INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.
Bioenergetics of young-of-year walleye and trophic interactions in experimental ponds

Madon, Sharook P., Ph.D.
The Ohio State University, 1993
BIOENERGETICS OF YOUNG-OF-YEAR WALLEYE AND TROPHIC INTERACTIONS IN EXPERIMENTAL PONDS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of the Ohio State University

By

Sharook P. Madon, B.Sc., M.Sc., M.S.

* * * * *

The Ohio State University

1993

Dissertation Committee: Approved by
David A. Culver Advisor
Roy A. Stein Department of Zoology
William J. Mitsch
To Alysha, Rohan and Sheila

For all the love, happiness and sacrifices
ACKNOWLEDGEMENTS

I very much appreciate the guidance, support, and friendship I received from my advisor, Dr. David A. Culver throughout my doctoral program here at The Ohio State University. I would like to extend my deepest gratitude to him for the opportunities he has provided me, and for the faith he placed in the projects I undertook. I would like to thank Dr. Roy Stein, one of the finest scientists I have known, who in spite of an ever busy schedule gave so much of his time to improve my dissertation research. Drs. William Mitsch and Bruce Vondracek served on my general examination committee, and provided many useful suggestions throughout my dissertation research. I would like to thank all of my friends here at Ohio State for their support, and for making my stay a pleasant experience.

I owe this research to many people who provided valuable technical support, often involving tedious work in the laboratory and field. In particular, I would like to thank Jianguang Qin, my colleague and fellow graduate student, for selflessly giving up many hours of his sleep during the all-night sampling stints. A very big thanks to
Jim Stoeckel, Donald Stoeckel, Lisa Jackson, Darcy Uetrecht, Molly Giere, Lisa DePinto, and Mike Grove who were actively involved in field sampling, laboratory analysis, and when weather permitted, bathing (voluntary and involuntary) in the ponds and drying out near campfires. Who says research is all dull work?! A very big thanks to Ruth Pontius who, in my absence, got all documents turned in to the Graduate School on time. Jim Stafford, Robert Hesterman, Patrick Howard, and Daryl Rinker at the Hebron State Fish Hatchery, and Dick Chittum and Morton Pugh at the St. Mary's Fish Hatchery, provided help and access to the experimental ponds.

This research was funded by Federal Aid in Sport Fish Restoration Project F-57-R and administered through the Ohio Division of Wildlife. Funding was also provided via the Osburn Fellowship through the Graduate School, and the Department of Zoology, The Ohio State University.

Thanks are due to my parents, grandmother, and brother for their support, and their trust in my ability to succeed in this country. I would also like to thank my mother-in-law for helping us with both our children, and for her gentle and cheerful presence in our house. Finally, no amount of thanks can express the gratitude I feel towards my wife and children for staying by me through thick and thin, and for their numerous sacrifices - to them I dedicate this work.
VITA

September 22, 1961. . . . . . . . Born - Bombay, India

1982. . . . . . . . . . . . . . . . . . . B.Sc., St. Xavier's College, University of Bombay, Bombay, India

1982-1984. . . . . . . . . . . . M.Sc., St. Xavier's College, University of Bombay, Bombay, India

1984-1987. . . . . . . . . . . . M.S., Research Assistant, SUNY - College of Environmental Science and Forestry, Syracuse, New York, USA

1988-present. . . . . . . . . . . Research and Teaching Associate, Department of Zoology, The Ohio State University, Columbus, Ohio, USA

PUBLICATIONS


FIELDS OF STUDY

Major Field: Zoology
Research Area: Aquatic Ecology
# TABLE OF CONTENTS

**DEDICATION** ............................................ ii  
**ACKNOWLEDGEMENTS** ...................................... iii  
**VITA** ................................................... v  
**LIST OF TABLES** .................................... ix  
**LIST OF FIGURES** ................................... xii  
**INTRODUCTION** .......................................... 1  

**CHAPTER**  

I. **BIOENERGETICS MODEL FOR LARVAL AND JUVENILE WALLEYE: AN IN-SITU APPROACH USING EXPERIMENTAL PONDS**  
   Introduction ........................................... 6  
   Methods and Materials .................................. 9  
   Results .................................................. 20  
   Discussion ............................................. 26  

II. **YOUNG-OF-YEAR WALLEYE ENERGETICS IN EXPERIMENTAL PONDS: DENSITY-DEPENDENT GROWTH AND RECRUITMENT**  
   Introduction ........................................... 60  
   Methods and Materials .................................. 62  
   Results .................................................. 73  
   Discussion ............................................. 80  

III. **ZOOPLANKTON-PHYTOPLANKTON INTERACTIONS IN EXPERIMENTAL PONDS: ZOOPLANKTON COMMUNITY STRUCTURE AND THE TROPHIC CASCADE**  
   Introduction ........................................... 115  
   Methods and Materials .................................. 118  
   Results .................................................. 123  
   Discussion ............................................. 127  

vii
APPENDIX

Bioenergetics Model. .................................. 154
LIST OF REFERENCES. .................................. 158
### LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Parameter values ((g \cdot g^{-1} \cdot d^{-1})) for the adult (Kitchell et al. (1977); Hewett and Johnson (1987); cited in Fox 1991), and young-of-the-year (this study) walleye bioenergetics model.</td>
<td>36</td>
</tr>
<tr>
<td>2. Equations relating instantaneous evacuation rates ((R, h^{-1})) of YOY walleye derived via three different methods, to wet body weight ((W, g)), and temperature ((T, ^\circ C)). Instantaneous evacuation rates are derived from 24 h feeding periodicity ((ERDIEL)), and from enclosure experiments using gut evacuation for all fish ((ERGUT)), and gut evacuation for larvae and stomach evacuation for larger fish ((ERGUTSTOM)). The number of experiments ((n)), and regression statistics are given for each equation.</td>
<td>38</td>
</tr>
<tr>
<td>3. Allometric relationships for resting metabolism ((R_{REST})) and total field metabolism ((R_{TOT})), for YOY walleye in ponds, scaled to 20(^\circ C), and optimal temperature via temperature-dependence function. All units are in (g \cdot g^{-1} \cdot d^{-1}), and (g) for wet body weight ((W)). Allometry for total field metabolism is provided for one low density ((LD)), and one high density ((HD)) fish pond. Number of estimates ((n)), and regression statistics are provided.</td>
<td>39</td>
</tr>
<tr>
<td>4. Partitioning of mean square error (proportions) into systematic (mean and slope) and random (residual) components for relationship between observed wet weight or food consumption and values predicted by a bioenergetics model for YOY walleye using parameters extrapolated from adult fish (Fox 1991) and measured for YOY walleye</td>
<td></td>
</tr>
</tbody>
</table>
(this study). The YOY model is simulated at activity levels of 2, 3, 4, and variable activity. Bonferroni joint confidence intervals for the null hypothesis of an intercept (\( \beta_0 \)) of 0 and a slope (\( \beta_1 \)) of 1, and a reliability index indicating factor (\( k > 1 \)) by which model predictions are within observed values, are given for each model simulation; CI is confidence interval.

5. Mean instantaneous growth rates of YOY walleye in low and high density ponds. Date is the mid-point of the time period between which growth rates were measured. Growth rate on each date is the mean rate calculated from 4 ponds of each fish density treatment, and standard errors are included in parenthesis. P-values are based on the t-test.

6. Instantaneous evacuation rates (R, \( h^{-1} \)), of walleye in hatchery ponds, calculated by fitting negative exponential curves to gut and stomach fullness (% body weight) of fish sampled serially from food-free enclosures in one low and one high fish density pond. N is the total number of fish sampled for each evacuation rate experiment. Temperature was the mean of enclosure water temperatures taken 2-4 times during the experiment.

7. Energy budget of YOY walleye calculated for one high and two low fish density ponds. Consumption (C ± 95% CI) was calculated based on predicted evacuation rates (R) and feeding periodicity data; estimates were adjusted to account for caloric differences between fish and zooplankton (0.75C). Growth (G) was estimated using the Ricker method, and waste losses were assumed to be 0.28*C. Total field respiration (\( R_{est.} \)), standard+active+SDA respiration) was estimated as \( R_{est.} = C - G - 0.28*C \), and adjusted via the temperature-dependent function to obtain respiration at optimal temperature (\( R_{opt.} \)). Units for all energy budget parameters are g.g'1.d'1. \( R_{opt.} \) was regressed against body weight (g, wet) for ponds 15 and 19; data from pond 18 was treated as an independent data
8. Weekly mean weight specific (g·g⁻¹·d⁻¹) and absolute (g·m⁻³·d⁻¹) consumption rates of YOY walleye in low and high density ponds. Absolute weekly consumption rates are compared for the early and late fish mortality simulations. Comparisons of mean consumption rates are made using the one-way ANOVA analysis at an alpha level of 0.05.

9. Clearance rates (ml·individual⁻¹·d⁻¹) of copepods estimated from in-situ grazing experiments using Haney's (1971) technique. n refers to the numbers of copepods used in the experiments.
LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURES</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Mean gut clearance (± SE) over time in selected enclosure experiments (only 2 of 18 such experiments shown here) for (A) 9 mm larvae (N=45) with undifferentiated guts and (B) 28 mm juveniles (N=50) with differentiated stomachs. Arrow indicates time when stomach evacuation was completed.</td>
<td>42</td>
</tr>
<tr>
<td>2. Relationship between evacuation rates and wet body weight of YOY walleye ($r^2 &gt; 0.60; p &lt; 0.02$). Evacuation rates were calculated using 3 different methods; from decline in gut-fullness at night in diel samples (ERDIEL), from enclosure experiments involving decline in gut fullness for all fish sizes (ERGUT), and from decline in gut-fullness of larvae, and stomach fullness of larger fish (ERGUTSTOM). Equations relating evacuation rates to body weight and temperature for each method are given in Table 2.</td>
<td>44</td>
</tr>
<tr>
<td>3. Growth (dashed line), and assimilation (solid line) rates of YOY walleye plotted versus wet body weight, in two low density (25 fish m$^{-3}$), and one high density (50 fish m$^{-3}$) fish ponds. Consumption rates (C) were calculated using evacuation rates derived via three different methodologies (ERDIEL, ERGUT, ERGUTSTOM; Figure 2), and adjusted for waste losses ($C - 0.28C$), to yield assimilation rates.</td>
<td>46</td>
</tr>
<tr>
<td>4. Allometry of total field metabolism, and resting metabolism of YOY walleye (this study), and resting metabolism of adult walleye (from Kitchell et al. 1977; Hewett and Johnson 1987). Field metabolism estimates were derived from field growth</td>
<td>xii</td>
</tr>
</tbody>
</table>
and consumption estimates for YOY walleye in (A) a low (25 fish·m²), and (B) a high
(50 fish·m²) density pond, and under assumed waste and SDA losses. Resting
metabolism for YOY walleye was measured in dark chambers. Regressions for the
relationships are in Table 3. All values are scaled to optimal temperature (27°C).

5. Relationship between (A) the activity
parameter (ACT = activity metabolism,
RACTOPT/resting metabolism, RREST)
and (B) P-value (proportion of maximum
consumption realized), and zooplankton
biomass, and (C) the relationship between
the activity parameter and P-value. All
values are scaled to optimal temperatures
for consumption (25°C) and respiration
(27°C).

6. In-situ maximum consumption allometry of
YOY walleye (this study) and adult walleye
(from Kitchell et al. 1977). Maximum
consumption rates of YOY walleye in three
low density (10 fish·m³) fish ponds at the
Hebron State Fish Hatchery, Hebron, Ohio,
were calculated from a daily energy budget
(see methods).

7. Comparison of observed mean wet weights
(symbols, 95% CI too small in most cases
to be visible, n=45 fish for each estimate)
of YOY walleye with growth trajectories
across age predicted from a bioenergetics
model for adult walleye (Fox 1991, adult
allometric parameters, except activity = 2),
and YOY walleye with constant activity of 2,
3, 4, and activity varied according to
zooplankton biomass (this study).
C indicates period when chironomids, and
not zooplankton, were the main diet,
thereby giving a poor fit between model
predictions and observed values because
activity was predicted from zooplankton
biomass.

8. Relationship between observed wet weights
and wet weights predicted from a
bioenergetics model for adult, and YOY
walleye (Table 1) at constant, and variable
activity levels. Errors are not systematic
if values fall along the 1:1 line. See
9. Relationship between observed food consumption and food consumption predicted from a bioenergetics model for adult, and YOY walleye at constant, and variable activity levels. Errors are not systematic if values fall along the 1:1 line. See Table 4 for partitioning of mean square errors, Bonferroni Joint Confidence Intervals, and Reliability Index tests. . . . 58

10. Relationship of walleye percent survival (top panel), biomass yield (middle panel) and walleye final mean body weights (bottom panel) vs. walleye harvest density in ponds at St. Mary's Hatchery, Ohio. . . . . . . . . . . . . . . 95

11. Mean weekly percent biomass composition of prey taxa in walleye diets in the low (upper panel) and high (lower panel) fish density ponds. . . . . . . . . . . . . 97

12. Correlations of Daphnia (upper panel) and Diaptomus (lower panel) abundances vs. walleye stocking and harvest density. . . . . . . . 99

13. Correlations of Bosmina (upper panel) and Cyclops (lower panel) abundances vs. walleye stocking and harvest density. . . . . . . 101

14. Growth curves calculated via the Ricker (1975) growth method, for each pond indicating daily changes in walleye wet body weight, in low (upper panel) and high (lower panel) fish density ponds. . . . . . . . 103

15. Feeding periodicity of larval and juvenile walleye in 2 low (ponds 15 and 18), and 1 high (pond 19) fish density pond based on changes in mean gut fullness (food biomass/fish biomass) of five fish sampled from ponds at 3-h intervals. Bars below x-axis indicate period of darkness. . . . . . . . 105

16. Test of the energy budget model showing deviations of the model predicted vs. observed weight specific consumption estimates from the 1:1 line (solid line)
where predicted values \( C_p \) = estimated values \( C_q \). The dashed line is the least squares fit to predicted vs. observed consumption estimates. The mean \( C_p/C_q \) ratio = 0.96. 

17. Seasonal patterns of predicted mean daily weight specific consumption (top panel), and cohort consumption in the early (middle panel) and late (bottom panel) mortality simulations in the low and high density ponds. Chironomids in the diet in weeks 5 and 6 were not included.

18. Seasonal trends in daily mean net (solid line) and gross production (dashed line) of zooplankton biomass in the early mortality (upper panel) and late mortality (lower panel) simulations in low and high fish density ponds. The area between the solid and dashed lines indicates the magnitude of walleye population consumption on preferred microcrustacean zooplankton.

19. Mean cumulative seasonal gross production of preferred zooplankton under the early mortality (upper panel) and late mortality (lower panel) simulations in the no, low, and high fish density ponds. P-values correspond to comparisons between adjacent bars.

20. Seasonal changes in mean zooplankton biomass during April 28 - June 9, 1989 in experiments conducted at four fish density treatment levels (n=2 ponds per treatment), at the Hebron State Fish Hatchery, Hebron, Ohio.

21. One-way ANOVA comparisons of time-weighted means of net and gross primary productivity, phytoplankton respiration rate, phytoplankton gross resource, edible and inedible phytoplankton biovolumes, and various zooplankton taxa in 1989. Comparisons are across four fish density treatments. Bar connecting treatments below each graph indicates no significant difference between those treatments. Error bars are \( \pm 1 \) SE.

22. Weekly changes in the resource base of edible algae (solid line) compared against predicted zooplankton community grazing
pressure (dashed line) in ponds treated with four fish density levels in 1989, at the Hebron State Fish Hatchery. Pond numbers are given against each line for edible algae and zooplankton grazing rates to facilitate comparisons. .............................................. 138

23. Seasonal changes in mean edible and inedible phytoplankton during April 28 - June 9, 1989 in experiments conducted at four fish density treatment levels (n=2 ponds per treatment), at the Hebron State Fish Hatchery, Hebron, Ohio. .............................................. 140

24. Weekly changes in mean net and gross photosynthesis and respiration rates of phytoplankton in 1989 at the Hebron State Fish Hatchery in ponds stocked at four fish density levels. Standard error bars are shown. .................................................. 142

25. Seasonal changes in mean zooplankton biomass during April 26 - June 5, 1990 in experiments conducted at two fish density treatment levels (n=2 ponds per treatment), and one unreplicated no fish pond, at the St. Mary's Fish Hatchery, St. Mary's, Ohio. .... 144

26. One-way ANOVA comparisons of time-weighted means of net and gross primary productivity, phytoplankton respiration rate, phytoplankton gross resource, edible and inedible phytoplankton biovolumes, and various zooplankton taxa in 1990. Comparisons are across three fish density treatments. Bar connecting treatments below each graph indicates no significant difference between those treatments. Error bars are ± 1 SE. ... 146

27. Weekly changes in the resource base of edible algae (solid line) compared against predicted zooplankton community grazing pressure (dashed line) in ponds treated with three fish density levels in 1990, at the St. Mary's Fish Hatchery. Pond numbers are given against each line for edible algae and zooplankton grazing rates to facilitate comparisons. .............................................. 148

28. Seasonal changes in mean edible and inedible phytoplankton during April 26 - June 5, 1990 in experiments conducted at tow fish density
treatment levels (n=2 ponds per treatment), plus one unreplicated no fish treatment, at the St. Mary's Fish Hatchery, St Mary's, Ohio.

29. Weekly changes in mean net and gross photosynthesis and respiration rates of phytoplankton in 1990 at the St. Mary's Fish Hatchery in ponds stocked at three fish density levels. Standard error bars are shown.
INTRODUCTION

Interactions between YOY fish and their zooplankton prey play a key role in determining YOY growth and survival, and ultimately year-class strength (Shepherd and Cushing 1980; Hunter 1981; Rice et al. 1987a; 1987b; Fortier and Harris 1989; Jenkins et al. 1991). In addition, YOY fish, via effects on zooplankton prey (Dettmers and Stein 1992), can dramatically alter the phytoplankton community structure (Carpenter et al. 1985). Evaluating the mechanisms underlying interactions between YOY fish, zooplankton, and phytoplankton can shed some light on the role of YOY fish in driving community dynamics.

One way to evaluate the interactions between YOY fish and zooplankton is to quantify the impact that YOY fish have on zooplankton through ontogeny. To this end, bioenergetics models have been implemented as powerful tools to assess ecological interactions between predators and prey (Stewart and Binkowski 1986; Hayward and Margraf 1987; Lyons and Magnuson 1987; Kitchell and Hewett 1987; Hewett and Stewart 1989; Stewart 1989). Bioenergetics models require detailed weight- and temperature-dependent physiological data for the species of concern and, given a measure of growth and the
thermal regime that the fish encounters, can predict amounts of food consumption in the field (Hewett and Johnson 1987). Although many models exist for large fish, few are developed specifically for YOY fish due to logistical difficulties encountered while working with larvae and early juveniles. This project has taken advantage of replicated ponds used to raise larval walleye for stocking for estimation of bioenergetic parameters. Mechanisms underlying interactions between YOY fish, zooplankton and phytoplankton can also be evaluated via pond experiments involving manipulations of fish density. Dynamics and responses of zooplankton and phytoplankton to varying degrees of predation under variable densities of YOY fish can shed light on the role of density-dependent processes in driving community dynamics.

My dissertation research focuses on (1) developing and testing a bioenergetics model for YOY walleye, and (2) quantifying and evaluating the mechanisms underlying interactions among YOY walleye (Stizostedion vitreum), zooplankton, and phytoplankton in experimental ponds. I chose walleye because it is an important game fish in North America (Hile 1937; Schweigert et al. 1977). Human activity in recent decades has led to dramatic declines in inland walleye populations in Ohio (Trautman 1981), and it is now common practice to stock hatchery raised walleye as fingerlings into inland waters (Schneider 1969; Chesire and Steele 1972; Forney 1975; Laarman 1978). The Ohio
Department of Natural Resources has also identified natural recruitment of walleye in Lake Erie as a key research area (personal communication, Joe Mion, Aquatic Ecology Laboratory, Ohio State University). Below, I provide a brief summary of my research on these problems and present an outline of how it is arranged in the chapters in my dissertation.

