. In contrast, low densities

of yellow perch and other small-bodied fishes could have allowed yellow perch in the pelagic embayments to expend less energy foraging (due to reduced activity rates). Activity rates of yellow perch in pelagic embayments also would be lower if the yellow perch spend less time foraging to avoid predators. Boisclair and Leggett (1989) found that energy allocated to activity was highly variable and could account for between 0 - 40% of the energy budget among yellow perch populations. They posited that such large differences could underlie variation in growth among populations. Unfortunately, activity rates for fishes are poorly known and difficult to quantify in the field (Boisclair and Leggett 1989).

Size-selective predation mortality also offers a feasible explanation for why size at age and growth rates were higher than model predictions for age 1 through 2 yellow perch across embayments, but particularly in South Sandy. High predation mortality of YOY and age 1 fishes also could explain a general pattern of age distributions in which frequency decreased most sharply after age 1. We hypothesized that the yellow perch population in South Sandy would be most likely to be affected by predation, because of the presence of walleye. Dominance of YOY yellow perch in South Sandy followed by a fairly uniform decrease in frequency with age and coupled with high predation pressure on age 1 and older yellow perch, supports this hypothesis. Uniform decrease in frequency with age in South Sandy compared to the other embayments also could be due to South Sandy being more isolated from Lake Ontario. Greater isolation could reduce immigration or emigration of individuals into or from the population. Discrepancies between observed and model growth rates were largest in the two pelagic embayments, with predation pressure on YOY and age 1 perch highest in Little Sodus and South Sandy, respectively, across embayments.

Size-selective mortality would remove slower growing (i.e., smaller) fish from the population to a greater extent than faster growing fish. Therefore, yellow perch growth would appear to be faster because surviving fish would be those who outgrew vulnerability to predation more quickly (Post and Prankevicius 1987). Although predation pressure on age 1 and older yellow perch in Sterling also is high, dense macrophyte beds, which are absent in pelagic-dominated Little Sodus and South Sandy, could provide some protection from predation. Additionally, the relative frequencies of prey fishes versus YOY yellow perch were greater in the two littoral embayments, Sterling and South Colwell, than in the two pelagic embayments. Greater availability of alternate prey could have reduced predation pressure on YOY yellow perch in the littoral embayments, where predation pressure was highest on fishes less than 90 mm TL. However, a model of walleye and yellow perch dynamics in Oneida Lake developed by Rose et al (1999) predicted greater predation pressure on YOY yellow perch when alternate prey fish availability was increased. Finally, greater predation pressure in the pelagic embayments could have reduced yellow perch activity levels compared to levels in littoral embayments.

Another explanation for faster than predicted yellow perch growth between ages 1 and 3 is the loss of slow growing individuals to emigration. The degree to which individuals within these populations migrate between the embayments and Lake Ontario is unknown. Stable carbon isotope data from Sterling suggest that most individuals collected during summer reside in the embayment, but that individuals may migrate into the embayments from Lake Ontario during fall (Chapter 2). Although not shown, a small number of individuals in Little Sodus and Sterling were

much larger at a given age than the majority of individuals, suggesting immigration of fish from Lake Ontario (or nearby embayments) that had experienced more rapid growth. Conceivably, slow-growing yellow perch may leave the embayments in search of greater prey availability; however, we did not sample and thus do not have data on prey availability or yellow perch growth in Lake Ontario nearshore habitat.

Model assumptions also might contribute to model underestimates of female and male growth between ages 1 and 3. Differences in observations and model predictions of growth rates to age 1 could be due to error from uncertainty in hatch date and starting the model with mean age 0+ lengths based on fish collected during September and April. Our model does not include YOY growth dynamics, which might have captured the benefits of greater zooplankton consumption in Little Sodus and South Sandy. However, mean lengths of YOY captured in each embayment were larger in Little Sodus and Sterling, the latter being dominated by littoral habitat and containing YOY yellow perch with a high proportion of amphipods in their stomachs.

Uncertainty in daily ration estimates also could influence model predictions. Daily ration estimates were based on diets of fish collected once a day on several sampling dates, as opposed to collecting multiple samples over a single, 24 hour period on multiple dates. Furthermore, high variability in ration estimates may have masked any differences in daily ration among embayments.

Additionally, mean prey compositions across sizes were included in the model, ignoring differences in prey composition among size classes within an embayment. For example, the proportion of amphipods, a high energy prey item, consumed was quite variable among length classes, except in Sterling. Discrepancies between

observed and predicted growth rates do not appear to reflect finer scale patterns in the proportions of prey consumed of different energetic value. For example, 90-120 mm TL fish in Sterling and South Sandy ate a relatively high-energy diet compared to the diet of similar-sized fish in Little Sodus and South Colwell. Despite these differences in prey energetics, growth rates for age 2 female and male perch in Little Sodus and Sterling were similarly higher than growth rates in South Colwell and South Sandy. To confirm this observation, we ran a version of the model in which prey composition was specified for fish less than 120 mm TL and for fish greater than 120 mm TL. Runs from both this and the original model produced similar results.

Despite differences among embayment yellow perch populations in relative incorporation of pelagic versus littoral energy, yellow perch had access to and consumed littoral and pelagic prey in all systems. Therefore habitat coupling may operate at the level of the food web as opposed to individual populations in these and possibly other systems. Such food web level effects possibly result in yellow perch populations being structured by varying degrees of both bottom-up and top-down processes. Low prey availability appeared to have limited yellow perch growth in all four embayments, resulting in slow growth rates and small size at age relative to other studies. Similarly slow growth in studies of yellow perch populations in other systems has been attributed to inadequate prey availability (Diana and Salz 1990, Heath and Roff 1996, Schaeffer et al. 2000). Therefore, yellow perch populations may be controlled primarily by bottom-up effects of prey availability. Our results suggest that within a given level of prey availability, however, populations in some systems may be influenced by top-down effects to a greater extent than in other systems.

The clearest pattern that emerged distinguishing the characteristics of yellow perch populations in pelagic-dominated embayments from those of populations in littoral-dominated systems was more rapid growth in pelagic-dominated systems. More rapid growth in pelagic-dominated systems could be due to size-selective mortality from predation. Large, deep lakes can better support large-bodied fishes (Holmgren and Appelberg 2000), Chapter 1), such as walleye and northern pike, which exert predation pressure on smaller-bodied fishes such as yellow perch. Walleye predation, in particular, has been shown to influence yellow perch populations in Oneida Lake, NY (Nielsen 1980, Rose et al. 1999), which is slightly deeper than the pelagic-dominated embayments in this study. As a result, top-down effects might be more likely to influence yellow perch growth to a greater degree in relatively large, deep systems. Shallow, vegetated systems can support more small-bodied fishes, by providing habitat for a diverse prey assemblage and protection from predation (Randall et al. 1996; Chapter 1). In these littoral-dominated systems, bottom-up effects and inter- and intraspecific competition for invertebrate prey might have a greater effect than predation on yellow perch growth and size structure. For example, yellow perch growth in a relatively shallow lake in northern Michigan improved with removal of white sucker, a competitive species (Hayes et al. 1992).

In conclusion, embayment yellow perch populations appeared to be sensitive to bottom-up and top-down processes to varying degrees, partly as a function of system morphometry and biological interactions with other species, such as walleye. We did not observe direct effects of differences in pelagic versus littoral energy flow on yellow perch populations. Instead, habitat coupling might operate at the level of the food web, by altering predator-prey and competitive interactions. Although we

focused on a single species for this study, we view this as a starting point for identifying mechanisms that underlie physicochemical and biological effects on fish community structure and function.

