THE PRACTICALITY OF METABOLIC MODELING TO PREDICT ECOSYSTEM PROPERTIES IN THE MIDDLE OCONEE RIVER

by

LINDSEY FIELDS

(Under the Direction of John R. Schramski)

ABSTRACT

Riverine ecosystems are shaped by hydro, wind, and to a lesser extent geothermal energies, and also through the work of living organisms via photosynthesis and metabolism. Environmental evaluation methods exist to assess environmental health like water quality and quantity, community abundance, and system diversity. However, biotic energy flows, storages, carrying capacities, and respective balances have not been fully explored as an additional and critical environmental health assessment tool. A mechanistic metabolic model was constructed of a small section of the Middle Oconee River (Athens, GA) to predict whole ecosystem properties that can be used to evaluate ecosystem functionality. Model sensitivities to data and assumptions were explored. In the study system, ecosystem biomass and carbon export were found to increase with food web complexity and decomposer trophic transfer efficiency. Metabolic models, currently expanding in larger geographic scale studies, also have robust discovery and educational merit in assessing more localized ecosystems.

INDEX WORDS: metabolic theory, Middle Oconee River, ecosystem model, energy, trophic web, carbon export
THE PRACTICALITY OF METABOLIC MODELING
TO PREDICT ECOSYSTEM PROPERTIES IN THE MIDDLE OCONEE RIVER

by

LINDSEY FIELDS
BA, Boston University, 2008
PhD, University of Rhode Island, 2013

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA
2018
THE PRACTICALITY OF METABOLIC MODELING
TO PREDICT ECOSYSTEM PROPERTIES IN THE MIDDLE OCONEE RIVER

by

LINDSEY FIELDS

Major Professor: John R. Schramski
Committee: C. Brock Woodson
E.W. Tollner

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
May 2018
DEDICATION

I dedicate this work to my family: Mom, Dad, Jimmy, Auntie, and Andy. Your endless love, encouragement, support, and belief in me has helped me in countless ways during my pursuit of this degree, and in everything else. Each one of you has been an unwavering support system and cheerleader, pushing me to achieve my goals. I love you all and cannot thank you enough for the roles you play in my life.
ACKNOWLEDGEMENTS

I extend my deepest gratitude to my mentor and major professor, Dr. John R. Schramski. Dr. Schramski, I am exceedingly grateful that you were willing to take a chance and welcome someone with an unorthodox background into your lab. I appreciate all of the guidance, support, and encouragement you have offered throughout my journey. Many thanks to my committee: Dr. C. Brock Woodson and Dr. E.W. Tollner. Dr. Woodson, I am forever thankful for your willingness to answer my endless questions about modeling, teaching, grading, classes, assistantships, and so on. Working with you both inside and outside of the classroom has been a pleasure and a wonderful learning experience. Dr. Tollner, I very much appreciate all of your enthusiasm and insight into my work, and I have thoroughly enjoyed working with you. There have been several other faculty members of the College of Engineering who have served as mentors and role models to me in various capacities, and each of them have further enriched my experience in the department. In particular, I thank Dr. Siddarth Savadatti and Dr. Mike Yoder for always going above and beyond to help, teach, and encourage me. Thanks also to Margaret Sapp, who helped me navigate every single deadline, form, guideline, and issue over the last two years. This was no small feat, and I truly appreciate all of your efforts.

Many thanks to our collaborators on this project for their insights, enthusiasm, and willingness to share data: Dr. Seth Wenger, Dr. Mary Freeman, Dr. Todd Rasmussen, Dr. Amy Rosemond, and Dr. Kit Wheeler. I am especially grateful to Caitlin Conn for sharing her data and taking time out of her extremely busy schedule to ensure I had everything I needed to develop the best model possible. Thanks to Dr. Kyle McKay for ensuring that the Middle
Oconee River became the focus of much-needed research efforts, and for the support of my model development.

I remain forever grateful to the academic family that I gained when I first embarked on my graduate school journey: Dr. Wally Fulweiler, Dr. Leanna Heffner, Dr. Courtney Schmidt, Dr. Brita Jessen, Dr. Autumn Oczowski, Dr. Laura Windecker, and Dr. Veronica Berounsky. You have all continued to inspire me more than you know. I will always be deeply grateful for Dr. Scott Nixon, who continues to play a critical and influential role in my development as a scholar and as a person.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>ACKNOWLEDGEMENTS</th>
<th>v</th>
</tr>
</thead>
<tbody>
<tr>
<td>CHAPTER</td>
<td></td>
</tr>
<tr>
<td>1 INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>2 BACKGROUND AND LITERATURE REVIEW</td>
<td>3</td>
</tr>
<tr>
<td>Organismal Metabolism</td>
<td>3</td>
</tr>
<tr>
<td>Metabolic Theory of Ecology (MTE)</td>
<td>5</td>
</tr>
<tr>
<td>Food Webs</td>
<td>9</td>
</tr>
<tr>
<td>Riparian Ecosystem Structure</td>
<td>11</td>
</tr>
<tr>
<td>Study Area</td>
<td>16</td>
</tr>
<tr>
<td>3 METHODS</td>
<td>21</td>
</tr>
<tr>
<td>Model Applications and Approach</td>
<td>21</td>
</tr>
<tr>
<td>Ecological Data Collection</td>
<td>29</td>
</tr>
<tr>
<td>Model Assumptions</td>
<td>31</td>
</tr>
<tr>
<td>4 RESULTS AND DISCUSSION</td>
<td>32</td>
</tr>
<tr>
<td>Food Web Structure and Complexity</td>
<td>32</td>
</tr>
<tr>
<td>Flow Variability and Assuming a Steady State System</td>
<td>36</td>
</tr>
<tr>
<td>Trophic Transfer Efficiency and the Microbial Loop</td>
<td>38</td>
</tr>
<tr>
<td>5 CONCLUSIONS</td>
<td>40</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>43</td>
</tr>
</tbody>
</table>
APPENDICES

A  INDIVIDUAL BODY MASS DATA .................................................................46
B  DIET MATRICES ...........................................................................................51
C  MATLAB CODE ...........................................................................................56
CHAPTER 1

INTRODUCTION

Energy flows in ecosystems and civilization are becoming increasingly important as landscape alterations, biomass losses, and nonrenewable energy consumption continue to increase (Day et al. 2009). Riverine ecosystems are arguably at the forefront of this importance, as over 50% of the world’s population lives within 3 km of surface freshwater bodies (Kummu et al. 2011), making rivers tightly linked to human activities. They exhibit complex and intricate energy transfer, and are shaped by numerous energies (e.g. hydro, wind, and geothermal energies) and biological activities (photosynthesis and metabolism).