Chapter I focuses on the development and testing of a bioenergetics model for YOY walleye in experimental ponds. My results indicate that larval and juvenile walleye have higher rates of gut evacuation, consumption and respiration than adults. Therefore, extrapolation of adult walleye parameters into YOY stages underestimated weight-specific physiological parameters for larval walleye. Activity costs of larval walleye were high and variable, and ranged from 1-5.5 times resting metabolic rates. Both activity metabolism, and food consumption, were positively correlated with zooplankton biomass, and activity metabolism and food consumption were linearly and positively correlated. My results indicate that activity should be modelled as a dynamic component of bioenergetics models, with variations in activity based on zooplankton biomass.

Chapter II evaluates the density-dependent growth of walleye, and zooplankton dynamics under variable predation in ponds stocked at 0, 25, and 50 walleye fry·m⁻³. I used an energy budgeting approach to quantify the impact of
planktivory by YOY walleye on zooplankton. Biomass yield of YOY walleye was correlated positively with fish harvest density, whereas mean final body weights did not differ with density. Mean instantaneous fish growth rates never differed between low and high density ponds, revealing that YOY walleye growth was density-independent. Even though mean seasonal abundances of preferred prey (Daphnia and Diaptomus) were correlated negatively with YOY stocking and harvest densities, both weight-specific consumption and population consumption by walleye in high-density ponds frequently exceeded that in low-density ponds, indicating higher zooplankton productivity at high fish densities. Seasonal gross biomass production (defined as production without fish predation) of preferred zooplankton in the high-density ponds exceeded production in no-fish and low-fish ponds. Thus, more zooplankton were available in the high density ponds, thereby buffering the effects of increased predation and maintaining walleye growth. I hypothesized that higher predation in the high-density ponds prevented algal overgrazing by zooplankton, increased algal biomass, and consequently increased zooplankton productivity. Walleye at densities of 25·m⁻³ did not influence zooplankton dynamics, and walleye <20 mm did not influence zooplankton production in either the high or low density ponds, even though mean weight-specific consumption was highest (40-139% body weight) in these fish due to high
evacuation rates. I concluded that larval walleye growth in natural systems may be density-independent simply because larval walleye are too rare to exert a predatory pressure sufficient to affect zooplankton dynamics.

In Chapter III, I tested the hypothesis generated in Chapter II that increased planktivory by YOY walleye in high density ponds increased phytoplankton biomass. Ponds were stocked at 3-4 fish density levels. I compared experiments between two years in which the size structure of the zooplankton differed; in 1989, the zooplankton community was dominated by small-bodied zooplankton such as cyclopoid copepods and *Bosmina*, whereas in 1990, large-bodied *Daphnia* and *Diaptomus* were dominant. Walleye did not suppress *Bosmina*, and although grazing by *Bosmina* on phytoplankton was considerable at the end of the 1989 experiment, edible phytoplankton biovolume did not differ between fish density treatments. Conversely, fish strongly suppressed *Daphnia* and *Diaptomus* in 1990, thereby preventing overgrazing of phytoplankton, and causing phytoplankton biomass to increase in the high-fish density treatments.

My dissertation highlights the complex changes and interactions during the ontogeny of early life stages of fish, and emphasizes the importance of trophic level interactions in regulating community dynamics and structure.
CHAPTER I

BIOENERGETICS MODEL FOR LARVAL AND JUVENILE WALLEYE:
AN IN-SITU APPROACH USING EXPERIMENTAL PONDS

Introduction

Bioenergetics models are used extensively to address problems of fisheries management (Stewart et al. 1981; 1983; Stewart and Iberra 1991), examine ecological interactions (Stewart and Binkowski 1986; Hayward and Margraf 1987; Lyons and Magnuson 1987; Kitchell and Hewett 1987; Hewett and Stewart 1989; Hewett 1989), and assess ecological risk involving effects of thermal stress and bioaccumulation of pollutants in fish populations (Hill and Magnuson 1990; Borgmann and Whittle 1992). These models are based on an energy balance equation where growth is modeled as consumption minus metabolic costs and losses as urine and feces. For many fish species, neither large fish nor larvae were used to develop models. Most use juvenile to late-juvenile sizes in lab experiments (Hewett and Johnson 1987). Relative to juvenile and adult fish, early life stages have high weight-specific consumption and metabolic rates (Mills and Forney 1981; Houde and Schekter 1893; Dabrowski 1986;
Dabrowski et al. 1988; Marmulla and Rösch 1990; Keckeis and Schiemer 1990; Houde and Zastrow, in press), and adult models generally yield poor predictions of growth and consumption of YOY fish (Post 1990).

The activity component of the bioenergetics model is poorly understood (Boisclair and Leggett 1989; Boisclair and Leggett 1991; Hewett et al. 1991; Lucas et al. 1991), and is usually assumed because of the logistic difficulty of quantifying activity metabolism in the field (Hewett and Johnson 1987). In addition, opinions differ as to whether activity should be measured as a constant (Hewett and Johnson 1987; Hewett et al. 1991) or as a variable component (Boisclair and Leggett 1987; Boisclair and Leggett 1991).

Both theoretical models (Ware 1975; 1978; Dabrowski et al. 1988; Dabrowski 1989; Dabrowski et al. 1989) and empirical studies (Hunter and Thomas 1974; Munk and Kiorboe 1985) have shown that swimming speed increases with food density. In addition, feeding rate typically increases with food density (Laurence 1977; Werner and Blaxter 1980; Houde and Schekter 1980; Mathias and Li 1982). Because metabolism correlates with swimming speed (Brett and Groves 1979; Dabrowski 1986; Rombough 1988; Kaufmann 1990; Boisclair and Tang, in press), active metabolism should increase with food density and feeding rate (Boisclair, in press). Activity costs could be particularly high and variable for planktivorous particulate feeders (Kerr 1971; Boisclair and Sirois, in press; Lucas
and Johnstone, in press), including many species of larval and juvenile fish, and directly related to food density. If this be true, then bioenergetic models must incorporate activity as a variable component. Failure of bioenergetic models to predict growth and consumption accurately in the past has often been attributed to errors induced when activity is modeled as a constant multiplier of standard metabolic rate (Minton and Mclean 1982; Boisclair and Leggett 1989; Boisclair and Leggett 1991).

Bioenergetic models (Kitchell et al. 1977; Hewett and Johnson 1987) have recently been developed to examine the growth, consumption, and production dynamics of YOY percids (Post 1990; Fox 1991). However, opinions differ on whether extrapolations of adult percid allometry to young-of-year (YOY) stages underestimate consumption and metabolic rates. Post (1990) reported that consumption and metabolic rates of YOY yellow perch were underestimated when derived from adult allometry. Conversely, Fox (1991) reported that YOY walleye did not have higher consumption or respiration rates than those predicted by allometric models based on adult fish. Species-specific physiological differences were implicated in the apparent discrepancy between YOY yellow perch and walleye models (Fox 1991).

In this study, I adapted Post's (1990) in-situ approach to develop a bioenergetics model for pond-reared YOY walleye. Metabolism of fish in the field in the in-situ
approach is calculated as the difference between measured consumption, growth and assumed waste losses, and the accuracy of field consumption estimates depends on evacuation rates (Elliot and Persson 1978). The goals of this research are to (1) develop allometric parameters of maximum consumption and metabolism specifically for larval and juvenile walleye, and (2) test whether observed growth and consumption dynamics of YOY walleye in ponds are adequately represented by allometric functions of consumption and metabolism in a bioenergetics model for adult walleye (Kitchell et al. 1977; Hewett and Johnson 1987; Fox 1991). (3) I also assessed three different methodologies involving calculation of evacuation rates in the field and enclosures. Finally, (4) I developed a submodel that included activity explicitly as a variable component to assess how variable activity influences the accuracy of a YOY walleye bioenergetics model.

Methods and Materials

Study area.

Experiments were conducted in 3 ponds (area=0.4–0.5 ha; depth=1-1.5 m) at the St. Mary's Fish Hatchery, St. Mary's, Ohio, during April 28 through June 5, 1990, and in 3 ponds at the Hebron Fish Hatchery, Hebron, Ohio, during April 22 through May 28, 1991. Ponds at the St. Mary's and Hebron Fish Hatcheries were filled with water from nearby Grand
Lake, and Buckeye Lake, respectively, 3-5 d before the experiments began, and therefore contained a natural assemblage of zooplankton.

All ponds at both hatcheries were treated with inorganic fertilizer sufficient to achieve a phosphate concentration of 0.03 mg P·L⁻¹ and inorganic nitrogen of 0.6 mg N·L⁻¹, resulting in a N:P ratio of 20:1. This N:P ratio was previously identified as an optimal nutrient regime for growth of small algae favored by zooplankton (Culver et al., in press). Walleye larvae (mean total length=8.0 mm, mean wet weight=0.0021 g) at St. Mary's Hatchery (1990) were stocked in two ponds at densities of 25 fish·m⁻³, and in one pond at 50 fish·m⁻³; at Hebron Fish Hatchery (1991), walleye larvae were stocked in all three ponds at 10 fish·m⁻³. In 1990, I determined stocking densities as:

\[ V = \frac{(SD \times 10)}{n} \]

where V represents the volume (ml) of larvae required to achieve the desired stocking density (SD), and n is the mean number of larvae counted in two to three 10 ml subsamples of larvae. In 1991, I used a commercial electronic fry counter to determine stocking density of larval walleye (Culver et al. 1992)
Zooplankton sampling:

Zooplankton were sampled every 2-3 days by towing a metered net (mouth diameter=50 cm, mesh=64 μm) for a distance of 8-13 m. During the tow, the net, attached to a 1.5 m pole, was lowered to the bottom of the pond and raised to the surface in a sigmoidal fashion to obtain a depth-integrated sample. Typical volumes sampled ranged from 1.5-2.5 m³. Samples were preserved immediately in 4% sucrose-formalin solution. In the laboratory, each zooplankton sample was diluted to 400-4000 ml. Two subsamples (2-10 ml) were then counted. Zooplankton were identified to species. For abundant taxa, I counted at least 100 individuals in each subsample; I counted all individuals in rare (< 5-10 individuals) taxa. Whenever possible, lengths (nearest 0.1 mm) of up to 20 individuals were measured for conversion to dry weight using length-weight regressions (Culver et al. 1985). Dry weights were converted to wet weights using a dry/wet weight ratio of 0.10 (Hewett and Johnson 1987).

Fish sampling:

I required field measurements of growth and consumption to develop allometric relationships for maximum consumption and field metabolism for YOY walleye. Estimating field consumption required information on gut evacuation rates and diel variation in feeding (Elliot and Persson 1978). Fish were sampled twice a week at 3 h intervals for a 24 h period.
from one high (50 fish·m⁻³) and two low (25 fish·m⁻³) density ponds in 1990 to estimate feeding periodicity and growth; in 1991 fish were sampled weekly from three low density ponds (10 fish·m⁻³) to estimate growth. In both years, during the first three weeks of the experimental period, larvae were captured with a dip-net (0.5 m diameter), and later with a seine, and preserved in 10% formalin.

Evacuation rates for YOY walleye were estimated via enclosure experiments conducted on days when diel samples were taken. I added 100-200 fish to food-free enclosures in one low fish and one high fish pond, either during midday or at dusk. Initially, 10 fish were preserved in 10% formalin; five fish were subsequently sampled from enclosures at 0.5-1 h intervals for 5-14 h depending on fish size and water temperature, and preserved in 10% formalin. Larger fish with differentiated stomachs were examined immediately under the microscope, and the time when stomachs of at least 80% of the fish were completely evacuated was noted. Water temperatures measured 2-4 times throughout the experiment.

I removed intestinal tracts from samples of 10 fish collected twice a week (N=120 fish), removed the food, and weighed empty intestinal tracts to the nearest 0.1 mg. I then quantified the relationship between fish wet weight and the wet weight of an empty intestinal tract. Intestinal tracts with food were removed from fish sampled for feeding
periodicity and enclosure experiments, and weighed to the nearest 0.1 mg. Food weights were estimated by subtracting predicted empty intestinal tract weights from intestinal tract plus food weight. Gut fullness, expressed as the ratio of food weight to fish weight, was calculated for fish collected during the feeding periodicity and evacuation rate enclosure experiments.

Energy densities:

No data exist on the energy density of YOY walleye. Tarby (1977) reported that the energy density of YOY yellow perch ranged from about 800 cal·g⁻¹ wet weight in June to 1,000 cal·g⁻¹ wet weight in October. During this period, moisture content decreased from 85 % to 78 %. Dry/wet weight data indicated that pond-reared YOY walleye (9-40 mm; 0.005-0.4 g wet weight) had a relatively constant moisture content of 85 % (Madon, unpublished data), allowing us to assume that larval walleye had a relatively constant energy density of 800 cal·g⁻¹ wet weight. I also assumed a constant energy density of 600 cal·g⁻¹ wet weight for zooplankton (Cummins and Wuychuck 1971; Hewett and Stewart 1987; Post 1990).

Evacuation rate methods:

I used three different methods to calculate evacuation rates. (1) ERDIEL: I calculated evacuation rates in two low
and one high density ponds (N=33; 11 feeding periodicity experiments in each pond) from maximal rate of decline in whole gut fullness from midnight to dawn when fish were presumably not feeding. The other two methods involved enclosure experiments conducted in one low and one high density pond. (2) ERGUT: I calculated evacuation rates for all fish sizes by fitting a negative exponential curve to the point when 80-90% of the gut was empty (i.e., when food in gut did not decline further). (3) ERGUTSTOM: this method differed from ERGUT in that evacuation rates for larger fish with differentiated stomachs were based only on stomach evacuation. Initial stomach fullness was calculated as the difference between the initial whole gut weight and the weight of the gut at time when stomachs were empty, and only stomach evacuation times were used.

For each method, evacuation rates were pooled for all ponds (n=3 ponds; ERDIEL), and enclosures (n=2 enclosures; ERGUT, ERGUTSTOM) as they did not differ (ANCOVA, p > 0.27 for both temperature and body weights as covariates, after test for homogeneity of slopes, p > 0.12). A relationship was developed for each method between evacuation rate, fish wet body weight, and temperature using multiple linear regression. Feeding periodicity and predicted evacuation rates were incorporated into the Elliot and Persson (1978) model to estimate daily consumption. Daily weight-specific growth rates were derived using the Ricker (1975) method as
presented in Yamashita and Bailey (1989) from 45 fish collected twice a week from each of three ponds.

I tested the validity of the three methods for calculating evacuation rates via an energy balance approach. I adjusted daily consumption (C) estimates to 0.75C (C_{adj}) to account for differences in caloric densities of YOY walleye and zooplankton prey. To obtain assimilation (A), I adjusted C_{adj} for fecal losses which were assumed to be 25% of consumption, a typical value for young fish (Brett and Groves 1979);

\[ A = C_{adj} - 0.25(C_{adj}). \]

Respiration.

Resting metabolic rates (R_{rest}) were measured for YOY walleye (0.0037-0.5807 g mean wet weight) in 250-500 ml bottles using Winkler titration. Temperatures of pond water during the experiment ranged from 17-26.5°C. I used trough, as well as pond-reared walleye to measure respiration rates. Walleye were isolated in dark 40-L food-free aquaria for at least 24 h before the experiment; aquaria were immersed in troughs receiving pond water.

Depending on body size, 1 to 14 walleye fry were transferred to each bottle (n=3) containing water from the aquaria; two control bottles (n=2) had no fish. Fish were incubated for 3-6 h, and temperatures during these
experiments ranged from 17-26°C. Initial dissolved oxygen content at the beginning of the experiment was measured (nearest 0.01 mg·L⁻¹). Fish usually settled down within 10 min of transfer to bottles, and activity was minimum. At experiment's end, water was siphoned into 100 ml bottles for Winkler titration. All fish were preserved in 10% formalin and their body weights measured (nearest 0.1 mg).

Total oxygen deficit in each bottle was adjusted for deficit in the controls, and $R_{\text{REST}}$ (g·g⁻¹·d⁻¹) was calculated using an oxycalorific value of 3.24 cal·mg⁻¹ O₂ (Elliott and Davidson 1975) and 800 cal·g⁻¹ fish tissue (Tarby 1977). $R_{\text{REST}}$ estimates were adjusted to 20°C ($R_{\text{REST}20°C}$) and optimal temperature ($R_{\text{RESTOPT}}$) using the temperature-dependent function (see Table 1), and regressed against mean body weight.

Total field respiration ($R_{\text{TOT}}$) was calculated as the difference between measured in-situ consumption ($C$) and growth ($G$), and waste losses (Table 1) (as per Post 1990) for one high (50 fish·m⁻³) and one low (25 fish·m⁻³) density pond in 1990. Calculated respiration rates were adjusted to respiration at 20°C ($R_{\text{TOT20°C}}$) and optimal temperature ($R_{\text{TOTOPT}}$) using the temperature-dependent function (Table 1). Relationships between $R_{\text{TOT20°C}}$, $R_{\text{TOTOPT}}$, and wet body weight were developed separately for the low and high fish density ponds.

Activity respiration ($R_{\text{ACT}}$) was calculated as the
difference between field consumption, growth, waste losses and SDA (assumed to be 10% of consumption, Tarby 1977). The activity parameter (ACT), calculated as $R_{ACTOPT}/R_{RESTOPT}$, and the proportion of maximum consumption ($P$ value = consumption/$C_{MAX}$ at optimal temperature) were related to zooplankton biomass (zooplankton were collected 1 day before measurements of growth and consumption) for one low and one high density pond.

**Maximum consumption.**

Allometric parameters for maximum consumption of YOY walleye were derived using Post's (1990) in-situ approach in three experimental ponds stocked with walleye fry at 10 fish·m$^{-3}$ during April 22 through May 28, 1991, at the Hebron Fish Hatchery. Growth was monitored by seining and weighing a sample of 10 fish; and daily weight-specific growth rates ($G$) were calculated using the Ricker (1975) growth method (in Yamashita and Bailey 1989). Respiration ($R_{EST}$) in these ponds was predicted via the low density in-situ model of respiration at optimal temperature ($R_{TOTOPT}$, Table 2), and adjusted to pond temperatures via the temperature-dependent function. Mean body weights of YOY walleye in the three ponds were larger than any sizes noted in ponds stocked with higher fish densities, and ranged from 0.634-0.824 g at the end of 6 wks. In addition, *Daphnia* and copepod densities
were commonly around 400-500 organisms·L⁻¹, and peaked at over 1000 individuals·L⁻¹. I therefore assumed that ad libitum feeding conditions in these ponds allowed for near maximal consumption of YOY walleye. Ambient maximum consumption estimates ($C_{\text{MAX}}$), adjusted for assumed 28% waste losses (Table 1) were calculated as:

$$C_{\text{MAX}} = (G + R_{\text{EST}})/0.72$$

Ambient maximum consumption estimates were adjusted to maximum consumption at 20 °C ($C_{\text{MAX20°C}}$) and optimal temperature ($C_{\text{MAXopt}}$) using the temperature dependence function (Table 1). The allometric relationship between $C_{\text{MAX20°C}}$, $C_{\text{MAXopt}}$, and body weight was represented by the line with the lowest intercept value that encompassed all $C_{\text{MAX}}$ values (Post 1990).