CHAPTER 4: Conclusions

In the research described herein, I explored how fish community structure and function in Lake Ontario embayments responded to external and internal environmental factors. Important external factors included nutrient and energy inputs from adjacent ecosystems. Important internal factors included embayment area, depth profile, and vegetation. With my research, I aimed to address the following questions: (1) which internal and external factors influence how much and where biomass is distributed in the fish community (i.e., structure); (2) which factors influence energy sources utilized by the fish communities (i.e., function); (3) are structural and functional responses related to each other? In brief, I found that different fish community characteristics were influenced by different external and internal environmental factors. Additionally, the relative importance of external and internal factors differed depending on the fish community characteristic considered. Internal factors generally were of greater importance than external factors for a larger number of responses considered. Finally, structural and functional responses appear to be related through trophic interactions. In this section, I consider my findings in the context of trophic interactions and, specifically, implications for bottom-up and top-down control in embayment ecosystems as they relate to the fish community.

Fish community structure differed among embayments for all three metrics considered, relative biomass, relative abundance, and size structure. Biomass increased with phosphorus loading and area. The relative importance of phosphorus loading and area differed among embayment hydrogeomorphic types. High levels of phosphorus loading in the two drowned-river mouth embayments seemed to outweigh the small size of those embayments. The effect of area and possibly other internal

factors such as habitat heterogeneity on biomass appeared stronger in protected embayments. Protected embayments received lower nutrient inputs than drowned-river mouth embayments, which could explain the greater importance of internal factors in these systems. If so, internal factors might operate within the constraints of external factors with respect to fish biomass. In contrast, an internal factor, percent vegetation, was the only factor that explained both fish abundance and size structure. A greater abundance of small-bodied fishes occurred in more vegetated systems. Therefore, in contrast to fish biomass, fish abundance and size structure were controlled almost entirely by internal factors. Considering these findings together, the amount of fish a system supports appears to be controlled externally by nutrient inputs (Figure 4.1a); i.e., via bottom-up processes. In contrast, the distribution of that biomass is controlled internally by vegetation (Figure 4.1b), via a combination of bottom-up and top-down processes. Vegetation likely influences fish abundance and size structure by providing complex habitat that favors small-bodied invertivorous fishes. Vegetated habitat both supports a diverse invertebrate prey assemblage and provides small-bodied fish protection from predation.

Both external and internal factors also influenced fish community function. As expected, availability and uptake of external energy sources by planktonic primary producers was determined by the strength of the embayments' connections to Lake Ontario and their watersheds. However, neither differences in nutrient concentrations nor water residence time influenced uptake of Lake Ontario versus watershed inputs. Internal factors, such as area and vegetation, also played a role by influencing the extent to which external subsidies extended into the embayments. Fish community reliance on pelagic versus littoral energy sources depended almost entirely on

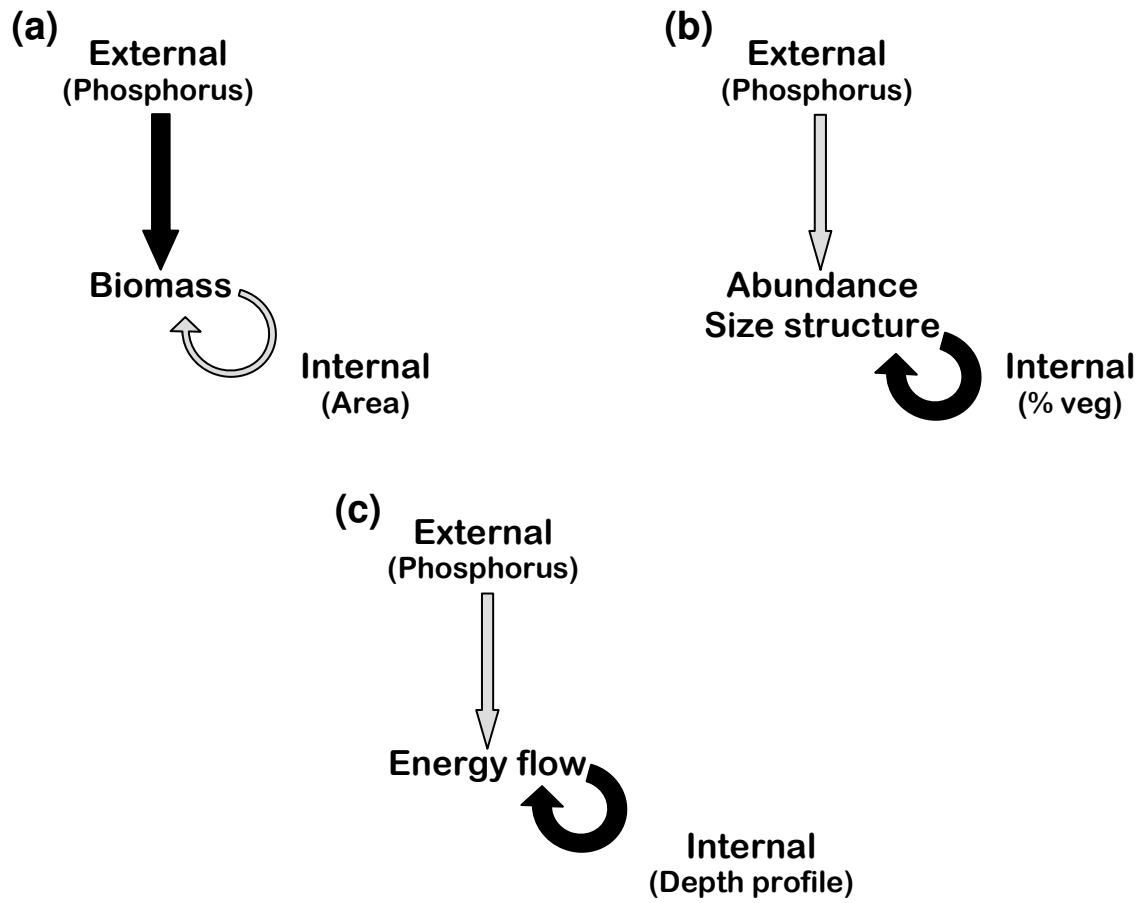


Figure 4.1. Relative importance of external and internal physicochemical factors on (a) fish community biomass, (b) fish community abundance and size structure, and (c) food web dynamics.

embayment depth profile, an internal factor. Again, nutrient loading and water residence time did not appear to influence internal habitat coupling. However, effects may not be evident when comparing only four embayments. Maximum trophic position also appeared to be determined by area as opposed to nutrient loading. Therefore, similar to fish abundance and size structure, fish community function appears to be more strongly influenced by internal factors than by external factors (Figure 4.1c).

Most likely, both bottom-up and top-down controls operate on fish community function. Fish diets were similar across embayments, suggesting that littoral prey were subsidized by pelagic primary producers in relatively large, deep embayments, a bottom-up effect. The availability of both pelagic and littoral invertebrate prey may subsidize invertivorous fishes, which could have important top-down effects. For example, the abundance of small-bodied fishes was high in Sterling. These fishes obtained about 60% of their energy from pelagic sources, yet zooplankton abundance in Sterling was low compared to other embayments (R. Doyle-Morin, Cornell University, unpublished data). The availability and consumption of both zooplankton and benthic invertebrates could have supported large enough populations of invertivorous fishes to enable them to graze down zooplankton populations.