Stream discharge (flow) is a primary driver of ecosystem function in rivers (Poff et al. 1997). Relating ecological processes to flow magnitude and variability is imperative to the understanding and management of riverine ecosystems. Though environmental evaluation techniques exist to assess the environmental health of rivers (e.g. stream discharge, water quality and quantity, community abundance, and system diversity), biotic energy flows, storages and carrying capacities, and balances have not been fully explored as an additional and critical environmental health assessment tool. Currently, a large collaborative project is quantifying the effects of flow variability on two key ecosystem functions in the Middle Oconee River (Athens, GA): (1) nutrient retention rate, and (2) secondary production of aquatic organisms. This entails many complex biological and ecological measurements and a multidisciplinary team of scientists and engineers. Part of this project, and the focus of this work, is to consider the role and
practicality of modeling energy storage and flow as the driver in these nutrient retention and production processes.

The underlying premise of this research lies in the knowledge that we can link the performance of individual organisms within an ecosystem to the storage and flux of carbon of the entire system using metabolic theory (Brown et al. 2004; Schramski et al. 2015). If we know or can reasonably estimate the gross primary production, environmental temperature, and food web composition of an ecosystem, we can use a metabolic derived model to predict whole ecosystem properties such as system biomass and carbon export and presumably assess ecosystem health and vitality. Metabolic theory has almost exclusively been applied to large ecosystems in a macro-ecological framework. Therefore, to assess the practicality of this approach for small ecosystems, a mechanistic metabolic model was constructed of a small section of the Middle Oconee River to predict whole ecosystem properties that can be used to evaluate ecosystem functionality and inform restoration efforts. The model was used to assess whether this type of model can be accurately transferred from larger, global-scale ecosystems (e.g. Schramski et al. 2015; Woodson et al. 2018) to smaller, more localized riverine ecosystems, and more generally applied to other rivers. Model sensitivities to data and assumptions were explored. The ultimate goal of this work was to build a solid foundation for a mechanistic metabolic model that can be applied to any river ecosystem as a simple, user-friendly tool for ecosystem assessment.
CHAPTER 2
BACKGROUND AND LITERATURE REVIEW

Life on Earth persists because of the flow of energy, and metabolism is the mechanism through which organisms process this energy (Brown et al. 2005; Schramski et al. 2015). In a natural ecosystem, energy and materials flow through the food web, and because of the energy stored in organic bonds that are formed and broken in exchanges of energy, we can essentially equate carbon to energy in these systems. Furthermore, this flow of carbon/energy through an ecosystem is dictated by the metabolism of the individual organisms in that system, and the total production within a trophic level is equal to the sum of its individuals (Schramski et al. 2015). In rivers, the ecosystem structure is complex, which lends to complexity in the food web and thus energy and material flows. Furthermore, a background knowledge of the specific riverine ecosystem is necessary to understand the more detailed nuances of ecosystem functionality for that system. This literature review addresses aspects that require some consideration for building a mechanistic metabolic model of the study area in the Middle Oconee River—organismal metabolism, the metabolic theory of ecology, food webs, riverine (riparian) ecosystem structure, and a description of the Middle Oconee River.

Organismal Metabolism

Metabolism is a complex series of enzyme-driven biochemical reactions that occur inside living organisms and collectively serves as the biological processing of resources and energy. This biological processing dictates the demands of organisms from their environment as well as
constrains resource allocation among organisms (Brown et al. 2004). Thus, the “speed of living” is characterized by the rate of biological metabolism (Brown et al. 2005), and knowledge of biological metabolism (i.e. the fluxes and stores of energy in the environment) is central to the understanding of ecosystem dynamics and anthropogenic impacts on natural systems (Schramski et al. 2015).

In general terms, energy is harnessed into biomass by autotrophs that comprise the base of the food web, is transferred and stored throughout trophic networks, and is released during respiration to fuel biological work (Brown et al. 2005; Schramski et al. 2015). Though metabolism is a biological process, it obeys the laws of thermodynamics along with the laws of mass and energy balance (Brown et al. 2004).

The metabolic characteristics of the individual organisms in an ecosystem influence many critical aspects of the ecosystems themselves, including biological and chemical composition, energy and material fluxes, population processes, and species diversity (Brown et al. 2004). Thus, in order to truly understand the dynamics of an ecosystem it is critical to be able to quantify the metabolic characteristics of its organisms in some way. Unfortunately, it is generally considered challenging and difficult to directly measure metabolic rates with an acceptable degree of accuracy and consistency (Brown et al. 2004). However, properties of individual organisms and their environments determine the rates of biological metabolism and many measurable things can impact the metabolism of both individuals and the system as a whole (Brown et al. 2004). Thus, researchers can take advantage of these relationships and identify predictors of individual metabolic rates.

At the individual level, there are many things that can impact rates of biological metabolism. Among them are: individual characteristics of organisms, interactions of organisms
with their environment, interactions among organisms, and the structure and composition of the community. Metabolic rates of individual organisms are generally driven by body size, temperature, and the availability of resources (Brown et al. 2005; Isaac et al. 2012). Organisms have a two-way interaction with their environment that directly impacts resource availability and thus individual metabolic rate; they obtain the necessary habitat and food sources from their environment, and in turn, have an impact on the biogeochemical cycles and surrounding physical environment. Similarly, the size and composition of a community can impact resource availability and predator/prey relationships. Thus, community composition and the food web structure of an ecosystem impacts the metabolic rates of individuals. With knowledge of these interactions, scientists have begun to establish top-down and bottom-up theoretical frameworks that help to mechanistically explain and predict individual metabolic rates and whole-ecosystem properties.

*Metabolic Theory of Ecology (MTE)*

There are two main theoretical frameworks used to describe the flow of energy and materials in ecosystems; one (Systems Theory of Ecology) takes a top-down approach, while the other (Metabolic Theory of Ecology) takes a bottom-up approach (Schramski et al 2015). The Systems Theory of Ecology was first established by Odum (1994) and takes a top-down approach to quantify energy/material flows through functional compartments within an ecosystem (Jørgensen 2009; Schramski et al 2015). The Metabolic Theory of Ecology (MTE) is complimentary to the Systems Theory of Ecology and is the focus of this research.