I tested the allometric relationship of $C_{\text{MAX}}$ developed for adult (Kitchell et al. 1977; Hewett and Johnson 1987; Fox 1991) and YOY walleye (this study) using $P$ values derived from field consumption estimates ($P$ value = Field consumption estimates adjusted to optimal temperature/$C_{\text{MAXopt}}$). I used Fox's (1991) estimate of field consumption for YOY walleye (Table 3 in Fox (1991)). Estimates for which growth was negative were not included. I also used field consumption estimates for YOY fish derived in this study to calculate $P$ values.
Model simulations.

A previous bioenergetics model for YOY walleye used allometric parameters of consumption and respiration derived from adult fish (Fox 1991). I used Fox's (1991) model, (henceforth called the adult model), and the YOY model derived from this study to estimate growth and consumption, and compared these estimates to observed growth and consumption in one independent low density pond. Growth in wet weight was predicted using observed consumption estimates; consumption was predicted by fitting predicted growth to observed growth to derive P-values, which were then incorporated into the model to derive consumption. The YOY model was simulated at activity (ACT) levels of 2, 3, 4, and variable activity, for both growth and consumption. I used zooplankton biomasses measured in the independent pond to predict variable activity levels (ACT) from the relationship between ACT and zooplankton biomass. For the consumption simulations, I used ACT predicted from the ACT - zooplankton biomass relationship, and used the ACT estimates to predict P values from the P value - ACT relationship.

I compared model predictions with observed values for weight and consumption using (1) partitioning of mean square error, (2) Bonferroni joint confidence intervals, and (3) the Leggett and William (1981) reliability index (see Rice and Cochran 1984, Wahl and Stein 1991 for details on these tests). In the first test, the mean square error of
predicted vs. observed values is partitioned into the mean, slope (systematic errors), and residual (random errors) components; proportions of the mean and slope components close to 0, and random component close to 1 indicate that the errors are not systematic. Bonferroni joint confidence intervals test the null hypothesis that the intercept and slope of the predicted vs. observed values are 0 and 1, respectively. The reliability index \( (k) \) indicates the model predictions being within a factor of \( k \) of observed values.

Results

Evacuation rates.

Negative exponential fits best described gut evacuation of YOY walleye over time in the enclosure experiments (Figure 1). Gut evacuation proceeded rapidly in the smallest larvae (within 0.5 h), but was considerably slower in larger fish at the same temperatures (Figure 1). However, relative to gut clearance, stomach evacuation was completed in a short period of time (Figure 1). Evacuation rates \( (R, \text{ } \text{h}^{-1}) \) using all three methods declined exponentially with body weight (Figure 2), and scaled linearly with temperature (Table 2). I tested for differences among these models (Table 2) using test of homogeneity of slopes and ANCOVA. All slopes were homogeneous \( (F < 1.29, p > 0.26) \); model ERGUTSTOM
consistently provided higher evacuation rates than either models ERDIEL or ERGUT (F > 43.74, p < 0.0001).

I calculated consumption using feeding periodicity data and evacuation rates derived via each of the three methods, and calculated assimilation as consumption adjusted for waste losses for a range of walleye sizes. I then compared assimilation with weight-specific growth rates across walleye body weights. Growth exceeded assimilation 40-90% of the time across body weights in all ponds when evacuation rates were derived from models ERDIEL and ERGUT (Figure 3). Only evacuation rates derived from model ERGUTSTOM resulted in assimilation estimates consistently higher than growth across body weights in all ponds (Figure 3).

Respiration.

The slope of the allometric relationship between resting metabolism and body weight for YOY walleye (Table 2) did not differ from that of -0.20 for standard metabolism for adult walleye (Kitchell et al. 1977, Table 3) at optimal temperature (test of slopes, t=0.214, p=0.5); however, YOY resting metabolism was 1.6 times higher than that of adults across the range of body weights examined (Figure 4).

The allometric relationship of total metabolism in the field was not significant across body weights in the high density pond (Figure 4, Table 3); however, field metabolism
differed between high and low density ponds (ANCOVA, F=4.32, p=0.05). Allometric relationships of field metabolism in both low and high density ponds were higher than resting metabolism (ANCOVA, F > 47.0, p < 0.0001). As body weights increased (0.0037-0.5807 g), the difference between mean field metabolism and YOY resting metabolism declined from 4.2X to 1.7X in the low density pond, but increased from 2.1X to 4.8X in the high density pond (Figure 4).

Both ACT and P value increased as a power of zooplankton biomass (Figure 5). ACT increased linearly with P value (Figure 5). The relationship with P value as the dependent variable was:

\[
P \text{ value} = 0.271 + 0.153(\text{ACT}); \ r^2=0.95, \ p<0.0001, \ n=20.
\]

Because correlations between two ratios (ACT and P value) could potentially be spurious (Jackson et al. 1990), I assessed the relationship between weight-specific active metabolism \( R_{\text{ACTOPT}} \) and weight-specific consumption \( C_{\text{OPT}} \) scaled to optimal temperature:

\[
R_{\text{ACTOPT}} = 0.436 - 0.034(C_{\text{OPT}}); \ r^2=0.91, \ p<0.0001, \ n=20
\]

The strong positive relationship in the above equation indicates that the correlations between the ratios ACT and P value are not spurious.
Maximum consumption.

The allometric relationship between CMAX and body weight (Figure 6) was:

\[ \text{CMAX_{CTO}} = 0.45 \ W^{-0.27} \]

\[ \text{CMAX_{20^{\circ}C}} = 0.35 \ W^{-0.27} \]

where \( \text{CMAX} \) is in units of \( g \cdot g^{-1} \cdot d^{-1} \) at optimum temperature for consumption (CTO, Table 1) and \( W \) is in g wet weight. The slope of the \( \text{CMAX_{CTO}} \) function for YOY walleye was the same as that for adult walleye (Kitchell et al. 1977, Table 1), but the intercept and the regression were 1.8 times higher (Table 1, Figure 6).

I calculated P values based on adult and YOY walleye \( \text{CMAX} \) allometry (Table 1) using field consumption estimates derived by Fox (1991), and consumption generated from one low and one high density pond (this study). The adult \( \text{CMAX} \) relationship yielded P values ranging from 0.1-1.45 for Fox's (1991) consumption estimates (P value > 1.0 for 4 of 26 consumption estimates), and 0.69-1.89 for estimates derived in this study (P values > 1.0 for 18 of 29 consumption estimates). Conversely, the reparameterized relationship for YOY walleye yielded P values ranging from 0.054-0.803 for Fox (1991) estimates, and 0.38-1.0 for estimates in this study.
Model Simulations.

I predicted wet weight and consumption by incorporating adult parameters of consumption and respiration with activity set at 2 times standard metabolism (Fox 1991), and the YOY model (this study). The YOY walleye model was run at various constant activities as well as variable activities. Predicted wet weights and consumption were compared with independent estimates of wet weights and consumption observed in one low density pond. Predicted wet weights were substantially overestimated by both the adult model and the YOY model with activity level of 2 times resting metabolism, and were underestimated by the YOY model with activity level set at 4 times resting metabolism (Figure 7). Conversely, wet weight predictions via either the YOY model with activity of 3 times resting metabolism or activity varied in accordance with zooplankton biomass, closely matched the observed growth curve in the pond (Figure 7). In the YOY model simulation with variable activity, the final predicted wet weight overestimated observed wet weight by 49%; this could have occurred because activity during the last week was predicted from crustacean zooplankton biomass, when actually, a large proportion of walleye diet consisted of chironomids. Since I were unable to establish a relationship between ACT and benthos biomass because of limited benthos biomass ranges,
predicting ACT based on crustacean zooplankton biomass may result in spurious activity levels when benthos are eaten. I therefore eliminated this data from further analysis.

I used partitioning of mean square errors derived via regressions of observed values of wet weight (Figure 8) and consumption (Figure 9) on predicted values to evaluate deviations between observed and predicted values. The adult model, and the YOY model with ACT of 2 and 4 times resting metabolism yielded regressions of observed on predicted wet weights, which deviated substantially from 1:1. Differences in the slope component accounted for the largest systematic errors; Bonferroni joint confidence intervals did include an intercept of 0, but not a slope of 1 (Table 4). The reliability index \( k \) for wet weight was 3.69 for the adult model, and 1.8 and 2.93 for the YOY model with ACT of 2 and 4, respectively (Table 4); this indicated that model predictions overestimated or underestimated mass by as much as an order of magnitude (Figure 8). Regressions of observed on predicted wet weights derived via the YOY model with ACT of 3 and variable activity, did not deviate substantially from the 1:1 line (Figure 8), and the largest errors were due to the random component (Table 4). In these cases, Bonferroni joint confidence intervals included an intercept of 0 and a slope of 1 (Table 4). The reliability index for the YOY model with variable activity \( (k=1.24) \) was marginally better than that for ACT of 3, indicating that
model predictions of wet weight were within 3-21% of observed values.

Regressions of observed consumption on consumption predicted via the adult, and YOY model with ACT of 2 deviated substantially from the 1:1 line (Figure 9), and the largest systematic errors were due to the mean component (Table 4). For these cases, Bonferroni joint confidence intervals included an intercept of 0, but not a slope of 1 (Table 4). The index \( k \) was 1.86 for the adult model, and 1.4 for the YOY model with ACT of 2 (Table 4), indicating that model predictions generally underestimated observed consumption by 11-135%. The YOY model with ACT of 3, 4, and variable activity did not deviate substantially from the 1:1 line (Figure 9), and the largest errors were due to the random component (Table 4). Bonferroni joint confidence intervals included an intercept of 0 and a slope of 1 for these simulations; the index \( k \) was 1.26, 1.30, and 1.32 for the ACT of 3, 4, and variable activity simulations, respectively, indicating that the model predicted reasonably accurately (Table 4).

Discussion

Evacuation rates.

The Elliot and Persson (1978) method for estimating fish daily ration in the field requires accurate estimates of gut evacuation rates (Ney 1990). Evacuations rates are
influenced by temperature (Persson 1979; 1981; 1982; 1986), fish body size, continuity of feeding, and stomach fullness (Noble 1973; Krasnopeyor 1989), and the quantity, type and size of prey eaten (Persson 1979; 1981; Mills et al. 1984). Laboratory-derived estimates of evacuation rates usually cannot account for all of the above factors, and may lead to large errors when applied to field estimates of stomach fullness to calculate daily ration (Ney 1990; Fox 1991).

Because of the shortcomings of applying laboratory-derived estimates of evacuation rates to field data, biologists have attempted to estimate evacuation rates directly from the field by fitting a negative exponential to decline in stomach fullness during periods when feeding presumably ceases (Post 1990; Fox 1991; Dettmers and Stein 1992).

Fitting negative exponentials to the decline in gut fullness of fish for feeding periodicity (ERDIEL) underestimated evacuation rates, causing estimates of weight-specific consumption to be lower than weight-specific growth. Underestimated evacuation rates would be a particular problem for larval fish which have short gut evacuation times due to a short, simple tube-like guts. In this study, larvae at 21°C cleared 80% of their guts within 0.5 h. Consequently, fitting a curve to field gut fullness data collected every 3 h (equivalent to assuming at least a 3 h evacuation time) would yield much lower estimates of gut evacuation rates and consumption. Evacuation rates for
larger larvae and juveniles with differentiated stomachs in my food-free enclosures also were underestimated when calculated based on whole gut evacuation times (ERGUT). Only by using much shorter stomach evacuation times could I improve estimates of evacuation rate (ERGUTSTOM). To estimate evacuation rates in field populations of larval fish which completely cease feeding during the post-dusk to dawn period, sampling every 15-30 min after dusk, instead of every 3 h, should yield better estimates of gut evacuation rates (Dettmers and Stein, 1992). Conversely, in fish populations such as YOY walleye, which may not always cease feeding in the post-dusk period (Madon and Culver, unpublished data), evacuation rates need to be calculated from fish placed into food-free enclosures. After stomach differentiation, only stomach evacuation rates need be used.

**Respiration.**

Resting metabolism of YOY walleye was higher than that of adults, although change with body size was similar. In general, weight-specific resting metabolism of larval fish is higher than that of adults (Kamler 1992). However, during the experiments to determine resting metabolism, it was not possible to acclimate YOY walleye to the test chambers; in addition, it was necessary to add more that one larva per chamber to produce a detectable oxygen deficit. The lack of acclimation to test chambers, and the possible
interactions among fish may have elevated metabolism of YOY walleye over resting levels, and may have contributed to some of the difference between YOY and adult resting metabolism.

Activity metabolism, a dynamic component of the energy budget, has been correlated positively with food availability and food consumption (Hunter and Thomas 1974; Kerr 1982; Kerr and Dickie 1985; Munk and Kiorboe 1985; Dabrowski et al. 1988; Boisclair and Leggett 1989; Boisclair and Sirois 1993). My results support these studies; active metabolism (ACT) and food consumption (P value) were correlated as powers of zooplankton biomass; active metabolism increased dramatically with food consumption. The large variation in the activity-zooplankton biomass relationship (Figure 5 A) probably reflects variations in feeding success at any given zooplankton biomass. At any given prey level, whether high or low, feeding bouts ending in failure to capture prey will prolong feeding activity, thereby increasing activity metabolism. Conversely, successful feeding will quickly lead to satiation, at least in juvenile fish, and thereby, reduced activity costs.

Total field metabolism (referred to as active metabolism, but also includes SDA costs) varied across fish body weight and with fish density. Variation of active metabolic rate with fish density reflected varying degrees of food availability and food consumption in the ponds.
Initially, activity costs were higher at low fish density than at high fish density because of higher food densities and food consumption in the low density pond (Madon and Culver, unpublished work). Near experiment's end, increased predation by walleye lowered zooplankton density, freeing zooplankton from intraspecific competition, which resulted in a compensatory increase in zooplankton production (Culver et al. 1992). Increased food availability and food consumption in the high density pond at experiment's end caused higher activity costs of fish.

Throughout the experiment, activity costs were highly dynamic, ranging from 1.03 to 5.47 times YOY resting metabolism. Larval fish generally exhibit higher active to resting metabolic ratios than adult fish, with values ranging from 1.5 to 15 depending on species and temperature (Brett and Groves 1979, Rombough 1988, Kamler 1992). Post (1990) reports that mean active metabolism in larval yellow perch is 4.4 times resting metabolism of adults; active metabolism of YOY walleye in my study, when compared to adult resting metabolism (same adult resting metabolism relationship used by Post; in Kitchell et al. 1977, Hewett and Johnson 1987) ranged from 1.65 to 8.75 times adult resting metabolism. Because I used fish smaller than Post's yellow perch, I cannot determine whether higher values of active metabolism are due to species differences or size differences. Fox (1991) assumed that the allometry for
standard metabolism of adult sauger (*Stizostedion canadense*) (Minton and McLean 1982) applied to YOY walleye, and assumed that active metabolism of YOY walleye in ponds was two times standard metabolism of adult sauger. My calculations indicate that the allometry for standard metabolism of adult walleye (Kitchell et al. 1977; Table 1, this study) yield metabolic rates that are about 1.2-1.5 times the Minton and McLean (1982) relationship (J·h⁻¹) for fish of 0.005-0.8 g wet weight at optimal temperature (assuming 4.181 J·cal⁻¹, a caloric density of 1000 cal·g⁻¹ wet weight, and oxycalorific value of 3,240 cal·g⁻¹ 0₂). Because the Kitchell et al. (1977) model for standard metabolism underestimates metabolism for YOY walleye, Minton and McLean’s (1982) model used by Fox (1992) leads to far greater underestimates of standard metabolism.

**Maximum consumption.**

Maximum weight-specific consumption of YOY walleye in my ponds exceeded adult consumption (Kitchell et al. 1977), although the slope of the allometric relationship for YOY and adult fish was similar. My results seemingly conflict with those of Fox (1991), who reported that extrapolation of adult consumption to YOY did not underestimate YOY maximum consumption. If I use consumption estimates derived by Fox (1991) for my data, then P values ranged from 0.1-1.89; P values > 1.0 indicate that the allometry for maximum
consumption is underestimated. Clearly, in agreement with Post (1990), back-extrapolation of adult rates underestimates YOY rates.

**YOY walleye model.**

Because dynamics of YOY fish are highly variable and poorly understood (Sissenwine 1984), bioenergetic models could be used as powerful tools in furthering understanding of growth and consumption dynamics of early life stages (Laurence 1977; Houde and Schekter 1983; Yamashita and Bailey 1989). My results agree with those of Post (1990) who reported that allometric parameters for adult fish underestimate consumption and respiration when extrapolated to YOY stages. Because both $C_{\text{MAX}}$ and metabolic costs were underestimated by the adult walleye model (Fox 1991), wet weight was overestimated and consumption was underestimated for YOY walleye.

There are differing opinions on whether activity should be modelled as a constant (Hewett and Johnson 1987; Hewett et al. 1991), or as a dynamic component (Boisclair and Leggett 1991) in bioenergetic models. Using the YOY model with ACT of 3 or ACT-variable, predicted from zooplankton biomass, improved model predictions of growth and consumption substantially. I emphasize here that using an ACT of 3 yielded model predictions close to observed values of growth and consumption for YOY walleye in my ponds simply
because ACT predicted from zooplankton biomass ranged from 1.47-3.0, with most values close to 3.0. Therefore, using a constant ACT of 3 in future modelling with YOY walleye may not always yield accurate model predictions. Planktivores, in general, have high metabolic costs associated with foraging for large numbers of small and mobile prey (Kerr 1971a; b; this study). I concur with Boisclair and Leggett (1989, 1991) that activity be modelled as a variable component of bioenergetic models, at least for actively feeding planktivores and benthivores, which include the early life stages of most fish species. Unfortunately, this entails collecting consumption and growth data to generate activity respiration for a range of prey abundances for prey of different types (i.e., separate relationships likely exist for crustacean zooplankton and benthos) as I have done here. This approach assumes that most field activity is related to food availability and consumption, and that activity costs related to all other activities (predator avoidance, position maintenance, etc.) are negligible. Accuracy of activity estimates depends on accurate consumption values, which in turn depends on precise measures of evacuation rates.

Although bioenergetics models have been used extensively to address consumption and growth patterns of fish in nature, only few field tests have provided good fits between model predictions and observed data (Rice and
Cochran 1984; Beauchamp et al. 1989). Other tests of bioenergetic models have indicated poor fits due to inaccurate model parameters, in particular, activity metabolism (Minton and McLean 1982; Boisclair and Leggett 1989; Wahl and Stein 1991) or inaccurate field estimates of consumption (Diana 1983). Post's (1990) in-situ approach for modifying allometric parameters of consumption and respiration, adapted to my ponds, adequately addressed allometry in YOY fish; the model, corrected for YOY parameters, provided good fits between observed and predicted estimates of growth and consumption. The in-situ approach is particularly valuable given the problems associated with extrapolating laboratory-derived physiological parameters to field data (MacKenzie et al. 1990).