Results from the yellow perch growth and size structure study confirm structural and functional observations from Chapters 1 and 2. They also provide insight into how structural and functional fish community characteristics are linked via trophic interactions. I had hypothesized that growth and size structure would be controlled via bottom-up effects of prey availability. I found this to be true in the two littoral

embayments, but not in the pelagic embayments. Instead, top-down control via predation appeared to influence yellow perch size structure and observed growth in the pelagic embayments. These results are consistent with our findings regarding fish community structure. The large, deep systems can support larger-bodied, piscivorous fishes and have less vegetation to provide small-bodied fishes with protection from those predators. In littoral embayments, where vegetation is quite dense, the type and availability of prey appears to underlie yellow perch growth and size structure. Therefore, trophic interactions were directly modified by internal factors, specifically embayment morphometry and vegetation. The role of external factors, such as nutrient loading and energy sources, and internal energy pathways may indirectly influence yellow perch population dynamics through effects on prey availability and composition.

In conclusion, embayment fish communities respond to physicochemical factors operating at multiple spatial scales (external and internal). Additionally, different community characteristics were sensitive to different factors. Effects of these factors on the fish community occur via trophic interactions and include both bottom-up and top-down control. External factors may operate primarily via bottom-up control by providing basal resources to food webs. Internal factors appear to influence fish communities by affecting trophic interactions, which can exert bottom-up or top-down effects on fish populations and their prey. These findings improve our understanding of how fish communities might respond to natural and anthropogenic changes in environmental conditions. Additionally, they identify what aspects of the community are influenced by factors that humans can control (e.g., nutrient loading and vegetation) versus what aspects are sensitive to factors we cannot control (e.g., area).

APPENDICES

Appendix 1.1. Length-weight regressions. Exponential (Exp) equations are of the form: $\text{weight} = a \cdot \text{length}^b$. Logarithmic (Log) equations are of the form: $\log_{10}\text{weight} = a \cdot \log_{10}\text{length} - b$. BS = Blind Sodus, FL = Floodwood, JU = Juniper, LS = Little Sodus, NS = North Sandy, SC = South Colwell, SS = South Sandy, ST = Sterling.

Species	Embayment	Equation	a	b	Length
American eel	all	Exp	0.0026	2.9800	cm TL
Brown bullhead	BS, FL, LS, SS, ST	Log	2.7142	4.1418	mm TL
	NS	Log	2.7894	4.3494	mm TL
	SC	Log	2.8756	4.5623	mm TL
Black crappie	all	Log	3.0084	4.8188	mm TL
Bluegill	BS	Log	3.8472	6.5039	mm TL
	FL	Log	2.3545	3.4013	mm TL
	LS	Log	3.0755	4.8679	mm TL
	NS	Log	3.2985	5.3488	mm TL
	SC	Log	3.2729	5.2573	mm TL
	ST	Log	3.1822	5.0415	mm TL
Bowfin	FL, LS, SC	Log	2.8695	4.6499	mm TL
	BS	Log	2.7392	4.2869	mm TL
	NS	Log	2.8813	4.6619	mm TL
	ST	Log	2.7985	4.4649	mm TL
Banded killifish	ST	Log	3.0410	5.0900	mm TL
Bluntnose minnow	NS	Exp	0.0011	3.1930	cm TL
Common carp	BS, FL, LS	Exp	0.0116	3.0250	cm TL
Central mudminnow	JU	Log	2.884	4.491	mm SL
Common shiner	BS, NS, SC, ST	Log	2.884	4.491	mm SL
Freshwater drum	BS	Log	3.320	5.740	mm FL
Grass pickerel	SC	Exp	0.0201	2.7520	cm TL
Golden shiner	FL, NS	Log	3.1462	5.3084	mm TL
	BS	Log	3.3488	5.7197	mm TL
	JU	Log	3.2665	5.5366	mm TL
	LS	Log	2.4878	3.9253	mm TL
	SC	Log	3.4962	5.9851	mm TL
	ST	Log	3.0960	5.2433	mm TL
Largemouth bass	BS	Log	3.0727	4.9909	mm TL
	FL	Log	2.9519	4.7123	mm TL
	LS	Log	3.1427	5.1771	mm TL
	NS	Log	3.1083	5.1054	mm TL
	SC	Log	3.0746	5.0535	mm TL
	SS	Log	2.5066	3.9708	mm TL
	ST	Log	2.9116	4.6848	mm TL

Longnose sucker	SS	Exp	0.0352	2.8420	cm TL
Logperch	NS	Log	2.8200	4.6600	mm TL
Northern pike	BS, FL, NS, ST	Log	1.8986	2.2267	mm TL
	SS	Log	1.3421	0.6234	mm TL
Pumpkinseed	JU	Log	3.1685	5.0254	mm TL
	BS	Log	3.2891	5.2627	mm TL
	FL	Log	2.8428	4.3624	mm TL
	LS	Log	3.2729	5.2390	mm TL
	NS	Log	3.3534	5.4220	mm TL
	SC	Log	3.0648	4.8479	mm TL
	SS	Log	3.0876	4.8562	mm TL
	ST	Log	3.1430	4.9676	mm TL
Rock bass	LS	Log	2.9900	4.6200	cm FL
Redbreast sunfish	LS	Exp	0.0204	3.0100	cm TL
Smallmouth bass	BS, FL, SS, ST	Exp	0.0120	3.0160	cm TL
Spottail shiner	BS, NS, SC, SS	Log	2.6391	4.3412	mm TL
Sand shiner	ST	Log	2.6391	4.3412	mm TL
Walleye	SS	Log	2.8881	4.7715	mm TL
White perch	SS	Exp	0.0082	3.1610	cm TL
Yellow perch	FL, JU	Log	3.0319	5.007	mm TL
	BS	Log	3.0867	5.1224	mm TL
	LS	Log	2.9736	4.8886	mm TL
	NS	Log	3.4652	5.9459	mm TL
	SC	Log	2.3369	3.6027	mm TL
	SS	Log	3.0676	5.0542	mm TL
	ST	Log	2.4058	3.6670	mm TL

Appendix 1.1 (Continued).

Species	Embayment	Source
American eel	all	Hurley, D.A. 1972. Journal of the Fisheries Research Board of Canada 29:535-543
Brown bullhead	BS, FL, LS, SS, ST	All embayments
	NS	NS
	SC	SC
Black crappie	all	All embayments
Bluegill	BS	BS
	FL	FL
	LS	All embayments
	NS	NS
	SC	SC
	ST	ST
Bowfin	FL, LS, SC	All embayments
	BS	BS
	NS	NS
	ST	ST
Banded killifish	ST	Fritz, E.S., and E.L. Garside. 1975. Canadian Journal of Zoology 53:361-369
Bluntnose minnow	NS	Small, J.W., Jr. 1975. Ecology 56:827-840
Common carp	BS, FL, LS	Runnström, S. 1952. Proceedings of the International Association of Theoretical and Applied Limnology 12:176-182
Central mudminnow	JU	Randall, R.G., and C.K. Minns. 2000. Canadian Journal of Fisheries and Aquatic Sciences 57:1657-1667
Common shiner	BS, NS, SC, ST	Randall, R.G., and C.K. Minns. 2000. Canadian Journal of Fisheries and Aquatic Sciences 57:1657-1667
Freshwater drum	BS	Randall, R.G., and C.K. Minns. 2000. Canadian Journal of Fisheries and Aquatic Sciences 57:1657-1667
Grass pickerel	SC	Kleinert, S.J., and D. Mraz. 1966. Wisconsin Conservation Department Technical Bulletin 37:1-39.
Golden shiner	FL, NS	All embayments
	BS	BS
	JU	JU
	LS	LS
	SC	SC
	ST	ST
Largemouth bass	BS	BS
	FL	FL
	LS	LS
	NS	NS
	SC	SC