MTE is an emerging mechanistic framework that takes a bottom-up approach for (1) quantifying individual metabolic rates and (2) predicting whole-ecosystem properties (Brown et
al. 2004; Sibley et al. 2012; Schramski et al. 2015). This framework of understanding is based on the idea that it is possible to use individual characteristics (i.e. body size and temperature) along with resource availability to understand how biological metabolism at the molecular and individual level can facilitate ecosystem-level properties (Sibley et al. 2012). Fundamentally, it equates energy and materials (e.g. carbon) as “ecological currencies” and exploits ecological relationships that are already well-established for individual metabolic rates (Brown et al 2004; Sibley 2012). MTE holds that these individual metabolic rates ultimately drive population-, community-, and ecosystem-level dynamics because it is metabolism that controls resource allocation to survival, growth, and reproduction (Sibley 2012).

The principals of metabolic scaling and allometry can be applied directly in the MTE framework by quantifying individual metabolic rates of organisms within an ecosystem. This is done using the metabolic theory equation, which predicts individual rates of production using allometric scaling of two of the primary factors that constrain metabolic rate: body size and temperature (Gillooly et al. 2001; Brown et al. 2004). The metabolic theory equation as described in Brown et al. (2004) and Schramski et al. (2015) is equation (1) below:

$$P_{\text{ind}} = P_o M^\beta e^{-E/kT}$$

Where $P_{\text{ind}}$ is individual production (kg C ind$^{-1}$ y$^{-1}$), $P_o$ is a coefficient determined from empirical data, $M$ is body mass (kg), $\beta$ is a mass scaling coefficient (~0.75), $E$ is activation energy (E=0.32 eV for photosynthesis and E=0.65 eV for respiration), $k$ is Boltzmann’s constant (8.62 x 10$^{-5}$ eV/K), and $T$ is environmental temperature (ectotherms) or internal body temperature (endotherms) in degrees Kelvin.

MTE in general is largely built on the initial work by Kleiber (1932) and his discovery that whole-organism metabolic rate could be scaled allometrically. Individual body mass causes
predictable variation of nearly all characteristics of organisms, and most of this variation can be described by allometric equations (Huxley 1932) with a specific biological scaling rate ($\beta$) of 0.75 for whole-organism metabolic rates (Kleiber 1932). Increasing temperature causes an exponential increase in metabolic rates as well as most other biological activities (Brown et al. 2004). The Boltzmann factor ($k$) describes how temperature impacts the kinetic energy of molecules and thus the reaction rate across the $0 \to 40^\circ C$ temperature range (Boltzmann 1872; Brown et al. 2004). Combining these two relationships yields the above metabolic theory equation (Gillooly et al. 2001). $P_o$ is a normalization constant independent of body size and temperature, and $E$ is the activation energy required for metabolism. $P_o$ and $E$ are typically determined from empirically measured body mass, temperature, and metabolic rate data for different groups of organisms (Brown et al. 2004). When applying this equation to the MTE, it is common to calculate the average individual production ($P_{ind}$) for an entire trophic compartment by using the appropriate $P_o$ and the average body mass ($M$) of all individuals within that trophic compartment (Schramski et al. 2015).

Starting with primary producers at the base of the food chain, the calculated $P_{ind}$ can be used to determine the population size ($N$) using equation (2) below if a measure of gross primary production (GPP) is known.

$$N \left( \frac{\# \text{ individuals}}{m^2} \right) = \frac{\text{NPP}}{P_{ind}}$$  \hspace{1cm} (2)

Where NPP is net primary production in kg C m$^{-2}$ y$^{-1}$ and is typically assumed to be 50% of GPP (Schramski et al. 2015; Zhang et al. 2009). For larger-scale analysis in aquatic ecosystems where only satellite-measured primary production is available, calculations can be adapted to incorporate photosynthetically active radiation (PAR) data and thus account for light penetration.
through the water column (Woodson et al. 2018). The total biomass within a trophic level (B) can then be calculated as in equation (3):

\[ B = N \times M_{\text{ind}} \]  

(3)

The average individual production (\(P_{\text{ind}}\)) of a trophic compartment can then be scaled to calculate the production of the entire trophic compartment (\(P_{\text{total}}\)) by multiplying by the total biomass within that compartment (B) as in equation (4):

\[ P_{\text{total}} = P_{\text{ind}} \times B \]  

(4)

In other words, the production rate of any trophic compartment is the sum of production of all individuals within that compartment (Schramski et al. 2015).

Carbon flow to the next trophic level is calculated by multiplying \(P_{\text{total}}\) by a trophic transfer efficiency (TTE). TTE is expressed as a fraction and represents the amount of energy (carbon) transferred between successive trophic compartments (Schramski et al. 2015). Literature values of TTE typically range between 0.01 and 0.2 (Schramski et al. 2010), though there is much uncertainty surrounding TTE estimates in general. Predator-prey body size relationships have been shown to influence TTE, with decreases in transfer efficiency as body size increases (Fig. 1) (Barnes et al. 2010).
Figure 1. Relationship between predator-prey mass ratios (PPMR), TTE, and predator mass observed in a meta-analysis of nearly 35,000 published predation events from 27 marine locations. Predators in this data set were primarily fish and squid in marine environments. From Barnes et al. (2010).

Food Webs

The structure and properties (e.g. trophic linkages) of the food web within an ecosystem play a critical role in driving energy flow through an ecosystem, as well as determine ecosystem resilience and species extinction (Petchey et al. 2012). Therefore, it is important to understand the organization and complexity of food webs.

The base of all food chains is comprised of autotrophic organisms, or organisms that fix light or chemical energy into carbon (Odum and Barrett 2005). All other organisms are considered heterotrophs, which require the consumption of organic materials for sustenance (Odum and Barrett 2005). The structure of a food web is formed when successive consumptions of organisms by other organisms create metabolically-driven linkages between different trophic
levels (Petchey and Dunne 2012). With each transfer, the quantity of energy decreases but the quality of energy increases (Odum and Barrett 2005). At each transfer, a large (typically 80-90%) portion of energy is lost as heat, which results in TTEs that are typically less than 20% (Odum and Barrett 2005).

Organisms are classified into specific trophic levels based on the number of steps between the sun (light energy) and what they consume for nourishment (Odum and Barrett 2005). Thus, from a functional perspective, green plants occupy the first (producer) trophic level, herbivores (primary consumers) occupy the second trophic level, primary carnivores (secondary consumers) occupy the third trophic level, and secondary carnivores (tertiary consumers) occupy the fourth trophic level (Fig. 2) (Odum and Barrett 2005). Organisms within a single population can be a member of multiple trophic levels depending on what they eat (e.g. omnivores), and these kinds of links between trophic compartments often add much complexity to the structure of a food web in a given ecosystem.