A field test for a YOY fish bioenergetic model that was not statistically rigorous, provided consumption estimates for YOY walleye 40% higher than observed values (Fox 1991). Predictions were improved when the Kitchell et al. (1977) standard respiration model was substituted with the more conservative model for adult sauger (Minton and McLean 1982) with a constant activity parameter of 2. However, the latter model failed to provide good fits between observed and predicted values of growth and consumption for YOY walleye in my ponds. Even though model predictions may be improved by changing a sensitive parameter such as activity,
predictions may not always be accurate because activity may depend on highly variable factors such as water temperature, prey mobility, prey distribution, prey availability, and the presence of other fish (see literature cited in Boisclair and Leggett 1989). Therefore, predicting activity from a prey availability parameter such as zooplankton biomass provides a strong biological basis for incorporating flexibility in the bioenergetics model to improve predictions.
Table 1. Parameter values \((g \cdot g' \cdot d')\) for the adult (Kitchell et al. (1977); Hewett and Johnson (1987); cited in Fox 1991), and young-of-the-year (this study) walleye bioenergetics model.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter description</th>
<th>Adult</th>
<th>YOY</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA</td>
<td>Intercept for maximum consumption</td>
<td>0.25</td>
<td>0.45</td>
</tr>
<tr>
<td>CB</td>
<td>Slope for maximum consumption</td>
<td>-0.27</td>
<td>-0.27</td>
</tr>
<tr>
<td>CTO</td>
<td>Optimum temperature for consumption</td>
<td>22</td>
<td>25</td>
</tr>
<tr>
<td>CTM</td>
<td>Maximum temperature for consumption</td>
<td>28</td>
<td>28</td>
</tr>
<tr>
<td>CQ</td>
<td>Slope of temperature dependence</td>
<td>2.3</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td><strong>Consumption</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RA</td>
<td>Intercept for maximum standard respiration</td>
<td>0.035 b</td>
<td>0.056</td>
</tr>
<tr>
<td>RB</td>
<td>Slope for maximum standard respiration</td>
<td>-0.20 b</td>
<td>-0.22</td>
</tr>
<tr>
<td>RTO</td>
<td>Optimal temperature for standard respiration</td>
<td>27 b</td>
<td>27</td>
</tr>
<tr>
<td>RTM</td>
<td>Maximum temperature for standard respiration</td>
<td>32 b</td>
<td>32</td>
</tr>
<tr>
<td>RQ</td>
<td>Slope for temperature dependence</td>
<td>2.1 b</td>
<td>2.1</td>
</tr>
<tr>
<td>ACT</td>
<td>Activity respiration multiplier</td>
<td>1.0</td>
<td>3.0</td>
</tr>
<tr>
<td>S</td>
<td>Specific dynamic action coefficient</td>
<td>0.172</td>
<td>0.1</td>
</tr>
</tbody>
</table>
Table 1. Continued

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter description</th>
<th>Adult</th>
<th>YOY</th>
</tr>
</thead>
<tbody>
<tr>
<td>FA</td>
<td>Fecal loss coefficient</td>
<td>0.158</td>
<td>0.25</td>
</tr>
<tr>
<td>UA</td>
<td>Urinary loss coefficient</td>
<td>0.0253</td>
<td>0.07</td>
</tr>
</tbody>
</table>

**Waste Losses**

* Original units in g O\textsubscript{2}·g\textsuperscript{-1}·d\textsuperscript{-1} (Hewett and Johnson 1987), are converted to g·g\textsuperscript{-1}·d\textsuperscript{-1} using oxycalorific value of 3,240 cal·g\textsuperscript{-1} O\textsubscript{2}, and predator caloric density of 1000 cal·g\textsuperscript{-1}.

* The adult walleye standard respiration model (J·h\textsuperscript{-1}) used in this study is: \(0.803 \cdot 10^\text{act} \cdot \text{Wass}\) (Minton and McLean 1982) with ACT=2.0 (Fox 1991); the Kitchell et al. (1977) model for which parameter values are given here yields standard respiration rates of 1.2-1.5 times Minton and McLean equation in the range of body weights observed in this study.

* ACT should preferably be varied according to zooplankton biomass (see discussion).
Table 2. Equations relating instantaneous evacuation rates ($R \cdot h^{-1}$) of YOY walleye derived via three different methods, to wet body weight ($W, \text{g}$), and temperature ($T, ^\circ\text{C}$). Instantaneous evacuation rates are derived from 24 h feeding periodicity (ERDIEL), and from enclosure experiments using gut evacuation for all fish (ERGUT), and gut evacuation for larvae and stomach evacuation for larger fish (ERGUTSTOM). The number of experiments ($n$), and regression statistics are given for each equation.

<table>
<thead>
<tr>
<th>Method</th>
<th>Equation</th>
<th>$n$</th>
<th>Regression Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$r^2$</td>
</tr>
<tr>
<td>ERDIEL</td>
<td>$\ln(R) = -1.884 + 0.883\ln(W) + 0.191\ln(W)^2 + 0.065(T)$</td>
<td>29</td>
<td>0.636</td>
</tr>
<tr>
<td>ERGUT</td>
<td>$\ln(R) = -4.561 + 0.461\ln(W) + 0.224\ln(W)^2 + 0.125(T)$</td>
<td>18</td>
<td>0.794</td>
</tr>
<tr>
<td>ERGUTSTOM</td>
<td>$\ln(R) = -1.515 + 0.219\ln(W) + 0.078\ln(W)^2 + 0.007(T)$</td>
<td>18</td>
<td>0.825</td>
</tr>
</tbody>
</table>
Table 3. Allometric relationships for resting metabolism ($R_{\text{rest}}$) and total field metabolism ($R_{\text{tot}}$), for YOY walleye in ponds, scaled to 20°C, and optimal temperature via temperature-dependence function. All units are in g·g⁻¹·d⁻¹, and g for wet body weight (W). Allometry for total field metabolism is provided for one low density (LD), and one high density (HD) fish pond. Number of estimates (n), and regression statistics are provided.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>T (°C)</th>
<th>Allometry</th>
<th>n</th>
<th>Regression Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$r^2$</td>
</tr>
<tr>
<td>$R_{\text{rest}}$</td>
<td>20</td>
<td>$R_{\text{restOC}} = 0.042 W^{0.22}$</td>
<td>24</td>
<td>0.686</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$R_{\text{restOPT}} = 0.056 W^{0.22}$</td>
<td>24</td>
<td>0.686</td>
</tr>
<tr>
<td>$R_{\text{tot}}$</td>
<td>20</td>
<td>LD: $R_{\text{TOTOC}} = 0.062 W^{0.41}$</td>
<td>10</td>
<td>0.600</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HD: $R_{\text{TOTOC}} = 0.221 W^{0.06}$</td>
<td>10</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td></td>
<td>LD: $R_{\text{TOTOPT}} = 0.083 W^{0.41}$</td>
<td>10</td>
<td>0.600</td>
</tr>
<tr>
<td></td>
<td></td>
<td>HD: $R_{\text{TOTOPT}} = 0.295 W^{0.06}$</td>
<td>10</td>
<td>0.032</td>
</tr>
</tbody>
</table>
Table 4. Partitioning of mean square error (proportions) into systematic (mean and slope) and random (residual) components for relationship between observed wet weight or food consumption and values predicted by a bioenergetics model for YOY walleye using parameters extrapolated from adult fish (Fox 1991) and measured for YOY walleye (this study). The YOY model is simulated at activity levels of 2, 3, 4, and variable activity. Bonferroni joint confidence intervals for the null hypothesis of an intercept ($\beta_0$) of 0 and a slope ($\beta_1$) of 1, and a reliability index indicating factor ($k > 1$) by which model predictions are within observed values, are given for each model simulation; CI is confidence interval.

<table>
<thead>
<tr>
<th>Model</th>
<th>Sources of error</th>
<th>Bonferroni joint CI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Slope</td>
</tr>
<tr>
<td>Adult</td>
<td>0.218</td>
<td>0.770</td>
</tr>
<tr>
<td>YOY: ACT=2</td>
<td>0.184</td>
<td>0.586</td>
</tr>
<tr>
<td>YOY: ACT=3</td>
<td>0.001</td>
<td>0.025</td>
</tr>
<tr>
<td>YOY: ACT=4</td>
<td>0.153</td>
<td>0.181</td>
</tr>
<tr>
<td>Model</td>
<td>Sources of error</td>
<td>Bonferroni joint CI</td>
</tr>
<tr>
<td>------------------</td>
<td>------------------</td>
<td>---------------------</td>
</tr>
<tr>
<td></td>
<td>Mean</td>
<td>Slope</td>
</tr>
<tr>
<td>YOY: ACT= variable</td>
<td>0.067</td>
<td>0.124</td>
</tr>
<tr>
<td>Adult</td>
<td>0.394</td>
<td>0.053</td>
</tr>
<tr>
<td>YOY: ACT=2</td>
<td>0.151</td>
<td>0.028</td>
</tr>
<tr>
<td>YOY: ACT=3</td>
<td>0.009</td>
<td>0.008</td>
</tr>
<tr>
<td>YOY: ACT=4</td>
<td>0.047</td>
<td>0.001</td>
</tr>
<tr>
<td>YOY: ACT= variable</td>
<td>0.038</td>
<td>0.021</td>
</tr>
</tbody>
</table>

**Food Consumption**
Figure 1. Mean gut clearance (± SE) over time in selected enclosure experiments (only 2 of 18 such experiments shown here) for (A) 9 mm larvae (N=45) with undifferentiated guts and (B) 28 mm juveniles (N=50) with differentiated stomachs. Arrow indicates time when stomach evacuation was completed.
A. Stomachs not differentiated

Mean wt.=0.0053g

$T = 21^\circ C$

$GC = 0.055 \cdot e^{-0.443 T_{\text{final}}}$

$p=0.018$

B. Stomachs differentiated

Mean wt.=0.1800g

$T = 21^\circ C$

$GC = 0.049 \cdot e^{-0.59 T_{\text{final}}}$

$p=0.0002$

Figure 1.
Figure 2. Relationship between evacuation rates and wet body weight of YOY walleye ($r^2 > 0.60; p < 0.02$).

Evacuation rates were calculated using 3 different methods; from decline in gut-fullness at night in diel samples (ERDIEL), from enclosure experiments involving decline in gut fullness for all fish sizes (ERGUT), and from decline in gut-fullness of larvae, and stomach fullness of larger fish (ERGUTSTOM). Equations relating evacuation rates to body weight and temperature for each method are given in Table 2.
Figure 2.
Figure 3. Growth (dashed line), and assimilation (solid line) rates of YOY walleye plotted versus wet body weight, in two low density (25 fish·m$^{-3}$), and one high density (50 fish·m$^{-3}$) fish ponds. Consumption rates (C) were calculated using evacuation rates derived via three different methodologies (ERDIEL, ERGUT, ERGUTSTOM; Figure 2), and adjusted for waste losses (C - 0.28C), to yield assimilation rates.
Walleye Growth (---) and Assimilation (----) Rates (g.g⁻¹.d⁻¹)

A. Low Fish Density

- ERGUTSTOM
- ERDIEL
- ERGUT

B. Low Fish Density

C. High Fish Density

Wet Weight of Walleye (g)

Figure 3.
Figure 4. Allometry of total field metabolism, and resting metabolism of YOY walleye (this study), and resting metabolism of adult walleye (from Kitchell et al. 1977; Hewett and Johnson 1987). Field metabolism estimates were derived from field growth and consumption estimates for YOY walleye in (A) a low (25 fish·m⁻³), and (B) a high (50 fish·m⁻³) density pond, and under assumed waste and SDA losses. Resting metabolism for YOY walleye was measured in dark chambers. Regressions for the relationships are in Table 3. All values are scaled to optimal temperature (27°C).
Respiration Rate of Walleye (g.g⁻¹.d⁻¹)

A. Low Fish Density

1.000

YOY Field Estimates

YOY Resting Estimates

Adult Resting

B. High Fish Density

1.000

YOY Field Estimates

YOY Resting Estimates

Adult Resting

Wet Weight of Walleye (g)

Figure 4.
Figure 5. Relationship between (A) the activity parameter (ACT = activity metabolism, $R_{ACT/\text{OPT}}$/resting metabolism, $R_{\text{REST/\text{OPT}}}$), and (B) P-value (proportion of maximum consumption realized), and zooplankton biomass, and (C) the relationship between the activity parameter and P-value. All values are scaled to optimal temperatures for consumption (25°C) and respiration (27°C).
Figure 5.
Figure 6. In-situ maximum consumption allometry of YOY walleye (this study) and adult walleye (from Kitchell et al. 1977). Maximum consumption rates of YOY walleye in three low density (10 fish·m$^{-3}$) fish ponds at the Hebron State Fish Hatchery, Hebron, Ohio, were calculated from a daily energy budget (see methods).
Figure 6.

\[ C_{\text{MAX}} \text{ of Walleye (g.g}^{-1}.d^{-1}) \]

\begin{align*}
\text{Wet Weight of Walleye (g)}
\end{align*}

YOY $C_{\text{MAX}} = 0.45 \ W^{-27}$

N=106

Adult $C_{\text{MAX}} = 0.25 \ W^{-27}$
Figure 7. Comparision of observed mean wet weights (symbols, 95% CI too small in most cases to be visible, n=45 fish for each estimate) of YOY walleye with growth trajectories across age predicted from a bioenergetics model for adult walleye (Fox 1991, adult allometric parameters, except activity = 2), and YOY walleye with constant activity of 2, 3, 4, and activity varied according to zooplankton biomass (this study). C indicates period when chironomids, and not zooplankton, were the main diet, thereby giving a poor fit between model predictions and observed values because activity was predicted from zooplankton biomass.
Figure 7.
Figure 8. Relationship between observed wet weights and wet weights predicted from a bioenergetics model for adult, and YOY walleye (Table 1) at constant, and variable activity levels. Errors are not systematic if values fall along the 1:1 line. See Table 4 for partitioning of mean square errors, Bonferroni Joint Confidence Intervals, and Reliability Index tests.
Figure 8.
Figure 9. Relationship between observed food consumption and food consumption predicted from a bioenergetics model for adult, and YOY walleye at constant, and variable activity levels. Errors are not systematic if values fall along the 1:1 line. See Table 4 for partitioning of mean square errors, Bonferroni Joint Confidence Intervals, and Reliability Index tests.
Predicted Food Consumption of Walleye (g,g⁻¹.d⁻¹)

ADULT: Fox (1991)

YOY: ACT=2

YOY: ACT=3

YOY: ACT=4

YOY: ACT=Variable

Observed Food Consumption of Walleye (g,g⁻¹.d⁻¹)

Figure 9.
CHAPTER II

YOUNG-OF-YEAR WALLEYE ENERGETICS IN EXPERIMENTAL PONDS:
DENSITY-DEPENDENT GROWTH AND RECRUITMENT

Introduction
Mechanisms driving recruitment variability in freshwater and marine systems have remained poorly understood (Sissenwine 1984). Fishery biologists have long recognized that the early life stages drive recruitment dynamics via variable production and typically low survival rates (Braum 1978; Sherman and Lasker 1981; Lasker 1981; 1987; Leiby 1984; Houde 1987; Cushing 1988). Both biotic factors (predation on eggs, larvae and juveniles, and starvation related to timing of food availability) and abiotic factors (fluctuations in temperature and salinity, and larval transport and retention) govern recruitment processes (Hunter 1981; Parrish et al. 1981; Creeco and Savoy 1985; Rice et al. 1987a; 1987b; Bailey and Houde 1989).

Density-dependent processes in these early-life stages are believed to be important to recruitment (Shepherd and Cushing 1980). Density-dependent control suggests that at
high larval fish abundances, zooplankton prey will be depleted, leading to intra- and inter-specific competition, which slows larval growth. Slow growth exposes larvae to longer periods of size-dependent predation (Miller et al. 1988), thereby causing high larval mortality. The implicit assumption in density-dependent control is that predation by larval fish affects zooplankton abundance, reducing food levels to where larval growth is reduced. Conversely, if prey resources were unaffected, no competition would occur and thereby, no reduction in larval growth. Studies that support density-dependent mechanisms via predatory impact of larval fish on zooplankton are abundant (e.g., Kiorboe et al. 1988; Bollens 1988; Savoy and Crecco 1988; Fortier and Harris 1989; Jenkins et al. 1991) as are those that refute it (Cushing 1983; Dagg et al. 1984; Peterson and Ausubel 1984; Monteleone and Peterson 1986; Jenkins 1987; Taggart and Leggett 1987). However, strong evidence for density-dependent regulation at the larval stage remains sketchy at best (Taggart and Leggett 1987; Houde 1989), and in fact, density-dependence seems to be more important in the juvenile stages (Houde 1987).

Herein, I examine the interaction between zooplankton dynamics and vital rates of walleye larvae and juveniles under varying densities in hatchery ponds. Research addressed three specific questions: (1) is growth of larval and juvenile walleye density-dependent, (2) if growth is
density-dependent, is growth reduced due to lower food availability, and (3) if food availability is lower at high fish densities, is this reduced availability due to fish consumption?

My approach involved developing an energy budget model based on the in-situ method of Post (1990) using two ponds, then testing the model consumption predictions against measured consumption from another pond, and finally using the model to predict consumption of zooplankton in all ponds. I also quantified zooplankton dynamics under changing predation pressures.

Methods and Materials

Experimental Design

Experiments were conducted in 10, 0.4-0.5 ha ponds (depth=1.5 m) during April 28 through June 5, 1990, at the St. Mary's State Fish Hatchery, St. Mary's, Ohio, USA. Experiments were part of a larger experiment to quantify the effects of fertilizer (inorganic and organic) and fish density manipulations on planktonic communities and fish production (Qin et al., unpublished manuscript). Ponds were filled with water from Grand Lake, St. Mary's, 4-5 d before the experiment began, and therefore contained a natural assemblage of zooplankton. Five ponds were treated weekly with organic fertilizer (alfalfa meal at 2.5 mg/L); five were treated with inorganic fertilizer (sufficient to
achieve a phosphate concentration of 0.03 mg P/L and
inorganic nitrogen of 0.6 mg N/L, resulting in a N:P ratio
of 20:1). Fish density treatments were crossed with
fertilizer treatments yielding the following design: For
each fertilizer treatment (five ponds), two ponds were
stocked with 25 walleye larvae per m³ (henceforth called low
density ponds), two with 50·m⁻³ (high density ponds). One
pond from each fertilizer treatment contained no fish.
Walleye larvae (age=2-3 d, mean total length=8.0 mm, mean
wet weight=0.0021 g) were stocked in all ponds on April 28;
stocking densities were determined by counting a subsample
(n=2-3, variability 5-10%) of a known volume of larvae (10-
20 ml, measured in a graduated cylinder) freed from as much
excess water as possible, and then measuring the appropriate
volume of larvae needed to achieve the required stocking
density. Ponds were drained on June 5-6 after a period of
approximately 6 weeks. The bottom of the ponds slope
towards the center, which leads to a concrete collection
well at one end where all fish are collected. Pond yield
was determined by weighing the total catch from each pond.
Mean wet weights were determined from a sample of 25-50
individuals; harvest densities were calculated as yield/mean
wet weight.

Zooplankton were sampled every 2-3 days by towing a
metered net (mouth diameter=50 cm, mesh=64 μm) for a
distance of 8-13 m. During the tow, the net, attached to a
5 foot wooden pole, was continually lowered to the bottom of the pond and raised to the surface in a sigmoidal fashion to obtain a depth-integrated sample. Typical volume sampled ranged from 1.5-2.5 m$^3$. Samples were preserved immediately in 4% sucrose-formalin solution. From two subsamples (2-5 ml) of each zooplankton sample, zooplankton were identified to species, counted, and measured ($N$=20, when possible, nearest 0.1 mm). For abundant taxa, I counted at least 100 individuals in each subsample; I counted all individuals in rare (< 5-10 individuals) taxa. Lengths were converted to dry weight using length-weight regressions (Culver et al. 1985). Dry weights were converted to wet weights using a dry/wet weight ratio of 0.10 (Hewett and Johnson 1987).

I tested the effects of fish density and fertilizer treatments on walleye growth, consumption, yield, survival, weights at harvest, zooplankton production and abundances using a two-way ANOVA with an alpha of 0.05. Because fertilizer treatment was insignificant for any variable tested, I combined ponds with organic and inorganic fertilizer treatments within each fish density treatment.

**Fish Diet Characterization**

I estimated mean proportional biomass contribution of zooplankton prey by genus and chironomids to total food biomass in fish diets on a weekly basis from five fish taken from each pond. Whole fish guts were dissected, prey
removed, identified to genus, counted, and measured (at least 10 taxon⁻¹) for conversion to biomass using length-weight regressions (Culver et al. 1985). Percent biomass contribution of each prey taxon to total diet was then calculated from mean individual weight and abundance.