	SS	SS
	ST	ST
Longnose sucker	SS	Magnin, E. 1964. <i>Naturaliste Canadien</i> 91:273-308
Logperch	NS	Randall, R.G., and C.K. Minns. 2000. <i>Canadian Journal of Fisheries and Aquatic Sciences</i> 57:1657-1667
Northern pike	BS, FL, NS, ST	All embayments
	SS	SS
Pumpkinseed	JU	All embayments
	BS	BS
	FL	FL
	LS	LS
	NS	NS
	SC	SC
	SS	SS
	ST	ST
Rock bass	LS	Randall, R.G., and C.K. Minns. 2000. <i>Canadian Journal of Fisheries and Aquatic Sciences</i> 57:1657-1667
Redbreast sunfish	LS	Swingle, W.E. 1965. Auburn University Agricultural Experiment Station. <i>Zoology-Entomology Series</i> 3:87p
Smallmouth bass	BS, FL, SS, ST	Funk, J.L., and G.C. Fleener. 1974. <i>Transactions of the American Fisheries Society</i> 103:757-771
Spottail shiner	BS, NS, SC, SS	All embayments
Sand shiner	ST	All embayments: Spottail shiner
Walleye	SS	SS
White perch	SS	St. Pierre, R., and J. Davis. 1972. <i>Chesapeake Science</i> 13:272-281
Yellow perch	FL, JU	All embayments
	BS	BS
	LS	LS
	NS	NS
	SC	SC
	SS	SS
	ST	ST

Appendix 1.2. Species captured in each embayment.

Family	Species	Common name	BS	LS
Amiidae	<i>Amia calva</i>	Bowfin	+	+
Anguillidae	<i>Anguilla rostrata</i>	American eel		
Atherinopsidae	<i>Labidesthes sicculus</i>	Brook silverside		+
Catostomidae	<i>Catostomus commersonii</i>	White sucker	+	
	<i>Catostomus catostomus catostomus</i>	Longnose sucker		
Centrarchidae	<i>Ambloplites rupestris</i>	Rock bass		+
	<i>Lepomis auritus</i>	Redbreast sunfish		+
	<i>Lepomis gibbosus</i>	Pumpkinseed	+	+
	<i>Lepomis macrochirus</i>	Bluegill	+	+
	<i>Micropterus dolomieu</i>	Smallmouth bass	+	+
	<i>Micropterus salmoides</i>	Largemouth bass	+	+
	<i>Pomoxis nigromaculatus</i>	Black crappie	+	+
Clupeidae	<i>Alosa pseudoharengus</i>	Alewife		+
	<i>Dorosoma cepedianum</i>	Gizzard shad	+	+
Cyprinidae	<i>Cyprinus carpio carpio</i>	Common carp	+	+
	<i>Luxilus cornutus</i>	Common shiner	+	
	<i>Notemigonus crysoleucus</i>	Golden shiner	+	+
	<i>Notropis atherinoides</i>	Emerald shiner		
	<i>Notropis heterodon</i>	Blackchin shiner		
	<i>Notropis heterolepis</i>	Blacknose shiner		
	<i>Notropis hudsonius</i>	Spottail shiner	+	+
	<i>Notropis stramineus</i>	Sand shiner		
	<i>Pimephales notatus</i>	Bluntnose minnow		
Esocidae	<i>Esox americanus vermiculatus</i>	Grass pickerel		
	<i>Esox lucius</i>	Northern pike	+	+
Fundulidae	<i>Fundulus diaphanus diaphanus</i>	Banded killifish		+
Ictaluridae	<i>Ameiurus nebulosus</i>	Brown bullhead	+	+
Lepisosteidae	<i>Lepisosteus osseus</i>	Longnose gar		
Moronidae	<i>Morone Americana</i>	White perch		
Percidae	<i>Etheostoma olmstedii</i>	Tessellated darter		
	<i>Percina caprodes</i>	Logperch		
	<i>Sander vitreus</i>	Walleye		
Petromyzontidae	<i>Petromyzon marinus</i>	Sea lamprey		
Sciaenidae	<i>Aplodinotus grunniens</i>	Freshwater drum	+	
Umbridae	<i>Umbra limi</i>	Central mudminnow		

Appendix 1.2 (Continued). Species captured in each embayment.

Family	Species	ST	JU	SS	NS	SC	FL
Amiidae	<i>Amia calva</i>	+		+	+	+	+
Anguillidae	<i>Anguilla rostrata</i>				+		
Atherinopsidae	<i>Labidesthes sicculus</i>	+			+		
Catostomidae	<i>Catostomus commersonii</i>						
	<i>Catostomus catostomus catostomus</i>			+			
Centrarchidae	<i>Ambloplites rupestris</i>			+			
	<i>Lepomis auritus</i>						
	<i>Lepomis gibbosus</i>	+	+	+	+	+	+
	<i>Lepomis macrochirus</i>	+		+	+	+	+
	<i>Micropterus dolomieu</i>	+		+	+		+
	<i>Micropterus salmoides</i>	+		+	+	+	+
	<i>Pomoxis nigromaculatus</i>	+		+	+	+	+
Clupeidae	<i>Alosa pseudoharengus</i>				+	+	+
	<i>Dorosoma cepedianum</i>			+			+
Cyprinidae	<i>Cyprinus carpio carpio</i>			+			+
	<i>Luxilus cornutus</i>	+			+	+	
	<i>Notemigonus crysoleucus</i>	+	+	+	+	+	+
	<i>Notropis atherinoides</i>	+					
	<i>Notropis heterodon</i>				+	+	
	<i>Notropis heterolepis</i>		+				
	<i>Notropis hudsonius</i>			+	+	+	+
	<i>Notropis stramineus</i>	+					
	<i>Pimephales notatus</i>				+		
Esocidae	<i>Esox americanus vermiculatus</i>					+	
	<i>Esox lucius</i>	+		+	+	+	+
Fundulidae	<i>Fundulus diaphanus diaphanus</i>	+			+	+	+
Ictaluridae	<i>Ameiurus nebulosus</i>	+	+	+	+	+	+
Lepisosteidae	<i>Lepisosteus osseus</i>	+		+			
Moronidae	<i>Morone Americana</i>			+	+		
Percidae	<i>Etheostoma olmstedii</i>		+				+
	<i>Percina caprodes</i>				+		
	<i>Sander vitreus</i>			+			
Petromyzontidae	<i>Petromyzon marinus</i>						+
Sciaenidae	<i>Aplodinotus grunniens</i>						
Umbridae	<i>Umbra limi</i>		+				

Appendix 2.1. IsoSource estimates of percent contribution of energy sources to each fish species. Sources for all embayments include lake site seston, lake site epilithon, stream site seston, and stream site epilithon. An additional source, stream site snail, was included in South Sandy. Lk = lake; St = stream; Med = median; IQR = interquartile range; GS = golden shiner; BB = brown bullhead; PS = pumpkinseed; YP = yellow perch; LMB = largemouth bass; NP = northern pike; BF = bowfin.