![Figure 2](image)

**Figure 2.** A simplified conceptual diagram of basic trophic level organization within an ecosystem.

British ecologist Charles Elton was one of the first researchers to establish principles of food webs. Elton (1927) observed that predators are typically larger in size than their prey, thus
establishing the importance of individual body size in determining trophic level composition and food web structure. Empirical relationships have since been established between mean prey and predator size across various animal taxa (Petchey and Dunne 2005). Body size is now known to be one of the most important factors driving the structure of food webs (Brown et al 2004; Petchey et al 2008), and size-based food webs relate food web structure to species body sizes. Though predators tend to be larger than their prey, there is much variation in the distribution of predator-prey body-size ratios in ecosystems (Brose et al. 2006). For instance, generalist predators eat prey of multiple sizes, and mega-consumers eat organisms that are much smaller in size (e.g. whales; Woodson et al. 2018). This kind of variation in diet preference can impact both the overall structure of the food pyramid and the overall biomass of an ecosystem (Woodson et al. 2018).

Size-spectra models use scaling arguments based on individual body size for predictions of ecosystem structure, while the metabolic theory model is based on trophic levels and relies on metabolic scaling and thermodynamic relationships (Woodson et al. 2018). Despite these differences, Woodson et al. (2018) found that both models yield similar predictions for ecosystems with size-based food webs and linear energy transfer, as long as large generalist predators and gigantic secondary consumers are not prevalent within the ecosystem. However, the presence of large generalist predators and/or gigantic secondary consumers is a common occurrence in many types of ecosystems (e.g. oceans and rivers).

Riparian Ecosystem Structure

The hydrology and geomorphology of rivers are complex, and this fosters a large degree of spatial heterogeneity in the structure and function of riverine ecosystems (Poff et al. 2006).
The natural flow of a river varies across timescales of hours to years, and tends to exhibit regional and seasonal regimes (Poff et al. 1997). Rivers also vary in size, shape, substrate/geology, and topography, and these geomorphic settings mediate physical and hydrologic structure and dynamics of the riverine ecosystem (Poff et al. 2006).

Ecological processes in riverine ecosystems are regulated by the magnitude, frequency, duration, timing, and rate of change of hydrologic flow regimes (Poff et al. 1997). In addition to hydrologic variation, the geomorphology of a river is an additive mechanism of control that drives ecological processes (Poff et al. 2006). Nearby land-use and anthropologic impacts (e.g. dams, urbanization, levees, groundwater pumping) also have an impact on riverine ecosystems as they play a major role in altering the ecology and health of fluvial ecosystems (Poff et al. 1997; Poff et al. 2006).

Though the base of the food chain in aquatic ecosystems is comprised of primary producers, rivers are unique in that the majority of this energy source does not always originate within the vicinity of its consumption, or even within the stream itself (Allan and Castillo 2007). This is supported by the fact that in many aquatic ecosystems, heterotrophic respiration exceeds gross primary production (Cole and Caraco 2001). In fact, an estimated 66% of consumed organic material is allochthonous (i.e. originated in a place other than where it’s found) coarse particulate organic matter (Allan and Castillo 2007). While phytoplankton form the base of many aquatic food webs in freshwater environments (Litchman 2005), organic material such as leaf fall and detritus, and the resulting bacterial/fungal biofilms, also contribute to the pool of available food for consumers in rivers (Allan and Castillo 2007). Organic material from upslope and upstream areas can largely or exclusively support high rates of ecosystem metabolism and rich food webs (Bernhardt et al. 2017). The potential rate of autochthonous (i.e. formed in its present
position) gross primary production (GPP) in a riverine ecosystem is maximized in rivers with clear, slow-flowing water with high light availability, but a lack of these characteristics does not indicate low biological rates in an area because of the potential contribution of allochthonous organic material (Bernhardt et al. 2007).

In addition to the heterogeneity in primary production, the food web structure in river ecosystems can be complex (Fig 3) and difficult to quantify for several reasons. First and foremost, there is a large degree of diet overlap and organisms that feed at multiple trophic levels (Allan and Castillo 2007). Additionally, individual species and feeding groups can often exhibit seasonal and/or geographical changes in diet (Allan and Castillo 2007). Methodologies for deciphering this complexity in riverine food webs are inadequate, and this has been a topic of research for decades (Jepsen and Winemiller 2002). Most data that are obtained regarding individual diets come from short-term feeding observations or stomach contents analysis that do not account for long-term variability (Jepsen and Winemiller 2002). Additionally, gut contents of invertebrates and smaller organisms are extremely difficult to distinguish (Allan and Castillo 2007). Stable isotope analyses can be used to reveal trophic structure within an ecosystem on a coarse level (i.e. poor taxonomic resolution) (Jepsen and Winemiller 2002). In other words, stable isotope analysis of fish tissue can reveal which trophic level they are eating at (food chain length), but not precisely what they are eating. Stable isotope data in combination with stomach content analysis can provide a much more complete view of the food web structure in an ecosystem, though it would not adequately address the diet preferences of very small organisms (e.g. insects) that play a critical role in riverine food webs.
Figure 3. A generalized riverine food web shown with interactions in the microbial food web (red lines). Adapted from Allan and Castillo (2007).

There is a paucity of food web studies in large riverine ecosystems, but much research has been conducted on classifying the overall ecosystem functionality of these systems (Hoeinghaus et al. 2007). In particular, there are three main general concepts of ecosystem
functioning that integrate biology, hydrography, and geomorphology to each one highlighting
different principal energy source that drives the fluvial food web (Hoeinghaus et al. 2007): The
River Continuum Concept, the Flood-Pulse Concept, and the Riverine Productivity Model. The
River Continuum Concept was developed by Vannote et al. (1980) and focuses on the physical
gradients along the length of a river. It proposes that this gradient of physical conditions results
in consistent organic matter dynamics that drive predictability of biological communities along
the length of a river (Vannote et al. 1980). Furthermore, it predicts that downstream communities
take advantage of inefficient upstream processing of organic material by assimilating the
downstream “leakage” of material (Vannote et al. 1980). The Flood-Pulse Concept is
complimentary to the River Continuum Concept and attempts to address its biggest limitations:
that it was developed on a small temperate stream but extrapolated to big rivers, and that it is
restricted to permanent, lotic habitats abut had been elaborated for the river basin (Junk et al.
1989). The Flood-Pulse Concept says that seasonal flood pulses in the river-floodplain systems
are what dictates ecosystem dynamics, and that fish yields and production are strongly related to
the accessibility of the floodplain (Junk et al. 1989). The Riverine Productivity Model was
developed by Thorp and Delong (1994) as an alternative to the River Continuum Concept and
Flood-Pulse Concept. It emphasizes the importance of labile autochthonous organic material and
direct organic inputs from the riparian zone to consumers relative to the more refractory
allochthonous material that is leaked from upstream due to inefficient processing (Thorp and
Delong 1994).