Energy Budget of YOY Walleye

I used the in-situ approach proposed by Post (1990) to develop energy budget parameters for YOY walleye in ponds, based on a mass-balance equation:

\[ C = G + R + W \]

where \( C \) = consumption, \( G \) = growth, \( R \) = respiration, and \( W \) = waste losses. I assumed waste losses to be 28% of consumption \((0.28C)\), as per Brett and Groves (1979). This assumption allows us to simplify the equation to:

\[ C = G + R + 0.28C \]

Units for all parameters in the above model are \( g \cdot g^{-1} \cdot d^{-1} \). I assumed that zooplankton prey had a caloric density of 600 cal\( \cdot g^{-1} \) wet weight of tissue, and YOY fish had 800 cal\( \cdot g^{-1} \) wet weight (Hewett and Johnson 1987; Tarby 1977). Consumption estimates were adjusted therefore to 0.75C.
**In-situ growth (G):**

Wet weights of at least 10 fish per pond, collected via seining from 10:00-13:00 h, were measured for each bi-weekly sample (nearest 0.1 mg). Daily growth (g) and daily weight-specific growth rates (g\cdot g^{-1}) were then estimated using the Ricker (1975) growth method (in Yamashita and Bailey 1989):

\[ W_t = W_0 e^{Gt}; \quad G = (\ln W_t - \ln W_0)/t, \]

\[ W_t = W_0 (1+k)^t, \text{ where } k = e^G - 1 \]

\( W_t \) is the mean wet weight on day \( t_2 \), \( W_0 \) is the mean wet weight on day \( t_1 \), and \( G \) is the instantaneous growth rate over \( t \) days. Weight specific growth rate (g\cdot g^{-1} \cdot d^{-1}) = [(W_t - W_0)/t]/W_0.

**In-situ consumption (C):**

In-situ consumption estimates required gut evacuation rates and diel variation in feeding, all as a function of body size. Fish were captured bi-weekly at 3-h intervals for a 24 h period from one high-density and two low-density ponds. During the first three weeks, larvae were captured with a dip-net (0.5 m diameter), and later with a seine. Fish were immediately preserved in 10% formalin for analysis of diel variation in feeding.
To estimate evacuation rates (N=11), I added 100-200 fish to food-free enclosures in one low fish and one high fish pond bi-weekly, either during midday or at dusk, on days when diel samples were taken. Initially, 10 fish were preserved in 10 % formalin; five fish were subsequently sampled from enclosures at 0.5-1 h intervals for 5-14 h depending on fish size, and preserved in 10 % formalin. Water temperatures measured 2-4 times throughout the experiment varied 2-5°C during the experiment. However, mean water temperature was assumed to adequately represent temperature the fish experienced during the experiment.

I removed the intestinal tracts from a bi-weekly sample of 10 fish (N=120 fish), recovered all food items, and weighed the empty intestinal tracts (nearest 0.1 mg). I then quantified how fish wet weight and the wet weight of an empty intestinal tract were related. Whole intestinal tracts were removed from fish sampled for the evacuation rate experiments, and food weight estimated by subtracting predicted empty intestinal tract weights from whole intestinal tract weight. Gut fullness, expressed as the ratio of food weight to fish weight, was calculated for each 0.5-1 h sample; instantaneous evacuation rates (R; h⁻¹) were calculated by fitting a negative exponential curve to the time-dependent gut fullness data. Evacuation rates were calculated based on whole intestinal tracts in small larvae with undeveloped stomachs, using 80-90% gut emptiness.
(coinciding with the flat portion of the negative exponential evacuation rate curve) as the cut-off point. In larger fish with differentiated stomachs I based the rates only on stomach evacuation, assuming that the fish would feed once its stomach was empty. Evacuation rates calculated from the enclosure experiments were pooled for both ponds as they did not differ statistically (ANCOVA, p > 0.05 for both temperature and body weights as covariates), and a predictive relationship was developed between evacuation rate, fish body weight, and temperature using a multiple linear regression model.

Feeding periodicity was determined following the method described in Post (1990). Five fish from each 3-h sample were weighed, whole intestinal tracts were removed, blotted, and weighed (nearest 0.1 mg). Gut fullness was calculated as described above; feeding periodicity was determined from the change in gut fullness over 24 h. Feeding periodicity and predicted evacuation rates were incorporated into the Elliot and Persson (1978) model to estimate daily consumption rates.

In-situ respiration (R):

For one low and one high fish density pond, total field respiration (standard + active + specific dynamic action costs) was calculated as the difference between measured in-situ consumption (C) and growth (G), and waste losses (W);
A second low density pond provided an independent test of the energy budget model predictions. Calculated respiration rates were adjusted to respiration at optimal temperature ($R_{opt}$) based on the temperature-dependence algorithm given in Hewett and Johnson (1987), where optimal temperature was 27°C. A relationship between $R_{opt}$ and wet body weight was developed separately for the low and high density ponds.

**Model consumption predictions:**

Daily walleye consumption for each of the eight experimental ponds was predicted using the estimated daily weight specific growth and respiration relationships developed for the low and high fish density ponds. Consumption estimates were adjusted for waste losses:

$$\text{Predicted } C = \frac{(G + R)}{0.72}$$

Respiration was adjusted for ambient pond temperatures using the temperature-dependent function.

Model consumption predictions were compared with measured consumption estimates from one independent low fish density pond to test how closely the model predictions matched the measured consumption estimates. Because it was logistically not possible to get independent data from
another high density pond, I could not test the model for this density level. I used two statistical tests to evaluate how closely model predictions matched observed consumption (Rice and Cochran 1984, Wahl and Stein 1991). Decomposition of mean square error (MSE) evaluated sources of errors in the model for predicting consumption:

\[ \text{MSE} = \frac{1}{n} \sum_{i=1}^{n} (P_i - A_i)^2 \]

\[ = (\bar{P} - \bar{A})^2 + (S_p - rS_A)^2 + (1 + r^2)S_A^2 \]

\[ = Z + S + R; \]

where \( n \) is the number of paired observations; \( P_i \) and \( A_i \) are predicted and observed data, respectively; \( \bar{P}, \bar{A}, S_p, \text{ and } S_A \) are means and standard deviations of \( P_i \) and \( A_i \); and \( r \) is their correlation coefficient. The mean square error representing the variance around the 1:1 line in the least squares regression of observed on predicted values can be partitioned as; (1) the mean component (\( Z \)) or error due to differences in means of observed and predicted values, (2) the slope component (\( S \)) or error resulted from the slope deviating from unity, and (3) the residual component (\( R \)) or the proportion of mean square error due to random error. Values of \( Z=0, S=0, \text{ and } R=1 \) indicate that errors are not systematic. In addition, I used Bonferroni joint confidence
intervals to test the null hypothesis that regression variables have an intercept of 0 and a slope of 1 (Neter et al. 1983). Finally, I used the reliability index ($k$), a number $\geq 1$, developed by Leggett and Williams (1981):

$$
k = \frac{1 + \sqrt{\frac{1}{n} \sum_{i=1}^{n} [(1 - y_i/x_i)/(1 + y_i/x_i)]^2}}{1 - \sqrt{\frac{1}{n} \sum_{i=1}^{n} [(1 - y_i/x_i)/(1 + y_i/x_i)]^2}}
$$

$x_1, x_2, \ldots, x_n$ represent model predictions, and $y_1, y_2, \ldots, y_n$ the corresponding observed values. The interpretation of this index is that the model predictions agree with observed values within a factor of $k$. The statistical interpretation is that the model is accurate within a factor of $k$ if about 68% of observed values lie between $1/k$ and $k$ times the predicted values (Leggett and Williams 1981). I also compared mean weekly estimates of weight specific and absolute consumption in the low and high density ponds to test whether consumption was lower in the high density ponds.

**Zooplankton Biomass Production and Fish Predation**

Standing crop biomass (wet weight, adjusted by dry/wet ratio of 0.10) of the most commonly found microcrustacean zooplankton in walleye diet (*Daphnia, Diaptomus*, and *Cyclops*, defined hereafter as preferred) were combined for
the pond zooplankton samples, and daily net biomass production (g wet wt·m⁻³·d⁻¹), defined as zooplankton production after fish related losses was calculated:

\[
\text{Daily net zooplankton biomass production (DNBP)} = \frac{(B_t - B_0)}{t}
\]

\(B_t\) is the standing crop biomass (g wet wt·m⁻³) on day \(t_2\), \(B_0\) is the standing crop biomass (g wet wt·m⁻³) on day \(t_1\), and \(t\) is time in days.

Next, for each pond, I calculated the daily absolute consumption (g food wet wt·m⁻³·d⁻¹) of preferred zooplankton biomass by fish throughout its ontogeny using the weight specific consumption estimates predicted by the model:

\[
\text{Daily absolute consumption (DAC)} = (PC\times\text{FWW})\times\text{PPMZ}\times\text{FD}
\]

PC is the predicted daily weight specific consumption (g·g⁻¹·d⁻¹), FWW is the mean fish wet weight (g), PPMZ represents the proportion of preferred microcrustacean zooplankton, and FD is fish density (numbers of fish·m⁻³). Although I knew seasonal fish survival from fish counts at pond draining, I did not know when mortality had occurred during the season. I therefore calculated FD based on two mortality simulations: (1) Early Fish Mortality, where all mortality was assumed to have occurred within a day of stocking the
ponds, and (2) Late Fish Mortality, where all mortality was assumed to have occurred a week before draining.

Daily gross zooplankton biomass production (g wet wt·m⁻³·d⁻¹), i.e., production without fish predation, was calculated by adding the daily absolute fish consumption (DAC) to daily net zooplankton production (DNBP):

\[ \text{Daily gross zooplankton biomass production (DGZBP)} = \text{DNBP} + \text{DAC} \]

Seasonal gross zooplankton production was calculated for each pond by summing daily gross production (DGZBP) estimates across the whole season.

Results
Survival and Yield at Harvest

Percent survival of YOY walleye (Table 5) did not differ with stocking (ANOVA, p=0.72) or harvest density (F=0.56, r²=0.05, p=0.48; Fig. 10). Mean harvest density in high density ponds (30.1 fish·m⁻³) was about twice that in low density ponds (16.3 fish·m⁻³). Yield of fish biomass (g fish·m⁻³) increased (F=10.03, r²=0.63, p=0.02) with harvest density (Fig. 10). Mean body weights at harvest, however, did not differ (F=2.66, r²=0.31, p=0.20) with increasing harvest density (Fig. 10).
Fish Growth and Diet Composition

Mean instantaneous growth rates of larval and post-larval walleye did not differ between low and high density ponds (Table 5). Microcrustacean zooplankton (daphnids and copepods) contributed substantially to YOY walleye diets during from weeks 1-4 (Fig. 11). The calanoid copepod, *Diaptomus oregonensis*, was most important, contributing 40-90% of walleye diets in both treatments. Cyclopoid copepods *Cyclops vernalis* and *Cyclops bicupidatus thomasi* (collectively termed *Cyclops*) never provided > 40% of the diet; they were rarely eaten in week 3. *Daphnia* ranged from 5 to 48% of walleye diets during weeks 1-4 for both treatments (Fig. 11). *Bosmina* were almost never eaten; they contributed < 10% of the diet. During the last 2 weeks of the experiment, chironomid larvae and pupae played a major role in the diet of YOY walleye, providing 50 to 92% of the walleye diet (Fig. 11). *Cyclops*, and to a lesser degree, *Diaptomus* and *Daphnia*, comprised the remainder of the diet in weeks 5 and 6.

Seasonal mean abundances of *Daphnia* declined with increasing stocking (F=26.04, r²=0.77, p=0.001) and harvest (F=42.83, r²=0.84, p=0.0001) density (Fig. 12). *Diaptomus* abundance was similarly inversely related with stocking (F=6.45, r²=0.45, p=0.035) and harvest (F=8.62, r²=0.52, p=0.019) densities (Fig. 12). Using linear regression,
Bosmina appeared to be unrelated to either stocking ($F=0.03$, $r^2=0.004$, $p=0.86$) or harvest ($F=0.20$, $r^2=0.03$, $p=0.664$) density; however, Bosmina abundances actually peaked in low fish density ponds, with similar low levels in no fish and high fish ponds (Fig. 13). Cyclops abundances were unrelated with either stocking ($F=0.001$, $r^2=0.0001$, $p=0.972$) or harvest ($F=0.50$, $r^2=0.06$, $p=0.498$) density (Fig. 13).

Energy Budget of YOY Walleye

In-situ growth:

Daily growth in weight (Fig. 14) and daily growth rates were derived using the Ricker growth method for all eight ponds. Daily growth rates were high in larvae <20 mm, ranging from 20 to 56% body weight·d$^{-1}$. Growth rates in larger fish (>20 mm) ranged from 2-20% body weight·d$^{-1}$.

In-situ consumption:

Evacuation rates (R) were calculated from enclosure experiments during the experiment at various temperatures and body weights (Table 6). Evacuation rates (·h$^{-1}$), fish wet body weight ($W$, g), and temperature ($T$, °C) for those dates were related as follows:

$$\ln(R) = -1.515 + 0.219\ln(W) + 0.078\ln(W)^2 + 0.077(T)$$

($r^2=0.83$, $F=21.97$, $p<0.0001$, $n=18$)
I used this relationship to predict evacuation rates associated with feeding periodicity (Table 7). Predicted evacuation rates (Table 7) were combined with feeding periodicity data (Fig. 15) to estimate daily consumption rates (Table 7). Confidence intervals (95%) around the consumption estimates were developed as described by Post (1990), and are conservative for consumption estimates (John Post, personal communication).

Feeding periodicity of YOY walleye varied with ontogeny (Fig. 15). Larvae about 9 mm fed continuously during the day, with a strong peak at dusk; feeding ceased at night. Mid-sized larvae (20 mm) fed continuously during the day; guts were never empty at night, suggesting that feeding did not cease at night. Food content levels were highest during daytime for fish > 20 mm.

Daily weight-specific consumption was highest in the smallest larvae but decreased rapidly with increasing fish size (Table 7). Consumption rates were highly variable.

**In-situ respiration:**

In-situ total field respiration ($R_{est.}$) was calculated as the difference between measured consumption and growth and assumed waste losses; it ranged from 7.5% of body weight in the largest fish to 69.4% in the smallest larvae (Table 7). Respiration at optimal temperatures ($R_{opt.}$) was calculated using the temperature-dependent function; the
relationships between \( R_{\text{opt.}} \) and fish body weight (\( W, g \)) in the low and high density ponds were:

Low density (Pond 15): \( R_{\text{opt.}} = 0.0827(W)^{-0.407} \)

\( (r^2=0.597, F=11.84, p=0.009, n=10). \)

High density (Pond 19): \( R_{\text{opt.}} = 0.2949(W)^{-0.056} \)

\( (r^2=0.029, F=0.239, p=0.638, n=10). \)

Although \( R_{\text{opt.}} \) and fish body weight were related in the low density ponds, they were not in high density ponds. However, respiration models differed between the two densities (ANCOVA, \( F=4.32, p=0.05 \)); therefore, two separate models were used to predict body weight-dependent respiration in the low and high fish density ponds.

**Model consumption predictions:**

Daily weight specific consumption rates, adjusted for waste losses, were predicted for all ponds using daily growth (Fig. 16) and respiration rates predicted from the low and high fish density models; respiration rates were adjusted to ambient temperatures using the temperature dependence function. Predicted consumption estimates agreed well with observed consumption estimates (Fig. 16) from one low density pond (pond 18, Table 3), with a mean predicted/observed consumption ratio of 0.96. Partitioning
of mean square errors from regressions of observed on predicted food consumption values indicated that 96.9% of MSE resulted from the residual component, whereas only 1.4% and 1.7% were due to the mean and slope component, respectively (i.e., Z=0.014, S=0.017, and R=0.969), thereby suggesting that errors in the model were not systematic. Bonferroni joint confidence intervals for the intercept and slope were 0.057 ± 0.392 and 0.832 ± 0.636, respectively, and included an intercept of 0 and slope of 1. The reliability index (k) indicated that model predictions of consumption were within a factor of 1.3 times observed consumption values.

Mean weekly estimates of daily weight specific consumption were lower in the high density ponds during the first 2 weeks, but treatments did not differ in week 3 (Table 8, Fig. 17). Conversely, during weeks 4 through 6, consumption estimates were higher in the high density ponds (Table 8, Fig. 17). However, absolute consumption (cohort consumption) of microcrustacean prey (excluding chironomids) was higher in the high density ponds in all weeks for both the early and late fish mortality simulations, except for week 1 in the early mortality simulation when no differences were found between the density treatments (Table 8, Fig. 17).
Zooplankton biomass production and fish predation

Seasonal net production of preferred zooplankton biomass did not differ between low and high density ponds (ANOVA, $F=0.58$, $p=0.475$). Consumption of YOY walleye <20 mm (before May 18) accounted for only 15-22% of the total seasonal consumption of preferred zooplankton biomass relative to individuals >20 mm, in both the early and late mortality simulations (Fig. 18). In addition, walleye consumed more zooplankton prey in high density ponds in both early and late fish mortality simulations.

Patterns of gross seasonal production of preferred zooplankton biomass were similar across treatments for early and late fish mortality simulations. Gross seasonal production increased across harvest density in both early ($F=7.49$, $p=0.026$, $r^2=0.483$) and late ($F=8.8$, $p=0.018$, $r^2=0.524$) mortality simulations. No fish and low fish ponds did not differ in gross seasonal production of zooplankton for early (Tukey HSD, $p=0.31$) or late (Tukey HSD, $p=0.18$) mortality simulations (Fig. ). In early fish mortality simulations, seasonal gross zooplankton production was 1.7 times higher in high density than in low density ponds (Tukey HSD, $p=0.027$), and 2.7 times higher than in no fish ponds (Tukey HSD, $p=0.035$) (Fig. 19). Similarly, under late fish mortality simulations, gross seasonal biomass production of preferred zooplankton was 1.8 times higher in high density ponds relative to low density ponds (Tukey HSD,
and 3.8 times higher than in no fish ponds (Tukey HSD, p=0.008) (Fig. 19).

Discussion

Fish yield at harvest would be expected to decline with increased fish densities, if density-dependent mechanisms controlled fish growth. However, in my experiments, yield of fish biomass increased with fish density. In addition, final mean body weights did not differ with fish density, suggesting lack of density-dependence. In similar pond experiments stocked with three walleye fry density levels (20, 40, and 60 fry·m⁻³), YOY walleye yield increased with fish density, even when mean final mean body weights were related inversely with fish density (Fox and Flowers 1990). Although analysis of total yield and body weight is useful in assessing the cumulative effect of fish densities, it provides little insight into the dynamics of growth through fish ontogeny. In my comparison of instantaneous growth rates of YOY walleye measured frequently, I found that rates did not differ between low and high fish density, indicating that growth dynamics of YOY walleye were density-independent.