Species	Lk Seston		Lk Epilithon		St Seston		St Epilithon		St snail	
	Med	IQR	Med	IQR	Med	IQR	Med	IQR	Med	IQR
Little Sodus										
GS	0.96	0.02	0.01	0.02	0.02	0.04	0.01	0.02		
BB < 300 mm	0.81	0.07	0.01	0.02	0.12	0.13	0.05	0.05		
PS	0.53	0.14	0.11	0.14	0.22	0.27	0.10	0.13		
YP	0.62	0.12	0.09	0.12	0.18	0.23	0.08	0.11		
LMB < 100 mm	0.66	0.10	0.08	0.11	0.16	0.21	0.07	0.09		
BB ≥ 300 mm	0.57	0.13	0.10	0.14	0.20	0.26	0.09	0.12		
NP	0.81	0.06	0.04	0.06	0.09	0.12	0.04	0.06		
LMB ≥ 100 mm	0.73	0.08	0.06	0.08	0.13	0.16	0.06	0.08		
BF	0.94	0.03	0.02	0.03	0.03	0.05	0.01	0.02		
South Sandy										
GS	0.13	0.19	0.05	0.07	0.13	0.18	0.06	0.09	0.54	0.12
BB < 300 mm					data out of range					
PS	0.17	0.24	0.06	0.09	0.16	0.22	0.08	0.12	0.42	0.16
YP	0.09	0.12	0.03	0.05	0.08	0.12	0.04	0.06	0.70	0.08
LMB < 100 mm	0.03	0.04	0.01	0.02	0.02	0.04	0.01	0.02	0.91	0.02
BB ≥ 300 mm	0.22	0.30	0.10	0.13	0.21	0.29	0.12	0.15	0.22	0.20
NP	0.39	0.30	0.16	0.12	0.38	0.29	0.20	0.15	0.34	0.20
WE	0.16	0.21	0.06	0.09	0.15	0.20	0.07	0.11	0.47	0.14
LMB ≥ 100 mm	0.21	0.28	0.08	0.11	0.19	0.27	0.10	0.14	0.30	0.19
BF	0.14	0.19	0.05	0.08	0.13	0.19	0.07	0.09	0.53	0.12
Sterling										
GS	0.22	0.28	0.18	0.24	0.25	0.07	0.25	0.32		
BB < 300 mm	0.20	0.25	0.16	0.21	0.33	0.06	0.22	0.29		
PS	0.21	0.27	0.17	0.22	0.29	0.06	0.24	0.30		
YP	0.17	0.23	0.42	0.06	0.14	0.19	0.19	0.25		
LMB > 100 mm	0.06	0.09	0.05	0.06	0.80	0.02	0.07	0.09		
BB ≥ 300 mm					data out of range					
NP	0.19	0.24	0.61	0.16	0.03	0.04	0.12	0.16		
LMB ≥ 100 mm	0.29	0.35	0.24	0.27	0.09	0.08	0.29	0.36		
BF	0.25	0.33	0.21	0.27	0.14	0.07	0.29	0.36		

South Colwell

GS	0.18	0.22	0.11	0.15	0.27	0.34	0.37	0.15
BB < 300 mm	0.10	0.14	0.06	0.08	0.16	0.20	0.64	0.09
PS	0.13	0.17	0.09	0.11	0.21	0.26	0.52	0.12
YP	0.13	0.17	0.09	0.11	0.21	0.26	0.52	0.12
LMB < 100 mm	0.05	0.07	0.89	0.04	0.03	0.04	0.01	0.03
BB \geq 300 mm	0.21	0.27	0.54	0.14	0.13	0.16	0.07	0.09
NP	0.29	0.35	0.21	0.20	0.27	0.32	0.16	0.16
LMB \geq 100 mm	0.12	0.16	0.08	0.11	0.19	0.25	0.56	0.11
BF	0.06	0.08	0.04	0.06	0.09	0.12	0.79	0.0

Appendix 3.1. Parameter values used to convert benthic invertebrate size (mm) to biomass (mg dry weight). All equations are of the form $M=a \cdot L^b$, where M =dry mass (mg) and a and b are regression coefficients. Equation and parameter values are from Benke et al. (1999). Measurements included body length (BL), head length (HL), head width (HW), telson width (TW), shell length (SL), and shell width (SW).

Taxon	Measurement	a	b
Decapoda	BL	0.0147	3.626
Amphipoda	BL	0.0058	3.015
	HL*	1.47	3.62
Gammaridae	HL	1.102	4.13
Hyallelidae	HL	1.3	2.9
Isopoda	BL	0.0054	2.948
Asellidae	HW*	0.6525	3.001
	TW	0.1661	2.8
Coleoptera	BL	0.0077	2.91
	HW	0.0077	3.14
Diptera	BL	0.0025	2.692
	HW	0.0025	2.791
Ceratopogonidae	BL	0.0025	2.469
	HW	2.7842	2.835
Chironomidae	BL	0.0015	2.617
	HW	1.172	2.371
Ephemeroptera	BL	0.0071	2.832
	HW	0.0071	3.319
Hemiptera	BL	0.0108	2.734
Lepidoptera Pyralidae	BL	0.0033	2.918
Odonata	BL	0.0078	2.792
	HW	0.0078	2.871
Coenagrionidae	BL	0.0051	2.785
Plecoptera	BL	0.0094	2.754
	HW	0.0094	3.094
Trichoptera	BL	0.0056	2.839
	HW	0.0056	3.252
Hydropsychidae	BL	0.0046	2.926
Leptoceridae	BL	0.0034	3.212
Insects (general)	BL	0.0064	2.788
	HW*	0.0064	3.043
Bivalvia (Unionidae)	SL	0.019308	2.822286
Gastropoda	SL	0.007667	3.001167
	SW	0.031775	2.933125

* mean of all families presented in Benke et al. (1999)

Appendix 3.2. Parameter values used to convert zooplankton size (mm) to biomass (ug wet weight). All equations are of the form $M=a \cdot L^b$, where M =wet mass (ug) and a and b are regression coefficients. Equation and parameter values are from Bottrell et al. (1976). If coefficients were not available for a particular taxonomic group, we assigned it the same coefficients as a similar group, based on size and shape; these are indicated by parentheses.

Taxon	<i>a</i>	<i>b</i>
Bosmina, Eubosmina	21.968	3.0395
Ceriodaphnia	12.966	3.338
Chydoridae (Ostracoda, Podocopa)	19.8	2.41
Cyclopoida (all Copepoda)	11.6	0.7825
Daphnia (unknown Cladocera)	14.01	2.54
Sida (Holopedium)	5.0743	3.0468

Appendix 3.3. Dry:wet weight ratios of prey. All values are from Cummins and Wuychuck (1971), with the exception of Gastropoda, which is from Hanson et al. (1997), and Other insect, which was chosen by the authors to reflect the mean value for insects; Bivalvia was assumed by the authors to be similar to Gastropoda.

Prey Taxon	Dry:wet
Amphipoda	75
Isopoda	75
Gastropoda	71
Bivalvia	71
Diptera	80
Ephemeroptera	80
Odonata	80
Trichoptera	81
Other insect	80

Appendix 3.4. Embayment-specific temperature coefficients. All equations are of the form

$$Temp = a - b \cdot \cos(2 \cdot \pi \cdot \frac{t}{365}) - c \cdot \sin(2 \cdot \pi \cdot \frac{t}{365}), \text{ where } t = \text{day of year.}$$

Embayment	<i>a</i>	<i>b</i>	<i>c</i>
Little Sodus	10.5	11.8	7.38
South Sandy	9.77	13.5	7.18
Sterling	9.90	13.5	5.43
South Colwell	8.71	15.0	6.63

Appendix 3.5. Model specifications.

Energy budget equation

Our model is a modification of the bioenergetics model developed by Kitchell et al. (1977):

$$C = G + W + M ,$$

where C is the energetic equivalent of prey biomass consumed, G is energy used for somatic and gonadal growth, W includes energetic losses to egestion and excretion, and M includes metabolic costs for maintenance and food ingestion. These terms are all expressed as specific rates ($\text{g wet} \cdot \text{g wet}^{-1} \cdot \text{d}^{-1}$). In the model presented here, G is allocated to three compartments as opposed to two; somatic growth (B), lipid storage (L), and gonadal growth (G). We include 5 state variables in the model: fish biomass, lipid weight, and gonad weight, and the proportions of assimilated energy shunted to lipid and gonad growth.