One final consideration that must be taken into account when discussing the ecosystem
and food web structure of riverine ecosystems is the potential contribution of the microbial loop.
The flux of carbon through the microbial food web is greater than historically thought (Allan and
Castillo 2007). These microbes act as decomposers and feed at multiple levels of the food web. They are consumed either directly as individual cells or biofilms by other organisms, or in association with larger particles of organic matter to which they are attached (Fig. 3) (Allan and Castillo 2007). The question remains whether a riverine microbial food web serves a role only in nutrient recycling and carbon remineralization, or if it also serves as an important energy pathway to higher trophic levels (Allan and Castillo 2007).

**Study Area**

The Middle Oconee River is a 6th order river in the upper Altamaha watershed with a drainage basin of 1031 km² (McKay 2014). It is situated in the Piedmont physiographic province in the Upper Oconee watershed, has a number of tributaries, and eventually joins with the North Oconee River in Athens to form the Oconee River before becoming the Altamaha River (Fig. 4) (Katz 2009; Pahl 2009). Based on data from a USGS stream gage (#02217500) located just downstream of the study site, the average daily discharge rate of the river ranges from 39 to 6660 cubic feet per second (cfs), with an annual average daily discharge of 571 cfs (Fig. 5).
Figure 4. Map of the Middle Oconee River shown with the location of USGS Stream Gages (red circles) and the withdrawal point for the Bear Creek Reservoir (green triangle). Modified from McKay (2014).

Figure 5. Average daily discharge of the Middle Oconee River. Dashed line represents the annual average daily discharge rate (571 cfs). Data are from USGS stream gage #02217500 located downstream of the study site (see Fig. 4 for location). Data downloaded from: http://waterdata.usgs.gov/nwis/inventory/?site_no=02217500
The Middle Oconee River plays an important role for the local community as it has 14 withdrawal points for drinking water supply, 5,467 in-stream impoundments, and 3 major surface reservoirs (Pahl 2009). When considered as a whole, the Oconee River Basin supports many important uses including drinking water, municipal and industrial uses, agriculture, and energy (Table 1). Despite this importance, the ecology and biology of the river has been largely unstudied to date. Very few extensive surveys have been conducted to identify the species composition in the river, two of which were conducted in the same area on a shoal (Grubaugh and Wallace 1995; Nelson and Scott 1962).

Table 1. Current uses of the Oconee River as described by the Georgia River Network (https://garivers.org/other-georgia-rivers/oconee-river.html).

<table>
<thead>
<tr>
<th>Category</th>
<th>Description</th>
</tr>
</thead>
</table>
| Drinking Water            | - Fourteen surface water intakes  
                           | - Municipal and privately owned public water systems supply drinking water for around 282,000 people in the state of Georgia                  |
| Municipal and Industrial  | - City of Athens has two surface water withdrawal permits that total 28 MGD (monthly average)                                              |
|                           | - Over one hundred facilities are authorized to discharge wastewater into the Oconee River Basin                                          |
| Agriculture               | - Irrigation of farmland in the Oconee River Basin requires around 4 billion gallons per year of water, and another 3.8 billion gallons of water per year for livestock operations |
|                           | - There are 559 agricultural water withdrawal permits in the Oconee River Basin                                                             |
| Energy                    | - Hydropower generation facilities dominate industrial surface water use  
                           | - Until recently, Georgia Power Company had a coal plant branch that withdrew water from Lake Sinclair                                           |
| Impoundments              | - Three major surface water reservoirs (Lake Oconee, Bear Creek, Lake Sinclair)                                                               |
|                           | - Hard Labor Creek Regional Reservoir is under construction                                                                                   |
|                           | - Upper Oconee contains nearly 5,500 small impoundments which cover 175 km²                                                                  |
The studies conducted by Nelson and Scott (1962) and Grubaugh and Wallace (1995) involved extensive biomass surveys on the same study area: a shoal adjacent to Ben Burton Park (Clarke County) that extends 500 m and that has an average width of 80 m (Fig. 4). USGS gauging station number 02217500 is located at a rock outcrop in the stream bed just downstream of the study site and has been collecting daily discharge and water temperature data since 1937 (Fig. 4). A second USGS gauging station is located upstream of the study area in Arcade, GA (USGS gage number 02217475) (Fig. 4). Drinking water intakes for the City of Athens, GA are also located immediately downstream of the study area (Fig. 4) (Grubaugh and Wallace 1995).

During the time period over which Nelson and Scott (1962) conducted their study, there were no industrial contributions to water pollution in the Middle Oconee River, and the upstream watershed was characterized by mostly woodland, cropland, and pasture, with a minimal contribution of roads and houses (Fig. 6) (U.S. Dept. of Interior 1951). Though there was little change in the shoals and adjacent riparian areas reported by Grubaugh and Wallace (1995), they noted substantial changes in land use practices in the river basin. Specifically, the amount of cropland had decreased to less than 20%, and the cropland dedicated to cotton and corn had been completely eliminated. By 2009, land cover remained predominantly forested, but the amount of agriculture decreased in favor of urban development and other uses (Fig. 6) (Pahl 2009).
Since the surveys conducted by Nelson and Scott (1962) and Grubaugh and Wallace (1995), a major water diversion was constructed in 2002 that is situated approximately 13.5 km upstream of the sampling site. Bear Creek Reservoir is a privately-owned, off-channel pump-storage, 204-ha reservoir that supplies water to four surrounding counties (Katz 2009). There is also now a low-head hydropower dam, Fall Line Hydro 2008, located 12.8 km upstream of the study area (Katz 2009).
CHAPTER 3

METHODS

This project entailed the adaptation of a mechanistic metabolic theory model for part of the Middle Oconee River (MOR) to predict whole-ecosystem properties such as biomass and carbon export rates from the ecosystem. Existing datasets from the MOR and sufficiently similar datasets from similar rivers (e.g. body sizes, temperatures, populations, etc.) were used to build the model. The model was used to assess whether this type of model can be accurately transferred from larger, global-scale ecosystems (e.g. Schramski et al. 2015; Woodson et al. 2018) to smaller, more localized riverine ecosystems, and more generally applied to other rivers. Further, model sensitivities to data and assumptions were explored. The ultimate goal of this work was to build a solid foundation for a mechanistic metabolic model that can be applied to any river ecosystem as a simple, user-friendly tool for river ecosystem assessment. It is hoped that this model can serve as a basis for future research and refinements.