*Daphnia* and *Diaptomus* were dramatically reduced by increased predation under high walleye densities. Conversely, abundances of *Bosmina* and *Cyclops*, the less preferred prey items, appeared unrelated to fish density.
However, trends in abundances of *Bosmina* across stocking and harvest density were highest in the low density ponds, with similar low abundances in the no fish and high fish ponds. Low *Bosmina* abundances in the no fish ponds can be attributed to high abundances of *Daphnia*, a superior competitor for algal resces, in the absence of fish predation; similarly, lower *Daphnia* abundance via predation in the low density ponds likely resulted in high abundance of *Bosmina*. Competitive exclusion of *Bosmina* by *Daphnia*, however, cannot explain the low abundances of *Bosmina* in the high density ponds where *Daphnia* abundances were low due to fish predation. Fish predation could not have caused the declining trend in *Bosmina* abundance between low and high density ponds, because *Bosmina* were rarely eaten. Fox and Flowers (1990) reported that the density of *Daphnia*, a preferred prey, varied inversely with walleye density, and that point estimates of food biomass in walleye stomachs in high density ponds were significantly lower than in low and medium density treatments. Point estimates of stomach fullness, however, may not necessarily be indicative of daily levels of food consumption. Fox and Flower's estimates of stomach fullness were determined from fish collected between 10:00-12:00 h and levels of stomach fullness during this time are variable among ponds (this study). In addition, such analyses involving correlations of preferred prey abundances/food consumption indices and
fish densities tend to imply that under high fish densities zooplankton prey resources became depleted, and that the reduced food availability is reflected in the lower food consumption at higher densities. The next logical implication is that lower food consumption will reduce fish growth.

In this study, however, growth did not vary with fish density, even though preferred zooplankton abundances varied inversely with fish density (we note here that the range of fish densities at harvest (12.9-34.4 m\(^3\)) was comparable to 10.5-42.7 fish m\(^3\) reported by Fox and Flowers (1990)). In fact, consumption in high density ponds frequently exceeded that in low density ponds, suggesting potentially higher food levels in high density ponds. Patterns of walleye growth and consumption are counterintuitive to, and cannot be reconciled with, patterns of preferred prey abundances across fish density observed in my experiment. I contend that correlations of zooplankton standing crop numbers/biomasses with fish density provide a static view of fish-zooplankton interactions, providing little insight into the dynamics of zooplankton under changing fish predation pressures.

Higher gross production of zooplankton in the high density ponds is consistent with the fact that growth did not decline with fish density, because more zooplankton biomass was available to support the greater fish biomass.
I hypothesize that the higher gross production of zooplankton biomass in the high density ponds resulted from higher levels of fish population consumption, which suppressed the abundance of zooplankton grazers, possibly preventing zooplankton from overgrazing their algal food resource. This in turn, may have increased the availability of algae to the zooplankton, leading to increased zooplankton production (Culver et al. 1984).

Seasonal zooplankton biomass production without fish predation did not differ between the no fish and low fish density ponds, implying that fish stocked at levels of 25·m$^{-3}$ had minimal impact on the dynamics of preferred zooplankton, relative to the high density levels. Although mean weight-specific consumption rates of walleye larvae < 20 mm were high (40-139% of body weight·d$^{-1}$) relative to larger individuals (23-47% of body weight·d$^{-1}$) across fish density treatments, mean absolute (cohort) consumption (g of food consumed·m$^{-3}$·d$^{-1}$) of individuals < 20 mm accounted for only 15-22% of the total cumulative seasonal consumption. Fish < 20 mm had little potential to regulate the abundance of zooplankton via predation. However, larger individuals may play a considerable role in zooplankton population regulation, actually reducing zooplankton abundances, especially at high densities.

In my experiments, walleye switched to chironomids during weeks 5 and 6. This switch appears to coincide with
the chironomid emergence rather than limited zooplankton prey (Fox et al. 1989). Fox (1989) reported that prey choice and consumption of YOY walleye were dictated by the biomass of chironomids in the benthos, and that walleye predominantly ate chironomids during peak emergence even when cladocerans and copepods were readily available.

In natural systems, walleye also switch to benthic macroinvertebrates, and then to fish as juveniles (Smith and Pycha 1960, Wolfert 1964, Forney 1966, Bulckley et al. 1976). Therefore, walleye may have little impact on microcrustacean prey rescues, because (1) as larvae they are too scarce (Forney 1975, Forney 1976, Mizera et al. 1981, Serns 1982), (2) have little influence on zooplankton via predation (this study), and (3) at larger sizes, they switch to insect larvae and ultimately fish. This is consistent with the view of Houde (1987) and Cushing (1983) who suggest that larvae may be too dilute, and place demands on prey rescues too small to adversely affect prey abundances.

I contend that there is very little evidence that density-dependent control is an important mechanism regulating recruitment in the larval stages, but may be more important in the juvenile stages of YOY fish. Larvae of other species, especially gizzard shad, *Dorosoma cepedianum*, which do reach high natural densities (Mizera et al. 1981), could have more impact on zooplankton rescues, in turn creating conditions for density-dependent growth and
recruitment. However, Dettmers and Stein (1992) showed that even high densities of larval shad (38 m$^{-3}$) in reservoirs with high zooplankton productivity had minimal impact on zooplankton production, relative to juveniles which had a considerable impact. Because gizzard shad continue as zooplanktivores as juveniles and adults (Dettmers and Stein, 1992) density-dependent control could govern recruitment, at least in the juvenile stages of this species.

Studies which have implied density-dependent mechanisms in larval fish population regulation are based either on circumstantial evidence (Fortier and Harris 1989), correlations of predator and prey abundances and predator growth (Jenkins et al. 1991), correlations based on stock-recruitment and mortality data (Savoy and Crecco 1988), or model simulations requiring extensive assumptions about zooplankton production and larval fish feeding (Bollens 1988; Jensen 1989). Jensen (1989), via a simulation model, identified density-dependent control in the larval stages as an important process regulating the recruitment of walleye. Jensen's model, however, did not explicitly include the dynamics of zooplankton prey via a numerical compensatory response to predation, and the model itself was based on the assumption that density-dependent controls regulate walleye population size. The possibility of zooplankton populations responding numerically to predation should be considered, especially in nutrient-rich waters such as inshore areas of
lakes, and estuaries, typical nursery areas for many fish species. Density-dependent growth of fish larvae via competition for food may most likely occur in oligotrophic environments where prey abundances and productivity are typically low (Jenkins et al. 1991). Dettmers and Stein (in press) showed that in reservoirs with low zooplankton productivity (at most 4 mg·m\(^{-3}\)·d\(^{-1}\)), relatively low densities of larval gizzard shad (3-7·m\(^{-3}\)) had considerable impact on zooplankton, whereas in reservoirs with high zooplankton productivity (exceeding 125 mg·m\(^{-3}\)·d\(^{-1}\)), even high densities of larval gizzard shad (38·m\(^{-3}\)) did not affect zooplankton populations considerably. More experimental and field evidence is needed with a variety of fish taxa and in systems of varying nutrient status to establish the importance of density-dependent control in regulating recruitment of marine and freshwater fish species. These studies should also include the natural gauntlet of predators of fish larvae.

This study illustrates that walleye larvae do not exhibit density-dependent growth and do not control zooplankton dynamics. Although juvenile walleye considerably influence zooplankton prey, increased zooplankton production compensates for increased consumption, preventing density-dependent growth. My results reveal that density-dependent control of larval fish recruitment in general require critical evaluation with additional field and mesocosm tests
before it can be accepted as a mechanism underlying recruitment.
Table 5. Mean instantaneous growth rates of YOY walleye in low and high density ponds. Date is the mid-point of the time period between which growth rates were measured. Growth rate on each date is the mean rate calculated from 4 ponds of each fish density treatment, and standard errors are included in parenthesis. P-values are based on the t-test.

<table>
<thead>
<tr>
<th>Date</th>
<th>Mean Instantaneous Growth Rates</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Low Density</td>
<td>High Density</td>
<td>P-value</td>
</tr>
<tr>
<td>April 28</td>
<td></td>
<td>0.13 (0.03)</td>
<td>0.18 (0.02)</td>
<td>0.18</td>
</tr>
<tr>
<td>May 4</td>
<td></td>
<td>0.23 (0.02)</td>
<td>0.20 (0.01)</td>
<td>0.21</td>
</tr>
<tr>
<td>May 6</td>
<td></td>
<td>0.18 (0.02)</td>
<td>0.15 (0.01)</td>
<td>0.27</td>
</tr>
<tr>
<td>May 12</td>
<td></td>
<td>0.05 (0.02)</td>
<td>0.05 (0.02)</td>
<td>0.99</td>
</tr>
<tr>
<td>May 16</td>
<td></td>
<td>0.14 (0.02)</td>
<td>0.09 (0.03)</td>
<td>0.09</td>
</tr>
<tr>
<td>May 19</td>
<td></td>
<td>0.14 (0.02)</td>
<td>0.11 (0.02)</td>
<td>0.34</td>
</tr>
<tr>
<td>May 23</td>
<td></td>
<td>0.08 (0.01)</td>
<td>0.09 (0.01)</td>
<td>0.71</td>
</tr>
<tr>
<td>May 26</td>
<td></td>
<td>0.10 (0.03)</td>
<td>0.10 (0.01)</td>
<td>0.96</td>
</tr>
<tr>
<td>May 30</td>
<td></td>
<td>0.07 (0.02)</td>
<td>0.08 (0.01)</td>
<td>0.69</td>
</tr>
<tr>
<td>June 2</td>
<td></td>
<td>0.06 (0.02)</td>
<td>0.10 (0.03)</td>
<td>0.28</td>
</tr>
</tbody>
</table>
Table 6. Instantaneous evacuation rates \((R, \text{h}^{-1})\), of walleye in hatchery ponds, calculated by fitting negative exponential curves to gut and stomach fullness (\% body weight) of fish sampled serially from food-free enclosures in one low and one high fish density pond. \(N\) is the total number of fish sampled for each evacuation rate experiment. Temperature was the mean of enclosure water temperatures taken 2-4 times during during the experiment.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Date</th>
<th>(N)</th>
<th>Mean Body Weight (g)</th>
<th>(T (\degree C))</th>
<th>Evacuation Rate ((R))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Density (Pond 18)</td>
<td>May 3</td>
<td>45</td>
<td>0.0078</td>
<td>13.7</td>
<td>1.22</td>
</tr>
<tr>
<td></td>
<td>May 7</td>
<td>59</td>
<td>0.0152</td>
<td>18.1</td>
<td>1.61</td>
</tr>
<tr>
<td></td>
<td>May 10</td>
<td>77</td>
<td>0.0274</td>
<td>13.0</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>May 14</td>
<td>70</td>
<td>0.0422</td>
<td>16.0</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>May 17</td>
<td>67</td>
<td>0.0566</td>
<td>16.6</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>May 21</td>
<td>60</td>
<td>0.0957</td>
<td>13.9</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>May 24</td>
<td>50</td>
<td>0.1128</td>
<td>22.3</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td>May 28</td>
<td>50</td>
<td>0.2030</td>
<td>18.0</td>
<td>0.72</td>
</tr>
<tr>
<td>High Density (Pond 19)</td>
<td>April 30</td>
<td>45</td>
<td>0.0053</td>
<td>20.8</td>
<td>3.22</td>
</tr>
<tr>
<td></td>
<td>May 3</td>
<td>52</td>
<td>0.0109</td>
<td>13.4</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>May 7</td>
<td>55</td>
<td>0.0181</td>
<td>18.1</td>
<td>1.47</td>
</tr>
<tr>
<td></td>
<td>May 14</td>
<td>50</td>
<td>0.0437</td>
<td>16.7</td>
<td>1.14</td>
</tr>
<tr>
<td></td>
<td>May 17</td>
<td>65</td>
<td>0.0580</td>
<td>17.0</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>May 21</td>
<td>64</td>
<td>0.0939</td>
<td>13.9</td>
<td>0.58</td>
</tr>
</tbody>
</table>
Table 6. Continued.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Date</th>
<th>N</th>
<th>Mean Body Weight (g)</th>
<th>T (°C)</th>
<th>Evacuation Rate (R)</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 24</td>
<td>53</td>
<td>0.1112</td>
<td>22.4</td>
<td>0.93</td>
<td></td>
</tr>
<tr>
<td>May 28</td>
<td>50</td>
<td>0.1586</td>
<td>17.8</td>
<td>0.73</td>
<td></td>
</tr>
<tr>
<td>May 31</td>
<td>50</td>
<td>0.1794</td>
<td>21.4</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td>June 4</td>
<td>55</td>
<td>0.2740</td>
<td>17.2</td>
<td>0.77</td>
<td></td>
</tr>
</tbody>
</table>
Table 7. Energy budget of YOY walleye calculated for one high and two low fish density ponds. Consumption \((C \pm 95\% \text{ CI})\) was calculated based on predicted evacuation rates \((R)\) and feeding periodicity data (Fig. 6); estimates were adjusted to account for caloric differences between fish and zooplankton \((0.75C)\). Growth \((G)\) was estimated using the Ricker method, and waste losses were assumed to be \(0.28*C\). Total field respiration \((R_{\text{K}}; \text{ standard\text{+}active\text{+}SDA respiration})\) was estimated as \(R_{\text{K}} = C - G - 0.28*C\), and adjusted via the temperature-dependent function to obtain respiration at optimal temperature \((R_{\text{opt}})\). Units for all energy budget parameters are \(\text{g.g}^{-1}.\text{d}^{-1}\). \(R_{\text{opt}}\) was regressed against body weight \((g, \text{ wet})\) for ponds 15 and 19; data from pond 18 was treated as an independent data set for testing the energy budget model. \(N = 45\) fish for each 24 h experiment.

<table>
<thead>
<tr>
<th>Pond</th>
<th>Date</th>
<th>Mean Body Weight (g)</th>
<th>T (°C)</th>
<th>R</th>
<th>C ± 95 % CI</th>
<th>G</th>
<th>R_{\text{K}}</th>
<th>R_{\text{opt}}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low Density</td>
<td>April 30</td>
<td>0.0052</td>
<td>20.3</td>
<td>2.87</td>
<td>1.374 ± 0.262</td>
<td>0.295</td>
<td>0.694</td>
<td>0.903</td>
</tr>
<tr>
<td>Pond 15</td>
<td>May 3</td>
<td>0.0113</td>
<td>14.6</td>
<td>1.22</td>
<td>0.566 ± 0.196</td>
<td>0.170</td>
<td>0.237</td>
<td>0.460</td>
</tr>
<tr>
<td></td>
<td>May 7</td>
<td>0.0212</td>
<td>17.9</td>
<td>1.19</td>
<td>0.490 ± 0.112</td>
<td>0.190</td>
<td>0.163</td>
<td>0.248</td>
</tr>
<tr>
<td></td>
<td>May 10</td>
<td>0.0357</td>
<td>12.3</td>
<td>0.65</td>
<td>0.364 ± 0.103</td>
<td>0.114</td>
<td>0.148</td>
<td>0.344</td>
</tr>
<tr>
<td></td>
<td>May 14</td>
<td>0.0549</td>
<td>16.6</td>
<td>0.81</td>
<td>0.549 ± 0.077</td>
<td>0.118</td>
<td>0.277</td>
<td>0.462</td>
</tr>
<tr>
<td>Date</td>
<td>Mean Body Weight (g)</td>
<td>T (°C)</td>
<td>R</td>
<td>C ± 95% CI</td>
<td>G</td>
<td>R_{min}</td>
<td>R_{max}</td>
<td></td>
</tr>
<tr>
<td>-----------</td>
<td>----------------------</td>
<td>--------</td>
<td>-----</td>
<td>------------</td>
<td>-----</td>
<td>---------</td>
<td>---------</td>
<td></td>
</tr>
<tr>
<td>May 17</td>
<td>0.0768</td>
<td>17.1</td>
<td>0.78</td>
<td>0.288 ± 0.099</td>
<td>0.128</td>
<td>0.080</td>
<td>0.129</td>
<td></td>
</tr>
<tr>
<td>May 21</td>
<td>0.1241</td>
<td>14.9</td>
<td>0.62</td>
<td>0.443 ± 0.060</td>
<td>0.100</td>
<td>0.218</td>
<td>0.414</td>
<td></td>
</tr>
<tr>
<td>May 24</td>
<td>0.1653</td>
<td>21.5</td>
<td>1.00</td>
<td>0.252 ± 0.168</td>
<td>0.104</td>
<td>0.078</td>
<td>0.094</td>
<td></td>
</tr>
<tr>
<td>May 31</td>
<td>0.2870</td>
<td>20.0</td>
<td>0.88</td>
<td>0.248 ± 0.154</td>
<td>0.051</td>
<td>0.127</td>
<td>0.169</td>
<td></td>
</tr>
<tr>
<td>June 4</td>
<td>0.3506</td>
<td>17.1</td>
<td>0.71</td>
<td>0.175 ± 0.140</td>
<td>0.051</td>
<td>0.075</td>
<td>0.121</td>
<td></td>
</tr>
<tr>
<td>April 30</td>
<td>0.0049</td>
<td>20.3</td>
<td>2.97</td>
<td>1.136 ± 0.275</td>
<td>0.247</td>
<td>0.571</td>
<td>0.743</td>
<td></td>
</tr>
<tr>
<td>May 3</td>
<td>0.0095</td>
<td>14.5</td>
<td>1.31</td>
<td>0.583 ± 0.202</td>
<td>0.167</td>
<td>0.253</td>
<td>0.494</td>
<td></td>
</tr>
<tr>
<td>May 7</td>
<td>0.0176</td>
<td>18.7</td>
<td>1.37</td>
<td>0.538 ± 0.135</td>
<td>0.212</td>
<td>0.176</td>
<td>0.253</td>
<td></td>
</tr>
<tr>
<td>May 10</td>
<td>0.0313</td>
<td>13.9</td>
<td>0.77</td>
<td>0.332 ± 0.095</td>
<td>0.096</td>
<td>0.143</td>
<td>0.293</td>
<td></td>
</tr>
<tr>
<td>May 14</td>
<td>0.0452</td>
<td>16.2</td>
<td>0.82</td>
<td>0.563 ± 0.082</td>
<td>0.123</td>
<td>0.284</td>
<td>0.487</td>
<td></td>
</tr>
<tr>
<td>May 17</td>
<td>0.0638</td>
<td>17.6</td>
<td>0.84</td>
<td>0.506 ± 0.100</td>
<td>0.122</td>
<td>0.242</td>
<td>0.377</td>
<td></td>
</tr>
<tr>
<td>May 21</td>
<td>0.1012</td>
<td>14.5</td>
<td>0.61</td>
<td>0.328 ± 0.115</td>
<td>0.118</td>
<td>0.118</td>
<td>0.230</td>
<td></td>
</tr>
<tr>
<td>May 24</td>
<td>0.1415</td>
<td>22.5</td>
<td>1.09</td>
<td>0.753 ± 0.098</td>
<td>0.140</td>
<td>0.402</td>
<td>0.462</td>
<td></td>
</tr>
<tr>
<td>Pond</td>
<td>Date</td>
<td>Mean Body Weight (g)</td>
<td>T (°C)</td>
<td>R</td>
<td>C ± 95% CI</td>
<td>G</td>
<td>R_r.</td>
<td>R_r.</td>
</tr>
<tr>
<td>----------</td>
<td>-------</td>
<td>----------------------</td>
<td>--------</td>
<td>----</td>
<td>-----------</td>
<td>------</td>
<td>-------</td>
<td>-------</td>
</tr>
<tr>
<td>High Density Pond 19</td>
<td>May 31</td>
<td>0.2867</td>
<td>24.7</td>
<td>1.27</td>
<td>0.405 ± 0.171</td>
<td>0.199</td>
<td>0.093</td>
<td>0.097</td>
</tr>
<tr>
<td></td>
<td>April 30</td>
<td>0.0060</td>
<td>20.5</td>
<td>2.68</td>
<td>1.045 ± 0.303</td>
<td>0.267</td>
<td>0.486</td>
<td>0.624</td>
</tr>
<tr>
<td></td>
<td>May 3</td>
<td>0.0122</td>
<td>14.2</td>
<td>1.14</td>
<td>0.407 ± 0.227</td>
<td>0.139</td>
<td>0.155</td>
<td>0.309</td>
</tr>
<tr>
<td></td>
<td>May 7</td>
<td>0.0205</td>
<td>18.7</td>
<td>1.29</td>
<td>0.522 ± 0.176</td>
<td>0.176</td>
<td>0.200</td>
<td>0.288</td>
</tr>
<tr>
<td></td>
<td>May 10</td>
<td>0.0333</td>
<td>14.2</td>
<td>0.77</td>
<td>0.245 ± 0.167</td>
<td>0.091</td>
<td>0.085</td>
<td>0.171</td>
</tr>
<tr>
<td></td>
<td>May 14</td>
<td>0.0472</td>
<td>16.3</td>
<td>0.82</td>
<td>0.558 ± 0.070</td>
<td>0.101</td>
<td>0.301</td>
<td>0.514</td>
</tr>
<tr>
<td></td>
<td>May 17</td>
<td>0.0629</td>
<td>17.7</td>
<td>0.85</td>
<td>0.391 ± 0.114</td>
<td>0.106</td>
<td>0.176</td>
<td>0.271</td>
</tr>
<tr>
<td></td>
<td>May 21</td>
<td>0.0940</td>
<td>14.6</td>
<td>0.62</td>
<td>0.506 ± 0.077</td>
<td>0.122</td>
<td>0.242</td>
<td>0.470</td>
</tr>
<tr>
<td></td>
<td>May 24</td>
<td>0.1327</td>
<td>22.8</td>
<td>1.12</td>
<td>0.792 ± 0.087</td>
<td>0.070</td>
<td>0.500</td>
<td>0.565</td>
</tr>
<tr>
<td></td>
<td>May 31</td>
<td>0.2291</td>
<td>21.5</td>
<td>0.99</td>
<td>0.403 ± 0.110</td>
<td>0.055</td>
<td>0.236</td>
<td>0.286</td>
</tr>
<tr>
<td></td>
<td>June 4</td>
<td>0.2833</td>
<td>17.5</td>
<td>0.73</td>
<td>0.312 ± 0.112</td>
<td>0.055</td>
<td>0.170</td>
<td>0.266</td>
</tr>
</tbody>
</table>
Table 8. Weekly mean weight specific $(g \cdot g^{-1} \cdot d^{-1})$ and absolute $(g \cdot m^{-3} \cdot d^{-1})$ consumption rates of YOY walleye in low and high density ponds. Absolute weekly consumption rates are compared for the early and late fish mortality simulations. Comparisons of mean consumption rates are made using the one-way ANOVA analysis at an alpha level of 0.05.