Consumption

To account for temperature effects on consumption (C ; $\text{g wet} \cdot \text{g wet}^{-1} \cdot \text{d}^{-1}$), we calculated C by multiplying B_{cons} by a temperature function, $f_{p,T}$ (Hanson et al. 1997), equation 2). Parameter values for this and all subsequent model equations are provided in Appendix 3.6.

$$C = f_{p,T} \cdot B_{\text{cons}} , \tag{3}$$

where

$$f_{p,T} = v_p^{x_p} \cdot e^{x_p \cdot (1 - v_p)}$$

and

$$z_p = \log(c_q) \cdot (c_{tm} - c_{to})$$

$$y_p = \log(c_q) \cdot (c_{tm} - c_{to} + 2)$$

$$x_p = \frac{z_p^2 \cdot (1 + (1 + \frac{40}{y_p})^{0.5})^2}{400}$$

$$v_p = \frac{c_{tm} - T}{c_{tm} - c_{to}}$$

Water temperature, T , is determined as described above.

Waste

Waste includes egestion (F) and excretion (U) defined by Hanson et al. (1997) as:

$$F = f_a \cdot T^{f_b} \cdot e^{f_g \cdot p} \cdot C \quad (4)$$

$$U = u_a \cdot T^{u_b} \cdot e^{u_g \cdot p} \cdot (C - F) \quad (5)$$

The proportion of maximum consumption (p) is:

$$p = \frac{C}{C_{\max} \cdot f_{p,T}},$$

where C_{\max} is the maximum consumption rate (g wet·g wet⁻¹·d⁻¹), such that.

$$C_{\max} = c_a \cdot W_{fish}^{c_b},$$

and W_{fish} is the weight (g) of the yellow perch.

Metabolism

Metabolic costs were calculated using a modified version of Hanson et al. (1997), in which

$$M = SMR \cdot ACT + SDA \cdot (C - F), \quad (6)$$

where SMR is the standard metabolic rate, ACT is the ratio of active to standard metabolism, and SDA (Appendix 3.6) is the energetic cost of food digestion.

$$SMR = R_{\max} \cdot f_{r,T},$$

where R_{\max} is maximum respiration and $f_{r,T}$ is a respiration temperature function.

$$R_{\max} = r_a \cdot y^{r_b}$$

and

$$f_{r,T} = v_r^{x_r} \cdot e^{x_r \cdot (1 - v_r)},$$

where

$$z_r = \log(r_q) \cdot (r_{tm} - r_{to})$$

$$y_r = \log(r_q) \cdot (r_{tm} - r_{to} + 2)$$

$$x_r = \frac{z_r^2 \cdot (1 + (1 + \frac{40}{y_r})^{0.5})^2}{400}$$

$$v_r = \frac{r_{tm} - T}{r_{tm} - r_{to}}.$$

$$ACT = (A + SMR) / SMR.$$

Kitchell et al. (1977) and Hanson et al. (1997) set $ACT = 1$, which assumes swimming activity in perch is negligible. However, several authors (Kerr 1982, Boisclair and Leggett 1989, Boisclair 1992, Boisclair and Sirois 1993) argue that assuming negligible active metabolism in actively foraging fish is incorrect and leads to erroneous bioenergetics estimates. Kerr (1982) proposed that active metabolism is positively and linearly related to ration (i.e. greater energy is exerted with greater foraging). Tests of this hypothesis have supported the positive nature of the relationship, suggesting it may be linear or logarithmic (Boisclair and Leggett 1989, Boisclair 1992). Therefore, in place of using the ACT parameter employed by Hanson et al. (1997), we included functions for active metabolism and ACT as described in Boisclair and Leggett (1989). Active metabolism is defined as:

$$A = \frac{\left(\text{Ration} \cdot f_{p,T} - \frac{SMR}{\tau} \right) \cdot R_{\max}}{C_{\max} - \frac{SMR}{\tau}},$$

where τ is the proportion of energy consumed that is assimilated for growth and metabolic processes minus SDA (Boisclair and Leggett 1989).

$$\tau = \frac{C - F - E}{C} - SDA,$$

and $SDA = 0.172$ (Hanson et al. 1997). ACT is then calculated as:

$$ACT = (A + SMR) / SMR.$$

Production

Energy available for growth (prod; $\text{g} \cdot \text{d}^{-1}$) was calculated as

$$\text{Prod} = W_{fish} \cdot (C - F - U - M), \tag{7}$$

This energy is then allocated to three compartments – state variables, lipids (L), gonads (G), and somatic tissue (B) – based on empirical data in the literature. We assumed that total lipids each year reach a pre-spawning mass equal to 14% of perch body weight (Hayes and Taylor 1994) and ovaries reach a pre-spawning mass equal to 20% of female perch body mass (Karås and Thoreson 1992, Hayes and Taylor 1994,

Henderson et al. 2000). Similarly, testes reach a pre-spawning mass that is 10% of male perch body mass (Hayes and Taylor 1994). Additionally, we assumed that fish can decide where to allocate energy (somatic biomass, lipid, biomass, or gonad biomass growth) instantaneously based on their current lipid:somatic biomass and gonad:somatic biomass ratios. To maintain these ratios, we created state variables for the fraction of production energy going to lipids (state variable L_{frac}) and gonads (state variable G_{frac}) at each time as follows.

$$\frac{d}{dt} L_{frac} = \alpha \cdot L_{frac} \cdot B_{frac} \cdot \left(L_{tar} - \frac{L}{B} \right),$$

$$\frac{d}{dt} G_{frac} = \alpha \cdot G_{frac} \cdot B_{frac} \cdot \left(G_{tar} - \frac{G}{B} \right),$$

and

$$B_{frac} = 1 - L_{frac} - G_{frac},$$

where α defines how rapidly (in days) allocation adjusts to positive or negative deviations from target lipid and gonad end-of-year ratios, L_{tar} is the target pre-spawning lipid:somatic biomass ratio, and G_{tar} is the target pre-spawning gonad:somatic biomass ratio before lipids are metabolized and shunted to gonadal growth (see below; Table 3.3). Somatic (B), lipid (L), and gonadal (G) growth in biomass ($\text{g}\cdot\text{d}^{-1}$) at each time step are:

$$\frac{d}{dt} B = B_{frac} \cdot \text{prod}, \tag{8}$$

$$\frac{d}{dt} L = L_{frac} \cdot \text{prod}, \tag{9}$$

and

$$\frac{d}{dt} G = G_{frac} \cdot \text{prod}. \tag{10}$$

We assumed that the majority of feeding, and subsequently, growth only occurs from 1 May through 30 September (Persson 1983). During winter, stored energy (i.e., lipids) is metabolized for maintenance and gonadal growth (Hayes and Taylor 1994, Henderson et al. 2000). To estimate the proportion of lipids required for winter maintenance (Lip.Metab; Appendix 3.7), the amount of mass-specific energy needed ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) for winter metabolism was divided by lipid biomass at the end of the growing season. The amount of mass-specific energy needed for winter metabolism was estimated by calculating waste and metabolic costs at 4 °C across a range of fish biomass at the end of the growing season and dividing by fish biomass. Proportions of

lipids required for winter maintenance differed among age classes, but were consistent across the embayments, regardless of size at age. Lipids also are metabolized for gonadal growth. To calculate this, we assumed that lipids drop to 4% body mass after spawning (Hayes and Taylor 1994) and calculated the amount of lipid mass metabolized for gonadal growth (Lip.gonad) as

$$\text{Lip.gonad} = L - \text{Lip.Metab} \cdot L - 0.04 \cdot B, \quad (11)$$

where L is lipid mass at the end of the growing season, Lip.Metab is the proportion of pre- lipid mass metabolized for winter maintenance, and B is perch biomass at the end of the growing season. Lip.gonad is added to gonad biomass at the end of the growing season to calculate total pre-spawning gonad biomass. Similar to lipid mass, gonad mass is assumed to drop to 2% of body mass after spawning (Hayes and Taylor 1994). We estimated female fecundity from empirical relationships between egg production and fish biomass (HendBiom; Henderson et al. 2000) and egg production and gonad biomass (HendGon; Henderson et al. 2000).

$$\text{HendBiom} = 209.19 \cdot B - 3604.5, \quad (12a)$$

$$\text{HendGon} = 574.2 \cdot G + 5495.9, \quad (12b)$$

Male model alterations.