Model Applications and Approach

The metabolic theory model developed for this research was an adaptation of a metabolic theory model published by Woodson et al. (2018) that predicts biomass density, abundance, production (as carbon uptake), and carbon export for each trophic compartment in the food web of the global ocean. The model follows computational methods as in Schramski et al. (2015) and was developed and adapted for the Middle Oconee River using MATLAB.
The mechanistic metabolic model assesses each grid as a computational cell in a given study area. Model inputs include water temperature and gross primary production, as well as information about the organisms present in the ecosystem, their individual body masses, and information about the ecosystem food web (described below). For each grid cell and trophic compartment, the model outputs include total biomass density, abundance, production (carbon uptake), and carbon export.

The mechanistic metabolic model for a shoal study area in the Middle Oconee River varied food web connectivity, primary producer composition, and TTEs for both decomposers and non-decomposers for a total of 27 different variations (Table 2; described in more detail below). The shoal area of the Middle Oconee River was used because it has the most associated available ecological data; it was the study site that was sampled historically by Nelson and Scott (1962), Grubaugh and Wallace (1995), and more recently by Conn (in prep). Total area was calculated using the average wetted widths of the river measured at three transects across the shoal around 15 times per month throughout 2016 – 2017 by Conn (in prep). Annual average water temperature of the study area was used as the temperature input (see details in “Ecological Data Collection” section below).
Table 2. Model parameter variations.

<table>
<thead>
<tr>
<th>Food Web Type</th>
<th>Primary Producer Trophic Structure</th>
<th>TTEs (decomposers)</th>
<th>TTEs (non-decomposers)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linear size-structured</td>
<td>All grouped into one compartment</td>
<td>0.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Generalist</td>
<td>Three separate compartments</td>
<td>0.1</td>
<td>0.01</td>
</tr>
<tr>
<td>Literature-approximated</td>
<td>(diatoms, filamentous algae, other macroalgae)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Only diatoms consumed</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

A size-structured classification of trophic levels was assigned to the study area using the best available data: (Nelson and Scott 1962; Grubaugh and Wallace 1995), the Oconee River (Evans 1994), and more general information from the literature about food web dynamics in riverine ecosystems (Allan and Castillo 2007). A species list was first compiled for the shoal environment specific to our study site (Nelson and Scott 1962; Grubaugh and Wallace 1995) and from fish present downstream in the Oconee River proper (Evans 1994). The individual body mass of each species and their endotherm or ectotherm designation was determined from the literature (Appendix A). Species were classified into appropriate trophic compartments of a size-structured food web (Table 3) based on their body mass. Distinctions between “large” and “small” groups for these trophic compartments were determined by calculating the 50th percentile in each group (insects and invertebrates, and fish, separately). Then, an average body mass for each of the trophic compartments was calculated by taking the geometric mean body size for all organisms classified into that specific trophic level (Table 3). The geometric mean was used rather than an arithmetic mean because body mass data were not normally distributed,
and use of a geometric mean eliminated any potential bias from very high or very low outliers (Costa 2010). The average body mass of bacterial decomposers was assumed to be the same as in Woodson et al. (2018).

Primary producers had large variability in average body mass of the species present. To account for the large size distribution in primary producers and the results and availability of biomass data for the study area, three different trophic structures were used in model runs (Table 2): (1) all primary producers were grouped into a single trophic compartment and eaten with essentially equal preference, (2) three separate compartments of primary producers were used where all compartments were eaten from, but with a higher preference towards consumption of diatoms, and (3) three separate compartments of primary producers were used, but the only primary producer consumed by higher trophic levels was diatoms. These delineations were based on relative size of primary producers, and also on the basis that it is generally known that macroalgae and filamentous algae comprise a very small proportion of consumer diets in river ecosystems (Allan and Castillo 2007). When primary producers were split into three trophic levels, it was assumed that the percent contribution of each type of primary producer to annual gross primary production corresponded to the percent of total wet biomass (Table 4).
Table 3. Trophic structure used for this metabolic theory model of the shoal study area in the Middle Oconee River.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Average Individual Body Mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary Producersa (diatoms, filamentous algae, and other macroalgae species)</td>
<td>N/Ab</td>
</tr>
<tr>
<td>Zooplankton, small insects and small invertebrates</td>
<td>$10^{-8}$</td>
</tr>
<tr>
<td>Large insects and invertebrates</td>
<td>$10^{-5}$</td>
</tr>
<tr>
<td>Small fish</td>
<td>$10^{-1}$</td>
</tr>
<tr>
<td>Large fish</td>
<td>$10^{0}$</td>
</tr>
<tr>
<td>Decomposers (bacteria)</td>
<td>$10^{-12}$</td>
</tr>
</tbody>
</table>

aData Due to large variability in the size of primary producers, the trophic structure of primary producers was varied for model inputs: all primary producers were grouped in a single trophic compartment or they were split between three trophic compartments. See description in text for additional details.

bBody mass data for primary producers was entered into the model as a total biomass measured via surveys of the study area. See description in text for additional details.