<table>
<thead>
<tr>
<th>Week</th>
<th>Consumption $(g \cdot g^{-1} \cdot d^{-1})$</th>
<th>Consumption $(g \cdot m^{-3} \cdot d^{-1})$</th>
<th>Consumption $(g \cdot m^{-3} \cdot d^{-1})$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fish Density</td>
<td>Early Mortality</td>
<td>Low</td>
</tr>
<tr>
<td>1</td>
<td>1.387</td>
<td>0.808</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>2</td>
<td>0.652</td>
<td>0.562</td>
<td>0.04</td>
</tr>
<tr>
<td>3</td>
<td>0.398</td>
<td>0.397</td>
<td>0.95</td>
</tr>
<tr>
<td>4</td>
<td>0.343</td>
<td>0.411</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>5</td>
<td>0.287</td>
<td>0.454</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>6</td>
<td>0.230</td>
<td>0.466</td>
<td>&lt;.01</td>
</tr>
</tbody>
</table>
Figure 10. Relationship of walleye percent survival (top panel), biomass yield (middle panel) and walleye final mean body weights (bottom panel) vs. walleye harvest density in ponds at St. Mary's Hatchery, Ohio.
Figure 10.
Figure 11. Mean weekly percent biomass composition of prey taxa in walleye diets in the low (upper panel) and high (lower panel) fish density ponds.
Figure 11.
Figure 12. Correlations of *Daphnia* (upper panel) and *Diaptomus* (lower panel) abundances vs. walleye stocking and harvest density.
Figure 12.
Figure 13. Correlations of *Bosmina* (upper panel) and *Cyclops* (lower panel) abundances vs. walleye stocking and harvest density.
Figure 13.
Figure 14. Growth curves calculated via the Ricker (1975) growth method, for each pond indicating daily changes in walleye wet body weight, in low (upper panel) and high (lower panel) fish density ponds.
Figure 14.
Figure 15. Feeding periodicity of larval and juvenile walleye in 2 low (ponds 15 and 18), and 1 high (pond 19) fish density pond based on changes in mean gut fullness (food biomass/fish biomass) of five fish sampled from ponds at 3-h intervals. Bars below x-axis indicate period of darkness.
Figure 15.
Figure 16. Test of the energy budget model showing deviations of the model predicted vs. observed weight specific consumption estimates from the 1:1 line (solid line) where predicted values ($C_p$) = estimated values ($C_o$). The dashed line is the least squares fit to predicted vs. observed consumption estimates. The mean $C_p/C_o$ ratio = 0.96.
Figure 16.
Figure 17. Seasonal patterns of predicted mean daily weight specific consumption (top panel), and cohort consumption in the early (middle panel) and late (bottom panel) mortality simulations in the low and high density ponds. Chironomids in the diet in weeks 5 and 6 were not included.
Figure 17.
Figure 18. Seasonal trends in daily mean net (solid line) and gross production (dashed line) of zooplankton biomass in the early mortality (upper panel) and late mortality (lower panel) simulations in low and high fish density ponds. The area between the solid and dashed lines indicates the magnitude of walleye population consumption on preferred microcrustacean zooplankton.
Zooplankton biomass production (g.m\(^{-3}\).d\(^{-1}\))

Low Density

Early mortality

High Density

Early mortality

Late mortality

Late mortality

Net production

Gross production (net production+walleye cohort consumption)

Figure 18.
Figure 19. Mean cumulative seasonal gross production of preferred zooplankton under the early mortality (upper panel) and late mortality (lower panel) simulations in the no, low, and high fish density ponds. P-values correspond to comparisons between adjacent bars.
Early mortality

Late mortality

Figure 19.
CHAPTER III

ZOOPLANDKTON-PHYTOPLANDKTON INTERACTIONS IN EXPERIMENTAL PONDS: ZOOPLANKTON COMMUNITY STRUCTURE AND THE TROPHIC CASCADE

Introduction

The trophic cascade hypothesis suggests that predation is a potent force regulating productivity and plankton community structure in freshwaters (Carpenter et al. 1985). Piscivore induced reduction in planktivore biomass increases biomass of large herbivores and reduces phytoplankton biomass (Hrbacek et al. 1961; Shapiro 1980; Shapiro and Wright 1984; Carpenter et al. 1987). Many recent studies demonstrate the trophic cascade from planktivores to phytoplankton (Mills and Forney 1983; Vijverberg and VanDensen 1984; McQueen et al. 1986; Mills et al. 1987; Vanni 1987; Dorazio et al. 1987; Vanni and Findlay 1990; Dawidowicz 1990). Generally, *Daphnia* species are the key herbivores in many trophic cascade studies (Carpenter and Kitchell 1984; Sommer 1985; Lampert et al. 1986; Elser et al. 1990; Gulati 1990; Vanni et al. 1990) because their relatively large body size contributes to high grazing rates.
on phytoplankton (Burns 1969; Knoechel and Holtby 1986; Wu and Culver 1991). Therefore, removal of large herbivores by planktivores enhances phytoplankton biomass via reduced zooplankton community grazing rates (Losos and Hetesa 1973; Lynch and Shapiro 1981; Schoenberg and Carlson 1984). Removal of large herbivores such as Daphnia also releases smaller zooplankton species such as Bosmina, copepods, and rotifers from competition for food resources (Vanni 1986). Small zooplankton species then become abundant under the absence or near-absence of Daphnia (Vaga et al. 1985).

The dominant zooplankters in fertilized hatchery ponds, stocked with larval walleye, are Daphnia, Bosmina, cyclopoid and calanoid copepods, nauplii, and rotifers (Qin and Culver 1992; Culver et al. 1992; Chapter II). In some years, small-bodied zooplankton with low individual grazing rates such as Bosmina, cyclopoid copepods, and rotifers dominate these ponds; in other years, ponds are dominated by Daphnia and calanoid copepods with higher individual grazing rates than the small bodied species (Knoechel and Holtby 1986; Culver et al. 1992). The trophic cascade from planktivores to phytoplankton may be prominent when the key species are large-bodied zooplankters with higher grazing rates, such as Daphnia and Diaptomus (Knoechel and Holtby 1986). It is, however, unclear whether the trophic cascade weakens when small zooplankters dominate ponds. Although these species have low individual grazing rates, they reach high densities
either because larval walleye prefer large species such as *Daphnia* and *Diaptomus*, or because by the time the small species become abundant, walleye have begun to consume chironomids (Chapter II). Therefore, it is of interest to test whether high densities of small species zooplankton would reduce phytoplankton due to high community grazing rates.

In Chapter II, I hypothesized that zooplankton production in high fish density ponds increased because planktivory by YOY walleye reduced the biomass of the dominant grazers, *Daphnia* and *Diaptomus*, thereby preventing overgrazing of algae and enhancing phytoplankton biomass. Increased phytoplankton resources then permitted zooplankton biomass to increase. In this study (1) I will test the above hypothesis that phytoplankton biomass increases under increased planktivory, and (2) I will compare whether the trophic cascade from planktivores to phytoplankton differs between ponds dominated by small and large species of zooplankton. Comparisons are made between 2 years; in 1989, the dominant zooplankton were *Bosmina* and cyclopoid copepods and in 1990, *Daphnia* and *Diaptomus*. Densities of larval walleye were manipulated in both years, and community grazing rates of zooplankton were compared against the available phytoplankton resource base (standing crop + net photosynthesis by edible algae) to determine impact on algal resources.
Methods and Materials

Experimental Design

Experiments were conducted in eight, 0.4-ha ponds (depth=1 m) during April 28 through June 9, 1989, at the Hebron Fish Hatchery, Hebron, Ohio, and in five, 0.4-0.5-ha ponds (depth=1.5 m) during April 26 through June 5, 1990, at the St. Mary's State Fish Hatchery, St. Mary's, Ohio. All ponds in 1989 and 1990 were filled with water from nearby lakes (Buckeye Lake, Hebron, in 1989, and Grand Lake, St. Mary's, in 1990) 4-5 d before experiments began. In both years, all ponds were fertilized weekly with inorganic fertilizer sufficient to achieve a phosphate concentration of 0.03 mg P·L⁻¹ and inorganic nitrogen of 0.6 mg N·L⁻¹, resulting in a N:P ratio of 20:1.

In 1989, ponds were stocked with four densities of walleye fry: 10, 20, 25 and 30 fish·m⁻³ (two ponds for each density) on April 28. On April 26 in 1990, two ponds were stocked at 25 walleye fry·m⁻³, two ponds at 50 fish·m⁻³, and one pond received no fish. In both years, ponds were drained at the end of the 6-week experimental period, and fish harvest densities were determined as described in Chapter II.

Sampling and Analysis

Zooplankton. In 1989, zooplankton were sampled every 2–3 d by towing a metered net (mouth diameter=0.5 m,
mesh=64μm) for a distance of approximately 5-20 m, yielding typical sample volumes of 1.0-4.0 m³. Net towing, preservation and enumeration methodologies for 1989 follow those described in Chapter I. Zooplankton sampling and enumeration for 1990 are described in Chapter I.

Individual clearance rates for each cladoceran species sampled in 1989 and 1990 were estimated using the model developed by Peters and Downing (1984):

$$\log V = 0.173 + 0.750 \log W - 0.434 \log S - 0.0003C + 0.014C_a$$

where $V =$ individual clearance rate (ml·animal⁻¹·d⁻¹), $W =$ animal mass (μg dry weight·animal⁻¹), $S =$ food concentration (wet mass, $10^6 \mu^3$·ml⁻¹), and $C$ and $C_a$ are volume of experimental vessel (ml) and volume of experimental vessel per animal (ml), respectively. Because $C$ and $C_a$ apply to short-term laboratory feeding experiments in Peters and Downing's (1984) regressions, and do not apply directly to our pond study, we used the mean values of $C$ and $C_a$ provided in Table 3 in Peter and Downing (1984).

For copepods, we used individual clearance rates measured in the western basin of Lake Erie, and the Bay of Quinte, Lake Ontario in 1976 (Table 9, Culver, unpublished data), using the technique of Haney (1971). Individual clearance rates for each species of cladocerans and copepods
were multiplied by population density (numbers·l⁻¹) of each species to obtain population clearance rates (ml·l⁻¹·d⁻¹).

Population clearance rates (ml of water cleared of particles per liter per day) of all zooplankton taxa were summed, converted to grazing rates (ml of phytoplankton grazed per liter per day), which were then used to estimate the amount of daily gross edible phytoplankton resource consumed by the zooplankton community.

**Phytoplankton.**

In both years, phytoplankton were sampled from a boat every 2-3 d by lowering a 1.5 m long PVC tube sampler (diameter=10 cm) to the bottom of the pond to obtain a sample of the whole water column. Samples were preserved immediately in 1% Lugol's solution. In the laboratory, algal cells and filaments were classified to genus and counted in sedimentation chambers on an inverted microscope (400x). At least 100 cells of the dominant taxa were counted in each sample and 30-50 cells were measured for each taxon. Dimensions measured depended on cell shape. Cell volume of each taxon was estimated by applying formulae best describing cell shape, and mean cell volume was multiplied by cell density to obtain population biovolume. Algae were further classified into inedible (blue-greens, colonial greens, and filaments) and edible (small greens, diatoms, flagellates) components.
Gross primary production of phytoplankton was measured by changes in dissolved oxygen in replicated (n=2) light and dark bottles. The whole water column was sampled with a tube sampler and mixed in a bucket. Light and dark bottles were filled with mixed water, and the bottles were incubated in-situ (0.5 m below surface) in each pond for 24 h. The modified Winkler method was used for determining the oxygen content in light and dark bottles (Wetzel and Likens 1979). Respiration rate was estimated by subtracting the amount of dissolved oxygen in dark bottles after incubation from the initial oxygen content, and net primary production was calculated by subtracting respiration from gross primary production.

Net primary production (mg O₂·l⁻¹·d⁻¹) was converted to wet phytoplankton biomass production (mg phytoplankton·l⁻¹·d⁻¹) (1 mg O₂ = 3.3 mg phytoplankton, Lind 1985) and then to volume (ml phytoplankton·l⁻¹·d⁻¹) assuming a specific gravity of 1 g·l⁻¹ for phytoplankton. The proportion of net photosynthesis by edible algae was calculated by multiplying total net photosynthesis by the proportion of standing crop represented by edible algae. The gross edible algal resource available to zooplankton grazers was calculated as the sum of the edible standing crop and net photosynthesis of edible algae.
Statistical Analysis.

Fish density effects on all phytoplankton and zooplankton variables were analyzed with one-way ANOVA on time-weighted means. Time-weighted means were calculated as stated in Vanni and Findlay (1990). Briefly, for each sampling interval, the average of observations on two sampling dates bracketing the interval were calculated, and then multiplied by the percent of total experimental time period represented by that interval. The sum of these products gave the time-weighted mean; thus, one time-weighted mean for each pond was obtained. For each fish density treatment (n=4 in 1989; and n=3 in 1990), ANOVAs were conducted on primary productivity and phytoplankton respiration rates, gross edible phytoplankton resource, edible and inedible phytoplankton biovolumes, and biomasses of zooplankton taxa. All computations were performed with the Multivariate General Linear Hypothesis (MGLH) procedure of SYSTAT version 5.01 (Wilkinson 1990). Tukey's HSD multiple comparisons were used on treatment time-weighted means whenever whole treatment effects were significant. Because F-tests with 2 df (1990), or 4 df (1989) have relatively low power, a higher Type I error level was set (alpha=0.10) to reduce the probability of making a Type II error (Winer 1971; Peterman 1990).
Results

Fish Harvest.

In 1989 at Hebron, ponds stocked with 10, 20, 25, and 30 fish·m⁻³ yielded mean harvest densities of 9, 15, 12, and 23 fish·m⁻³, respectively. In 1990, ponds stocked 25 and 50 fish·m⁻³ yielded harvest densities of 16 and 32 fish·m⁻³. Maximum harvest densities were, therefore, approximately 2 times minimum for both years.

Hebron, 1989.

Zooplankton. All treatments were dominated by Cyclops vernalis, cyclopoid copepodites, and nauplii during the first 4 weeks (April 28 through May 25); Bosmina dominated the zooplankton community during weeks 5-6 (Fig. 20). Chydorus sphaericus was the other dominant cladoceran in the last 2 weeks, although its biomass was < 10% of zooplankton biomass, except in the 25 fish·m⁻³ treatment (HD=12 fish·m⁻³), where it contributed > 50% (Fig. 20). Daphnia constituted about 1-3% of the zooplankton biomass in all treatments; it was never dominant. Daphnia biomasses, however, were significantly higher in the lowest fish density treatment (p=0.08, Fig. 21), but did not differ among the three higher density treatments (p>0.90, Fig. 21). Biomass of Cyclops vernalis was highest in the lowest fish density treatment and differed from all three higher fish density treatments (p=0.001, Fig. 21). No differences
occurred in *Cyclops vernalis* biomasses among the three higher density treatments (*p*>0.65, Fig. 21). Fish density did not influence biomass of *Bosmina* (*p*=0.25), *Chydorus* (*p*=0.43), cyclopoid copepodites (*p*=0.22), or nauplii (*p*=0.19; Fig. 21).

When copepods were the dominant grazers, zooplankton community grazing was low (weeks 1-4), and copepod grazing generally accounted for an average of 2-10% of the available edible algal resource base (Fig. 22). Conversely, grazing by *Bosmina* was high in all treatments (except the 25 fish⋅m$^{-3}$ treatment) in weeks 5-6, and accounted for 50-100% of the edible algal resource base.

**Phytoplankton.**

Biovolumes of inedible algae peaked in all fish density treatments 2-3 weeks after fish stocking, and declined sharply thereafter; by week 6 (June 2-9), inedible algae represented only 2-10% of the total algal biovolume (Fig. 23). Fish density did not influence inedible algae biovolumes (*p*=0.58, Fig. 21).

Biovolume of edible algae peaked twice during the 6-week experiment in all treatments. The first peak coincided with the peak in inedible algal biovolumes in weeks 2-3, followed by a decline in week 4 (May 19-25); the second peak in edible algae occurred in week 6, when highest biovolumes were achieved, except in the lowest fish density treatment.
Fish density did not influence edible algal biovolumes \((p=0.18, \text{ Fig. 21})\).

Net and gross photosynthesis and respiration rate of phytoplankton peaked in weeks 3 and 5 in all treatments (Fig. 24). Net and gross primary productivity declined sharply whereas respiration rate declined moderately in week 6 across all treatments (Fig. 24). Fish density did not influence net \((p=0.38)\) or gross \((p=0.47)\) photosynthesis, or respiration rates \((p=0.39)\) of phytoplankton (Fig. 21). In addition, the gross edible phytoplankton resource potentially available for zooplankton grazing \((\text{net production of edible algae} + \text{edible algae standing crop})\) did not differ among densities \((p=0.12, \text{ Fig. 21})\).

St. Mary's, 1990

**Zooplankton.** The no fish treatments were dominated through the 6 week period by *Daphnia* and *Diaptomus* (Fig. 25). *Daphnia* biomass stayed at a relatively constant level for the first five weeks, and peaked in the last week (Fig. 25). *Bosmina*, *Cyclops vernalis*, cyclopoid copepodites, and nauplii were far less dominant in the no fish ponds (Fig. 25). Conversely, *Daphnia* biomasses were greatly reduced in the low fish and high fish treatments, and *Diaptomus*, followed by *Bosmina*, cyclopoid copepods, and nauplii were dominant (Fig. 25). *Daphnia* biomasses differed significantly among all treatments, with the lowest biomass
in the high fish treatment ($p<0.04$, Fig. 26). *Diaptomus* biomasses did not differ between the no fish and low fish treatments, but were lower in the high fish treatment than in the no fish ($p=0.06$) and low fish ($p=0.08$) treatments (Fig. 26). Fish density did not have a significant impact on *Bosmina*, *Cyclops*, cyclopoid copepodites and nauplii biomasses ($p>0.31$, Fig. 26).