We altered the model to create a male version by decreasing G_{frac} to 0.004, for a gonad:body weight ratio of about 13% (Hayes and Taylor 1994). We assumed activity rates were higher for males, to account for slower growth compared to females, despite lower allocation of energy to gonads. We multiplied active metabolism, A , by 3.0 to reflect reasonable differences in size at age based on reports in the literature (Tanasichuk and Mackay 1989, Henderson et al. 2000) and otolith data.

Appendix 3.6. Description and values for parameters used in the model. All parameter values are from Hanson et al. (1997).

Term	Description	Value
c_a	Intercept of C_{max} (effect of mass on consumption)	0.25
c_b	Slope of C_{max} (effect of mass on consumption)	-0.27
c_q	Slope for temperature effect on consumption	2.3
c_{tm}	Maximum observed temperature preference	28
c_{to}	Optimum temperature for consumption and growth	23
f_a	Intercept for the proportion of consumption egested	0.158
f_b	Coefficient for temperature effect on egestion	-0.222
f_g	Coefficient for effect of feeding level (p) on egestion	0.631
u_a	Intercept for the proportion of consumption excreted	0.0253
u_b	Coefficient for temperature effect on excretion	0.58
u_g	Coefficient for effect of feeding level (p) on excretion	-0.299
r_a	Intercept of R_{max} (effect of mass on respiration)	0.0108
r_b	Slope of R_{max} (effect of mass on respiration)	-0.2
r_q	Slope for temperature effect on respiration	2.1
r_{tm}	Maximum (lethal) temperature for respiration	33
r_{to}	Optimum temperature for respiration	28
SDA	Specific dynamic action; energy required for food digestion and absorption	0.172
α	Adjustment rate of production energy allocation to lipids and gonads	0.02
L_{tar}	Target lipid:somatic biomass ratio	0.14
G_{tar}	Target gonad:somatic biomass ratio before lipid contribution	
	Female	0.11
	Male	0.0042

Appendix 3.7. Proportion of lipids required for winter maintenance (*Lip.Metab*), based on the amount of mass-specific energy needed for winter metabolism and lipid biomass at the end of the growing season.

Year	1	2	3	4	5	6	7
Proportion	0.071	0.054	0.047	0.042	0.040	0.038	0.036

Appendix 3.8. Otolith weight (g) at age (y) estimates for YOY, female, and male yellow perch in each study embayment. Emb = embayment. YOY were not identified as female or male.

Emb	Age	Mean weight	
		Female	Male
LS	0	3.38	3.38
LS	1	5.69	6.30
LS	2	20.3	17.9
LS	3	31.2	25.8
LS	4	43.6	36.5
LS	5	48.8	47.6
LS	6	64.6	54.4
LS	7	96.9	58.3
SS	0	3.38	3.38
SS	1	3.59	3.46
SS	2	15.1	17.0
SS	3	30.1	26.1
SS	4	41.9	
SS	5		
SS	6		
SS	7		
ST	0	5.32	5.32
ST	1	7.78	7.36
ST	2	22.0	16.3
ST	3	35.6	25.3
ST	4	48.2	26.7
ST	5	64.4	35.3
ST	6	96.9	
ST	7		
SC	0	4.53	4.53
SC	1	3.74	3.78
SC	2	13.6	11.0
SC	3	18.1	16.8
SC	4	25.8	
SC	5	31.7	
SC	6	38.7	
SC	7		

Appendix 3.9. Literature estimates of yellow perch length at age. Age is in years, length is in mm TL.

Age	Length	Source	Location
0		Jobes (1952)	Lake Erie (all waters)
1	93.98	Jobes (1952)	Lake Erie (all waters)
2	170.18	Jobes (1952)	Lake Erie (all waters)
3	215.9	Jobes (1952)	Lake Erie (all waters)
4	241.3	Jobes (1952)	Lake Erie (all waters)
5	264.16	Jobes (1952)	Lake Erie (all waters)
6		Jobes (1952)	Lake Erie (all waters)
7		Jobes (1952)	Lake Erie (all waters)
0		Jobes (1952)	Saginaw Bay, MI
1	76.2	Jobes (1952)	Saginaw Bay, MI
2	134.62	Jobes (1952)	Saginaw Bay, MI
3	203.2	Jobes (1952)	Saginaw Bay, MI
4	241.3	Jobes (1952)	Saginaw Bay, MI
5	271.78	Jobes (1952)	Saginaw Bay, MI
6	304.8	Jobes (1952)	Saginaw Bay, MI
7	325.12	Jobes (1952)	Saginaw Bay, MI
0		Jobes (1952)	Green Bay, WI
1	71.12	Jobes (1952)	Green Bay, WI
2	116.84	Jobes (1952)	Green Bay, WI
3	160.02	Jobes (1952)	Green Bay, WI
4	200.66	Jobes (1952)	Green Bay, WI
5	228.6	Jobes (1952)	Green Bay, WI
6	259.08	Jobes (1952)	Green Bay, WI
7	284.48	Jobes (1952)	Green Bay, WI
0		Jobes (1952)	NW Lake Michigan, WI
1	71.12	Jobes (1952)	NW Lake Michigan, WI
2	114.3	Jobes (1952)	NW Lake Michigan, WI
3	152.4	Jobes (1952)	NW Lake Michigan, WI
4	180.34	Jobes (1952)	NW Lake Michigan, WI
5	215.9	Jobes (1952)	NW Lake Michigan, WI
6	246.38	Jobes (1952)	NW Lake Michigan, WI
7		Jobes (1952)	NW Lake Michigan, WI
0		Jobes (1952)	Lake of the Woods, MN
1	99.06	Jobes (1952)	Lake of the Woods, MN
2	137.16	Jobes (1952)	Lake of the Woods, MN
3	175.26	Jobes (1952)	Lake of the Woods, MN
4	205.74	Jobes (1952)	Lake of the Woods, MN
5	233.68	Jobes (1952)	Lake of the Woods, MN
6	266.7	Jobes (1952)	Lake of the Woods, MN
7	299.72	Jobes (1952)	Lake of the Woods, MN
0		Keast (1977)	Saginaw Bay, MI
1	115	Keast (1977)	Green Bay, WI
2	144.5	Keast (1977)	Green Bay, WI
3	181	Keast (1977)	Green Bay, WI