Table 4. Percent contribution of each primary producer trophic compartment to overall autochthonous GPP in the metabolic theory model.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Percent Contribution to GPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms</td>
<td>0.001%</td>
</tr>
<tr>
<td>Filamentous algae</td>
<td>2.4%</td>
</tr>
<tr>
<td>Other macroalgae</td>
<td>97.6%</td>
</tr>
</tbody>
</table>

A series of three different food webs with varying degrees of complexity were established for the study area to examine the sensitivity of the model to changes in food web structure (Table 2). The simplest food web titled the “linear size-structured” food web has organisms within each trophic compartment feed exclusively from the next lowest trophic compartment. A more complex food web, the “generalist” food web, entailed each trophic level feeding from all trophic levels below with equal preference. The most complex food web was the “literature-approximated” food web, in which the dietary preferences of organisms within each trophic level were approximated as a “best estimate” based on information found in the scientific literature (see Appendix A for sources). These food webs were constructed for both primary...
producer trophic compositions (Figs. 7, 8). For each food web configuration, a diet matrix was constructed that assigned a diet preference (as percent of total diet) to every trophic compartment (see Appendix B for all diet matrices). These diet matrices were pulled directly into the model. It was the intention of these diet matrices to encompass a large range in differences, with the knowledge that actual trophic structure in the MOR is likely somewhere in between.
Figure 7. Food web structures used for model variations in which all primary producers were grouped into a single trophic compartment. Food web complexity varied from least complex (top) to most complex (bottom).
Figure 8. Food web structures used for model variations in which primary producers were split into three different trophic compartments. Food web complexity varied from least complex (top) to most complex (bottom).
TTEs of both decomposers and non-decomposers were varied to explore potential resultant variations in model outputs (Table 2). Decomposer TTE was varied between 10% and 40% as in Schramski et al. (2015), while non-decomposer TTE was varied between 1% and 10% (Woodson et al. 2018).

In equation (1), the normalization constant \( P_o \), activation energy \( E \), and mass scaling exponent \( \beta \) are estimated from empirically measured body mass, temperature, and metabolic rate data for different groups of organisms (Table 5).

### Table 5. Metabolic scaling coefficients used in MOE shoal study area metabolic model. Values are from Brown et al. (2004) and Woodson et al. (2018) and references therein and represent the best available values in the literature.

<table>
<thead>
<tr>
<th>Level</th>
<th>( P_o )</th>
<th>( E ) (eV)</th>
<th>( \beta )</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 (autotrophs)</td>
<td>1.32E(^9)</td>
<td>0.32</td>
<td>1.036</td>
</tr>
<tr>
<td>1 (zooplankton, small insects, and invertebrates)</td>
<td>2.16E(^9)</td>
<td>0.65</td>
<td>0.96</td>
</tr>
<tr>
<td>2 (large insects and invertebrates)</td>
<td>2.16E(^9)</td>
<td>0.65</td>
<td>0.75</td>
</tr>
<tr>
<td>3 (small fish)</td>
<td>2.16E(^9)</td>
<td>0.65</td>
<td>0.79</td>
</tr>
<tr>
<td>4 (large fish)</td>
<td>2.16E(^9)</td>
<td>0.65</td>
<td>0.79</td>
</tr>
<tr>
<td>5 (decomposers)</td>
<td>1.32E(^9)</td>
<td>0.32</td>
<td>1.036</td>
</tr>
</tbody>
</table>

**Ecological Data Collection**

Input data included measurements taken from the study area and literature values of similar circumstances whenever site data was not available. For example, gross primary production (GPP) was assumed to be 0.01 kg C m\(^{-2}\) y\(^{-1}\), which was a mid-range value based on a meta-analysis of annual GPP estimates from deciduous forest streams at similar latitudes.
Collaborating scientists from University of Georgia’s (UGA’s) River Basin Center (RBC) led by Caitlin Conn collected significant ecological and environmental data from the MOR shoal study area in 2016 and 2017 (ref. forthcoming dissertation by C. Conn *in prep*) which was also the same study site used in Nelson and Scott (1962) and Grubaugh and Wallace (1995) (Fig. 4,9). C. Conn’s methods are briefly summarized here for completeness. In the study area, three transects were visited approximately monthly for eighteen months in 2016 – 2017 (Fig. 9). Wetted width of the river, sampling depth, turbidity, and biomass of primary producers including diatoms, filamentous algae, red algae (*Lemanea* species), riverweed (*Podostemum* species), and pondweed (*Potamogeton* species) were measured and documented.

*Figure 9.* Transect sampling locations where environmental data were collected. This is the same location as surveys conducted by Nelson and Scott (1962) and Grubaugh and Wallace (1995).
Where biomass sampling of macro-producers was accomplished using methods modified from Pahl (2009) as described in Conn (in prep) to obtain measurements of ash-free dry mass, this model used an average wet weight of each species from the entire sampling period as model inputs for primary producer biomass (kg C m$^{-2}$ y$^{-1}$). Because actual measurements of primary producer biomass were available, and because it is extremely difficult to quantify an average body mass for macroalgae, values for primary producer group mass density and gross primary production (GPP) were entered directly into the model rather than calculating a rate of individual production using the equation for metabolic scaling. Water temperature was continuously recorded every ten minutes from Dec 2016 to Dec 2017 immediately downstream of the study site, and an annual average water temperature value was used for the body temperature of all ectotherms in calculations of individual production as described above.

**Model Assumptions**

Major assumptions for model construction were: (1) the study area remains in steady-state over the course of a year, (2) there is a constant (average) daily discharge rate and thus a constant wetted perimeter within the study area, (3) all organisms in each trophic compartment have the same body mass (average mass of all individuals), and (4) the constant parameters and input values used in model calculations are an accurate representation of the study area. The impact of these assumptions was addressed to varying degrees in different model scenarios and model inputs outlined in Table 2.
CHAPTER 4
RESULTS AND DISCUSSION

There are several difficulties associated with choosing model parameters for a mechanistic metabolic model of a riverine ecosystem, which ultimately translate into underlying model assumptions. Each assumption should be taken into careful consideration when applying this type of model to a river, because it has the potential to heavily impact model outputs. In this study, many of these concerns were initially approached by developing various ranges of model scenarios in an attempt to capture the corresponding variation of model outputs. Using this sensitivity approach, we were able to evaluate the feasibility of adapting a mechanistic metabolic model to small sections of riverine systems to determine (1) if the adapted model can be generally and effectively applied specifically to the MOR ecosystem, and (2) which parameters the model is most vulnerable to. Below is a description of some of the key difficulties and assumptions associated with the application of a mechanistic metabolic model to river ecosystems, along with an assessment of how this model dealt with each one.

Food Web Structure and Complexity

Fluvial food webs have a high level of complexity and diet overlap, and it is often difficult to classify species into a particular trophic level (Allan and Castillo 2007). Adding to this complexity are the seasonal changes that impact river flow rate, and geomorphology that allow for various substrate types and microhabitats throughout the river, all of which result in varying communities and food web structures. Though this effort and model did not address
seasonal changes that arise from flow variability, changes in primary producer trophic structure and food web complexity were examined.