In the no fish and low fish treatments, *Daphnia* and *Diaptomus* grazed 25-95% of the phytoplankton resource base in weeks 1-2, and 5-6 (Fig. 27). Conversely, grazing pressure on phytoplankton was low in the high fish treatment for the first 5 weeks (2-5%), and increased to 30% in week 6 (Fig. 27).

**Phytoplankton.**

Biovolumes of inedible algae remained relatively constant through six weeks (Fig. 28), and did not differ among treatments ($p=0.56$, Fig. 26). Biovolumes of edible algae peaked during the first week, then declined, and remained relatively constant for the remaining 5 weeks in the 0 (no fish) and 25 fish·m$^{-3}$ (low fish) treatments (Fig. 28). Conversely, edible algae peaked during weeks 1 and 6 in the 50 fish·m$^{-3}$ (high fish) treatment (Fig. 28). Biovolumes of edible algae did not differ between the no fish and low fish density treatments ($p=0.67$), but were
significantly higher in the high fish, than in the no fish and low fish treatments (p<0.08, Fig. 26).

Net photosynthesis was negative during weeks 1-2 in all treatments, with additional periods of negative net production in weeks 4, 5, and 6 for the high fish, low fish, and no fish treatments, respectively (Fig. 29). Gross photosynthesis and respiration peaked in weeks 3 and 5 for all treatments, and gross photosynthesis was negative in week 6 in the no fish pond (Fig. 29). Overall, there were no significant effects of fish density on net and gross photosynthesis, and respiration rate (p>0.46, Fig. 26). Gross edible phytoplankton resource did not differ between the no fish and low fish treatments; however, the phytoplankton resource available to zooplankton was higher in the high fish treatment than in the no fish (p=0.09) and low fish (p=0.04) treatments (Fig. 26).

Discussion

The zooplankton community differed markedly between experiments at Hebron in 1989, and at St. Mary’s in 1990. In contrast to 1990 when Daphnia and Diaptomus were the most dominant species in the ponds, Daphnia were never abundant in 1989, even though fish densities (both stocking and harvest) were relatively lower in 1989. In ponds where Daphnia were abundant, Bosmina biomasses were low. In the absence of Daphnia, Bosmina thrived, and were the most
dominant species in all ponds in 1989. These differences in zooplankton community structure allowed comparison of the trophic cascade from planktivores to phytoplankton between the two years.

Because grazing rates of zooplankton increase exponentially with body size (Burns 1969; Peters and Downing 1984; Knoechel and Holtby 1986), smaller zooplankton such as Bosmina, Chydorus, and cyclopoid copepods have much lower individual grazing rates than *Daphnia* (Zankai and Ponyi 1986; Wu 1991). Large species such as *Daphnia* competitively reduce abundance of, and exclude small species by monopolizing phytoplankton resources (Brooks and Dodson 1965; Lynch 1979). Conversely, in the absence of large species, small species typically thrive (Kerfoot and DeMott 1980; DeMott and Kerfoot 1982; Vanni 1986; Vaga 1986). In the 1989 Hebron experiment, *Daphnia* biomass never exceeded 1-3% of zooplankton biomass at any fish density and all ponds were dominated by small-bodied zooplankton. *Cyclops vernalis* and cyclopoid copepodites were most abundant in weeks 1-4, whereas *Bosmina* and *Chydorus* peaked in weeks 5-6. Adult cyclopoid copepods are primarily predaceous on *Bosmina*, cyclopoid copepodids, and nauplii (Fryer 1957; McQueen 1969; Dodson 1974), and only graze on phytoplankton as copepodites and nauplii. Therefore, grazing pressure on phytoplankton was low during the first 4 weeks of the experiment. Grazing on phytoplankton increased considerably
in weeks 5-6, and often exceeded the phytoplankton resource base. Most grazing in weeks 5-6 was due to *Bosmina*. Although *Bosmina* individuals have relatively low individual grazing rates, the high biomass this species attained in the absence of *Daphnia* contributed to high community grazing rates.

Fish density did not influence primary productivity, phytoplankton respiration, biovolumes of edible or inedible algae, and the edible phytoplankton resource base. Even with low *Daphnia* biomass, fish had an impact on *Daphnia*. *Daphnia* biomass was highest in ponds stocked with the lowest fish density; ponds stocked at higher fish densities (20, 25 and 30 fish·m⁻³) had lower *Daphnia* biomass. My results agree with those of other studies which report similar effects of larval walleye on *Daphnia* (Fox 1989; Fox and Flowers 1990; Qin and Culver 1992). Consumption by larval walleye also reduced biomass of *Cyclops vernalis*. Fish density did not influence *Bosmina*, *Chydorus*, cyclopoid copepodids, or nauplii. YOY walleye generally prefer larger prey items, and small zooplankton such as *Bosmina*, copepodites and nauplii are not consumed (Chapter II, Fox 1989; Qin and Culver 1992). Because the dominant grazer (in terms of community grazing) *Bosmina*, was unaffected by planktivory, phytoplankton biomass did not increase at high fish densities. In fact, *Bosmina* densities peaked in weeks 5-6, and *Bosmina* populations seemed capable of overgrazing
phytoplankton across treatments. If the ponds had been left longer than 6 weeks, *Bosmina* may have overgrazed the algae and then crashed.

Dominant grazers in the 1990 St. Mary's experiment were *Daphnia* and *Diaptomus*. At high densities, adult *Diaptomus* could have considerable population grazing effects on phytoplankton (McQueen 1970). Although individual grazing rates of *Diaptomus* adults were one-fifth that of *Daphnia*, grazing of *Diaptomus* populations on phytoplankton was considerable when *Diaptomus* densities peaked in my experiment. Primary productivity and phytoplankton respiration rates did not differ with fish density. However, without walleye, *Daphnia* and *Diaptomus* reached high densities, and consequently reduced edible algal biomass. *Daphnia* and *Diaptomus* collectively grazed up to 100% of the edible phytoplankton in weeks 1, 5, and 6. Conversely, predation by YOY walleye in the low and high fish density treatments strongly suppressed *Daphnia* and *Diaptomus* (walleye diet data in Fig. 11, Chapter II) and reduced grazing on phytoplankton. Grazing on phytoplankton decreased by as much as 90% in the high fish density treatments, and consequently, the biomass of edible algae increased under increased zooplanktivity.

Although the trophic cascade from planktivores to zooplankton has been demonstrated repeatedly in lake, pond, and enclosure experiments (Mills and Forney 1983; Mills et
al. 1987; Qin and Threlkeld 1990; Faafeng et al. 1990; Diana et al. 1991), the link between planktivores and phytoplankton is not clearly understood (McQueen et al. 1986; Qin and Threlkeld 1990; Diana et al. 1991). Several studies report zooplankton effects on phytoplankton may be dependent on lake trophic status (McQueen et al. 1986; Vanni 1987). Based on comparative and experimental studies, McQueen et al. (1986) proposed that zooplankton effects would be greatest on nutrient-limited phytoplankton in oligotrophic systems. Conversely, Carney and Elser (1990), using data from lakes along a trophic gradient suggested that zooplankton effects would be greatest in lakes with intermediate productivity. Zooplankton effects on phytoplankton are postulated to be weakest in eutrophic and hypereutrophic systems (McQueen et al. 1986). All ponds in my experiments were fertilized at a constant regime of 600 ug N·L⁻¹ and 30 ug P·L⁻¹ and were therefore eutrophic. In this study, I show that zooplankton community structure plays an important role in the strength of the cascade from planktivores to phytoplankton. In my 1990 experiment at St. Mary's, where ponds were dominated by large species of zooplankton such as *Daphnia* and *Diaptomus*, which have high individual grazing rates, the trophic cascade from zooplanktivores to phytoplankton is prominent, and phytoplankton biomass increases under increased zooplanktivory. Conversely, in 1989 at Hebron, when ponds
were dominated by small species with low individual grazing rates, such as *Bosmina*, the link between planktivores and phytoplankton weakened. However, small species of zooplankton can reach very high densities in the absence of *Daphnia*, because they are released from food competition, and as this study demonstrates, can ultimately overgraze phytoplankton resources. Because YOY walleye in my experiments did not prey on *Bosmina*, fish density did not affect phytoplankton biomass. However, if *Bosmina* are heavily preyed on by planktivorous fish, such as when other preferred food resources are depleted, then increased planktivory may lead to increased phytoplankton biomass via reduced biomass of zooplankton. This study demonstrates that size-related zooplankton community structure, as well as ontogenetic shifts in diet of planktivorous fish are important in determining the trophic cascade from planktivores to phytoplankton.
Table 9. Clearance rates (ml·individual⁻¹·d⁻¹) of copepods estimated from in-situ grazing experiments using Haney’s (1971) technique. n refers to the numbers of copepods used in the experiments.

<table>
<thead>
<tr>
<th>Type</th>
<th>n</th>
<th>Clearance Rate</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cyclops vernalis</em></td>
<td>7</td>
<td>0.293</td>
<td>W. Basin, Lake Erie</td>
</tr>
<tr>
<td><em>C. bicupidatus</em></td>
<td></td>
<td>0.293</td>
<td>--</td>
</tr>
<tr>
<td><em>thomasi</em></td>
<td></td>
<td></td>
<td>--</td>
</tr>
<tr>
<td><em>Diaptomus</em></td>
<td>10</td>
<td>0.612</td>
<td>W. Basin, Lake Erie</td>
</tr>
<tr>
<td>Cyclopoid</td>
<td>42</td>
<td>0.058</td>
<td>W. Basin, Lake Erie</td>
</tr>
<tr>
<td>copepodids</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calanoid</td>
<td>11</td>
<td>0.403</td>
<td>W. Basin, Lake Erie</td>
</tr>
<tr>
<td>copepodids</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclopid</td>
<td></td>
<td>0.0042</td>
<td>Lake Ontario, Bay of Quinte</td>
</tr>
<tr>
<td>nauplii</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calanoid</td>
<td></td>
<td>0.0080</td>
<td>Lake Ontario, Bay of Quinte</td>
</tr>
<tr>
<td>nauplii</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* clearance rate for *C. bicupidatus* *thomasi* assumed to be the same as that estimated for *C. vernalis*. 
Figure 20. Seasonal changes in mean zooplankton biomass during April 28 through June 9, 1989 in experiments conducted at four fish density treatment levels (n=2 ponds per treatment), at the Hebron State Fish Hatchery, Hebron, Ohio. Numbers in parenthesis are mean harvest densities (number of fish·m$^{-3}$).
Figure 20.
Figure 21. One-way ANOVA comparisons of time-weighted means of net and gross primary productivity, phytoplankton respiration rate, phytoplankton gross resource, edible and inedible phytoplankton biovolumes, and various zooplankton taxa in 1989. Comparisons are across four fish density treatments. Bar connecting treatments below each graph indicates no significant difference between those treatments. Error bars are ± 1 SE. Mean harvest densities for ponds stocked with 10, 20, 25, and 30 fish·m⁻³ are 9, 15, 12, and 23 fish·m⁻³, respectively.
Figure 21.
Figure 22. Weekly changes in the resource base of edible algae (solid line) compared against predicted zooplankton community grazing pressure (dashed line) in ponds treated with four fish density levels in 1989, at the Hebron State Fish Hatchery. Pond numbers are given against each line for edible algae and zooplankton grazing rates to facilitate comparisons. Numbers in parenthesis are mean harvest densities (number of fish·m⁻³).
Figure 22.
Figure 23. Seasonal changes in mean edible and inedible phytoplankton during April 28 - June 9, 1989 in experiments conducted at four fish density treatment levels (n=2 ponds per treatment), at the Hebron State Fish Hatchery, Hebron, Ohio. Numbers in parenthesis are mean harvest densities (number of fish·m⁻³).
Figure 24. Weekly changes in mean net and gross photosynthesis and respiration rates of phytoplankton in 1989 at the Hebron State Fish Hatchery in ponds stocked at four fish density levels. Standard error bars are shown. Numbers in parenthesis are mean harvest densities (number of fish·m⁻³).
Figure 24.
Figure 25. Seasonal changes in mean zooplankton biomass during April 26 - June 5, 1990 in experiments conducted at two fish density treatment levels (n=2 ponds per treatment), and one unreplicated no fish pond, at the St. Mary's Fish Hatchery, St. Mary's, Ohio. Numbers in parenthesis are mean harvest densities (number of fish·m$^{-3}$).
Figure 25.
Figure 26. One-way ANOVA comparisons of time-weighted means of net and gross primary productivity, phytoplankton respiration rate, phytoplankton gross resource, edible and inedible phytoplankton biovolumes, and various zooplankton taxa in 1990. Comparisons are across three fish density treatments. Bar connecting treatments below each graph indicates no significant difference between those treatments. Error bars are ± 1 SE. Mean harvest densities for ponds stocked with 25 and 50 fish·m⁻³ were 16 and 32 fish·m⁻³, respectively.
Figure 26.
Figure 27. Weekly changes in the resource base of edible algae (solid line) compared against predicted zooplankton community grazing pressure (dashed line) in ponds treated with three fish density levels in 1990, at the St. Mary's Fish Hatchery. Pond numbers are given against each line for edible algae and zooplankton grazing rates to facilitate comparisons. Numbers in parenthesis are mean harvest densities (number of fish·m$^{-3}$).
Figure 27.
Figure 28. Seasonal changes in mean edible and inedible phytoplankton during April 26 - June 5, 1990 in experiments conducted at tow fish density treatment levels (n=2 ponds per treatment), plus one unreplicated no fish treatment, at the St. Mary's Fish Hatchery, St Mary's, Ohio. Numbers in parenthesis are mean harvest densities (number of fish·m$^{-3}$).
Figure 28.
Figure 29. Weekly changes in mean net and gross photosynthesis and respiration rates of phytoplankton in 1990 at the St. Mary's Fish Hatchery in ponds stocked at three fish density levels. Standard error bars are shown. Numbers in parenthesis are mean harvest densities (number of fish·m⁻³).
APPENDIX

BIOENERGETICS MODEL
APPENDIX

BIOENERGETICS MODEL

The most common use of the bioenergetics model (Hewett and Johnson 1987) is to predict consumption (C), given estimates of growth (G), and losses as respiration (R), specific dynamic action (S), feces (F), and urine (U).

\[ C = (R + S) + (F + U) + G \]

Units for all parameters are grams of prey per gram of predator per day, wet weights. The primary factors affecting the above energy budget are water temperature, fish weight, and energy densities of predator and prey. Specific rates are adjusted for energy densities of both predator and prey.

**Consumption:** Consumption is determined by modifying the maximum specific feeding rate as an allometric function of body weight, by a temperature-dependence function and a proportionality constant representing prey availability.

\[ C = C_{\text{max}} * F(T) * P\text{-value} \]

\[ C_{\text{max}} = a * W^{-b} \]
where:

\[ C_{\text{max}} = \text{maximum specific feeding rate (g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}) \]
\[ W = \text{fish weight (g)} \]
\[ a = \text{intercept of the allometric function} \]
\[ b = \text{slope of the allometric function} \]
\[ C = \text{specific consumption rate (g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}) \]
\[ P\text{-value} = \text{proportionality constant} \]
\[ F(T) = \text{temperature-dependence function} \]

The temperature-dependence function is an algorithm dependent on the optimal and maximal temperatures, and \( Q_{10} \), for consumption. This function ranges from near 0 at low temperatures, to 1 at optimal temperature for consumption, and back to 0 at maximum temperature.

**Respiration:** Respiration is determined by multiplying the resting metabolic rate, an allometric function of weight, by the temperature-dependence function for respiration, and the activity factor. The temperature-dependence function is a number from 0 to 1, based on an algorithm which incorporates the optimum and maximum temperature, and \( Q_{10} \), for resting metabolism. The activity parameter is a number, usually from 1-3 (but up to 5.5 for walleye larvae, see Chapter I) that adjusts resting metabolism to metabolic values in the field. Losses as specific dynamic action are calculated separately as a constant proportion of assimilation, and added to respiration to yield total metabolic rate.
\[ R = a W^b \cdot r(T) \cdot ACT \]

\[ S = SDA \cdot (C - F) \]

where:

- \( R \) = specific rate of respiration (g·g⁻¹·d⁻¹)
- \( W \) = fish weight (g)
- \( a \) = intercept of the allometric weight function
- \( b \) = slope of the allometric weight function
- \( r(T) \) = temperature-dependence function
- \( ACT \) = activity parameter
- \( S \) = energy loss via specific dynamic action
- \( SDA \) = proportion of assimilated energy lost to specific dynamic action.
- \( C \) = specific feeding rate
- \( F \) = specific rate of egestion

**Egestion and Excretion:** Both egestion (\( F \)) and excretion (\( U \)) are modelled as constant proportions of consumption (\( C \)) and assimilation (\( C - F \)), respectively.
LIST OF REFERENCES


Boisclair, D. In press. The relationship between feeding and activity rates for actively foraging juvenile brook charr (Salvelinus fontinalis Mitchill). Canadian Journal of Fisheries and Aquatic Sciences.


Hile, R. 1937. The increase in the abundance of the yellow pike-perch Stizostedion vitreum (Mitchill) in lakes Huron and Michigan, in relation to the artificial propagation of the species. Transactions of the American Fisheries Society 66:143-159.


prediction of cladoceran community filtering rates. 
Limnology and Oceanography 31:1-16.

Krasnopyor, E. V. 1989. Gut evacuation rate in the bream, 

Laarman, P. N. 1978. Case histories of stocking walleyes 
in inland lakes, impoundments, and the Great Lakes -
100 years with walleye. Pages 254-260. In Selected 
Coolwater Fishes of North America. R. L. Kendall, 
editor. American Fisheries Society Special 
Publication, Number 11, Washington, D. C.

Phytoplankton control by grazing zooplankton: A study 
on the spring clear-water phase. Limnology and 
Oceanography 31:478-490.

Lasker, R. 1981. The role of a stable ocean in larval fish 
survival and subsequent recruitment. Pages 80-87. In 
Marine Fish Larvae. Editor R. Lasker. Washington Sea 
Grant Program.

Lasker, R. 1987. Use of fish eggs and larvae in probing some 
major problems in fisheries and aquaculture. 
Transactions of the American Fisheries Society 
Symposium 2:1-16.

Laurence, G. C. 1977. A bioenergetic model for the 
analysis of feeding and survival potential of winter 
flounder, Pseudopleuronectes americanus, larvae during 
the period from hatching to metamorphosis. United 


Leiby, M. M. 1984. Life history and ecology of pelagic fish 
eggs and larvae. Pages 121-140. In Marine Plankton 
Life Cycle Strategies. Editors K. A. Steidinger and L. 
M. Walker. CRC Press Inc. Boca Raton, Florida, USA.

2nd edition. Kendall/Hunt Publishing Company, Dubuque, 
Iowa. 199 p.

fertilization and carp fry on the composition and 
dynamics of plankton. Hydrobiological Studies 3:173-
217.


McQueen, D. J., J. R. Post, and E. L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems.


Qin, J., and S. T. Threlkeld. 1990. Experimental comparison of the effects of benthivorous fish and
planktivorous fish on plankton community structure. Archives fur Hydrobiologia 119:121-141.


Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-


Wu, L. 1991. Trophic interactions in a large-lake ecosystem: ontogeny of fish diet, zooplankton summer dynamics, and phytoplankton succession. Ph.D. dissertation. The Ohio State University, Columbus, Ohio, pp 123.