4		Keast (1977)	Green Bay, WI
5		Keast (1977)	Green Bay, WI
6		Keast (1977)	Green Bay, WI
7		Keast (1977)	Green Bay, WI
0		Keast (1977)	Lake Erie
1	151	Keast (1977)	Lake Erie
2	187	Keast (1977)	Lake Erie
3	216	Keast (1977)	Lake Erie
4	234	Keast (1977)	Lake Erie
5	236.5	Keast (1977)	Lake Erie
6		Keast (1977)	Lake Erie
7		Keast (1977)	Lake Erie
0		Keast (1977)	Bay of Quinte, L. Ontario
1		Keast (1977)	Bay of Quinte, L. Ontario
2		Keast (1977)	Bay of Quinte, L. Ontario
3	172	Keast (1977)	Bay of Quinte, L. Ontario
4	182	Keast (1977)	Bay of Quinte, L. Ontario
5	202	Keast (1977)	Bay of Quinte, L. Ontario
6	216	Keast (1977)	Bay of Quinte, L. Ontario
7	239	Keast (1977)	Bay of Quinte, L. Ontario
0		Keast (1977)	various
1	119	Keast (1977)	various
2	159	Keast (1977)	various
3	182	Keast (1977)	various
4	204	Keast (1977)	various
5	220	Keast (1977)	various
6	240	Keast (1977)	various
7		Keast (1977)	various
0		Keast (1977)	Massachusetts ponds
1	108	Keast (1977)	Massachusetts ponds
2	124	Keast (1977)	Massachusetts ponds
3	128	Keast (1977)	Massachusetts ponds
4	135	Keast (1977)	Massachusetts ponds
5	146	Keast (1977)	Massachusetts ponds
6	162	Keast (1977)	Massachusetts ponds
7		Keast (1977)	Massachusetts ponds
0		Keast (1977)	Connecticut
1	135	Keast (1977)	Connecticut
2	176	Keast (1977)	Connecticut
3	203	Keast (1977)	Connecticut
4	223	Keast (1977)	Connecticut
5	239	Keast (1977)	Connecticut
6	252	Keast (1977)	Connecticut
7		Keast (1977)	Connecticut
0		Keast (1977)	Clayton Lake, VA
1	124	Keast (1977)	Clayton Lake, VA
2	191	Keast (1977)	Clayton Lake, VA

3	223	Keast (1977)	Clayton Lake, VA
4		Keast (1977)	Clayton Lake, VA
5		Keast (1977)	Clayton Lake, VA
6		Keast (1977)	Clayton Lake, VA
7		Keast (1977)	Clayton Lake, VA
0		Keast (1977)	L. Memphremagog, Que.
1	110	Keast (1977)	L. Memphremagog, Que.
2	162.5	Keast (1977)	L. Memphremagog, Que.
3	195	Keast (1977)	L. Memphremagog, Que.
4	227.5	Keast (1977)	L. Memphremagog, Que.
5	257.5	Keast (1977)	L. Memphremagog, Que.
6	270	Keast (1977)	L. Memphremagog, Que.
7	275	Keast (1977)	L. Memphremagog, Que.
0		Keast (1977)	Heming Lake, Mani.
1	71	Keast (1977)	Heming Lake, Mani.
2	86	Keast (1977)	Heming Lake, Mani.
3	124	Keast (1977)	Heming Lake, Mani.
4	142	Keast (1977)	Heming Lake, Mani.
5	170	Keast (1977)	Heming Lake, Mani.
6	213	Keast (1977)	Heming Lake, Mani.
7	231	Keast (1977)	Heming Lake, Mani.
0		Keast (1977)	Lake Opinicon
1	96	Keast (1977)	Lake Opinicon
2	119	Keast (1977)	Lake Opinicon
3	136	Keast (1977)	Lake Opinicon
4	151	Keast (1977)	Lake Opinicon
5	167	Keast (1977)	Lake Opinicon
6	186	Keast (1977)	Lake Opinicon
7	208	Keast (1977)	Lake Opinicon
0	70	Rose et al. (1999)	Oneida Lake, 1958-1990
1	140	Rose et al. (1999)	Oneida Lake, 1958-1990
2	155	Rose et al. (1999)	Oneida Lake, 1958-1990
3	205	Rose et al. (1999)	Oneida Lake, 1958-1990
4	240	Rose et al. (1999)	Oneida Lake, 1958-1990
5	255	Rose et al. (1999)	Oneida Lake, 1958-1990
6	275	Rose et al. (1999)	Oneida Lake, 1958-1990
7	280	Rose et al. (1999)	Oneida Lake, 1958-1990
0		Hayes and Taylor (1994)	Little Bear Lake, MI
1		Hayes and Taylor (1994)	Little Bear Lake, MI
2	110	Hayes and Taylor (1994)	Little Bear Lake, MI
3	120	Hayes and Taylor (1994)	Little Bear Lake, MI
4	130	Hayes and Taylor (1994)	Little Bear Lake, MI
5	140	Hayes and Taylor (1994)	Little Bear Lake, MI
6	170	Hayes and Taylor (1994)	Little Bear Lake, MI
7		Hayes and Taylor (1994)	Little Bear Lake, MI
0		Hayes and Taylor (1994)	Douglas Lake, MI
1		Hayes and Taylor (1994)	Douglas Lake, MI

2	115	Hayes and Taylor (1994)	Douglas Lake, MI
3	125	Hayes and Taylor (1994)	Douglas Lake, MI
4	130	Hayes and Taylor (1994)	Douglas Lake, MI
5	135	Hayes and Taylor (1994)	Douglas Lake, MI
6	160	Hayes and Taylor (1994)	Douglas Lake, MI
7		Hayes and Taylor (1994)	Douglas Lake, MI
0		Schaeffer et al. (2000)	Sag Bay 1929-30
1	75	Schaeffer et al. (2000)	Sag Bay 1929-30
2	130	Schaeffer et al. (2000)	Sag Bay 1929-30
3	210	Schaeffer et al. (2000)	Sag Bay 1929-30
4	245	Schaeffer et al. (2000)	Sag Bay 1929-30
5	275	Schaeffer et al. (2000)	Sag Bay 1929-30
6	290	Schaeffer et al. (2000)	Sag Bay 1929-30
7	310	Schaeffer et al. (2000)	Sag Bay 1929-30
0		Schaeffer et al. (2000)	Sag Bay 1943-55
1	70	Schaeffer et al. (2000)	Sag Bay 1943-55
2	110	Schaeffer et al. (2000)	Sag Bay 1943-55
3	145	Schaeffer et al. (2000)	Sag Bay 1943-55
4	190	Schaeffer et al. (2000)	Sag Bay 1943-55
5	225	Schaeffer et al. (2000)	Sag Bay 1943-55
6	265	Schaeffer et al. (2000)	Sag Bay 1943-55
7	280	Schaeffer et al. (2000)	Sag Bay 1943-55
0		Schaeffer et al. (2000)	Sag Bay 1968-71
1	85	Schaeffer et al. (2000)	Sag Bay 1968-71
2	155	Schaeffer et al. (2000)	Sag Bay 1968-71
3	190	Schaeffer et al. (2000)	Sag Bay 1968-71
4	230	Schaeffer et al. (2000)	Sag Bay 1968-71
5	250	Schaeffer et al. (2000)	Sag Bay 1968-71
6		Schaeffer et al. (2000)	Sag Bay 1968-71
7		Schaeffer et al. (2000)	Sag Bay 1968-71
0		Schaeffer et al. (2000)	Sag Bay 1986-88
1	115	Schaeffer et al. (2000)	Sag Bay 1986-88
2	130	Schaeffer et al. (2000)	Sag Bay 1986-88
3	160	Schaeffer et al. (2000)	Sag Bay 1986-88
4	175	Schaeffer et al. (2000)	Sag Bay 1986-88
5	190	Schaeffer et al. (2000)	Sag Bay 1986-88
6	210	Schaeffer et al. (2000)	Sag Bay 1986-88
7	225	Schaeffer et al. (2000)	Sag Bay 1986-88

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