In all model scenarios where non-decomposer TTE was set to 10%, there was a trend of increasing biomass output with increasing food web complexity (Table 6). The most complex food web with the largest number of trophic linkages (the literature-approximated food web) produced the largest biomass output, while the simpler linear size-structured food web generated the least amount of biomass output (Table 6). Additionally, with this increased total biomass there was a shift in contribution from smaller trophic levels (e.g. zooplankton, small insects and invertebrates) to larger trophic levels (e.g. small and large fish) (Fig. 10a,b). Introducing added complexity into the food web also shifted biomass distributions from a typical pyramid structure

Table 6. Model outputs of total biomass shown for three food webs (linear size-structured, generalist, and literature-approximated), three primary producer trophic composition (all primary producers in a single trophic compartment, three separate primary producer trophic compartments, and diatoms only), three decomposer TTEs, and two non-decomposer TTEs efficiencies.

<table>
<thead>
<tr>
<th>Non-decomposer TTE</th>
<th>Decomposer TTE</th>
<th>Linear Size-Structured</th>
<th>Generalist</th>
<th>Literature-Approximated</th>
<th>Linear Size-Structured</th>
<th>Generalist</th>
<th>Literature-Approximated</th>
<th>Linear Size-Structured</th>
<th>Generalist</th>
<th>Literature-Approximated</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.1</td>
<td>0.1</td>
<td>3.04</td>
<td>3.14</td>
<td>3.24</td>
<td>3.02</td>
<td>3.14</td>
<td>3.23</td>
<td>1.89</td>
<td>1.89</td>
<td>1.89</td>
</tr>
<tr>
<td>0.1</td>
<td>0.4</td>
<td>3.12</td>
<td>3.16</td>
<td>3.30</td>
<td>3.04</td>
<td>3.14</td>
<td>3.25</td>
<td>1.89</td>
<td>1.89</td>
<td>1.89</td>
</tr>
<tr>
<td>0.01</td>
<td>0.4</td>
<td>2.01</td>
<td>2.00</td>
<td>2.02</td>
<td>2.00</td>
<td>2.00</td>
<td>2.01</td>
<td>1.89</td>
<td>1.89</td>
<td>1.89</td>
</tr>
</tbody>
</table>

where there is a reduction in biomass with increasing individual body mass (Fig. 11a), to a less straightforward relationship between individual body mass and trophic biomass (Fig. 11b,c). These results are consistent with mechanistic metabolic model applications to the global ocean, where the presence of large generalist predators and gigantic secondary consumers added
additional complexity to the food web and resulted in a substantial increase in total biomass output along with irregularly-shaped biomass distributions (Woodson et al. 2018).
Figure 10. Model outputs of biomass for each trophic compartment shown for models in which (a) primary producers were grouped into a single trophic compartment, (b) primary producers were in three distinct trophic compartments, and (c) diatoms were the only primary producers consumed. In all cases, decomposer TTE was 0.4.
Figure 11. Trophic biomass plotted against average individual body mass for (a) linear size-structured, (b) generalist, and (c) literature-approximated food web structures. Values are shown for decomposer TTE of 10% and 40%. Non-decomposer TTE was fixed at 10% in all cases.

Flow Variability and Assuming a Steady State System

Stream discharge in rivers changes across multiple timescales, and this variability is an important driver of ecological processes. In developing the mechanistic metabolic model of the MOR, this variability was not taken into account for the sake of initial model development and simplicity. The average wetted with of the study area across a full annual cycle was used to calculate the size of the study area, and this area was treated as a constant size throughout the year. The shoal study area where literature and field data were collected was approximately
1,385 m². In future model exploration and expansion, seasonal flow variability would be an ideal next step, as it is known to change the community composition of different substrate areas and micro-habitats. However, significant environmental data would need to be assembled, especially seasonal surveys of species composition to capture seasonal community variation.

Rivers are open ecosystems, which means that organisms are continually entering and exiting the system, leading to a steady input of allochthonous material in the form of leaf litter and falling wood debris that provides an additional food source to primary consumers (e.g., ~66% of primary consumer energy comes from this allochthonous coarse particulate organic matter (Allan and Castillo 2007)). This model assumed steady-state conditions in both flow and organic matter throughput, meaning that the gross primary production (0.1 kg C m⁻² y⁻¹) entered into the model was assumed to account for both allochthonous and autochthonous contribution of organic material to the system. It should be noted that ecosystems may not ever reach steady-state conditions, so model outputs that result from a steady-state model should be considered as the ecosystem operating at carrying capacity (Woodson et al. 2018).

Model generated results revealed extreme model sensitivity to initial primary producer biomass or GPP estimates that correspondingly alter energy flow throughout the entire food chain (Fig. 10). However, there was little change in overall system biomass when relative feeding preference was varied between different groups of primary producers (see Appendix B for diet matrices); for example, in cases where higher trophic levels consumed all species of primary producers, relative diet preference between the different types of primary producers did not have an impact on overall biomass production (Fig. 10a,b). Limiting the available food supply to a smaller biomass (diatoms only) resulted in reduced outputs of overall biomass and a large reduction in population of higher trophic levels (Fig. 10c). In other words, biomass outputs
were virtually identical between scenarios where all primary producers were grouped into a single trophic compartment and when they were split into three separate trophic compartments with variable feeding preference, but were roughly 33% less when only diatoms were consumed (Table 6) (regardless of how decomposer TTE and non-decomposer TTE was varied).

Based on general knowledge of riverine ecosystems (e.g. Allan and Castillo 2007), it is highly unlikely that all primary producers are consumed by higher trophic levels with equal preference in either the Middle Oconee River or in riverine ecosystems in general. For example, macroalgae is typically not a large portion of the total organic material consumed in fluvial ecosystems (Allan and Castillo 2007). However, results of these different model scenarios reveal the importance of knowing the overall amount of primary producer biomass in the system that is actually available for consumption by higher trophic levels. Intuitively, reducing the available organic material for higher trophic compartments causes a reduction in overall biomass output, as well as a shift to smaller populations of larger organisms (Fig. 10c).

**Trophic Transfer Efficiency and the Microbial Loop**

There is wide variation of TTEs reported in the literature, and a detailed assessment of TTE in the MOR fell outside of the scope of this study. However, decomposer and non-decomposer TTEs were varied according to values typically used in modeling and whole-ecosystem analyses (e.g. Schramski et al. 2015, Woodson et al. 2018). Also, the role of the microbial loop especially requires consideration with relation to TTE as there is debate as to whether the microbial loop serves as an important energy transfer pathway in fluvial ecosystems, or if it simply plays a role in nutrient cycling (Allan and Castillo 2007).
Decreasing non-decomposer TTE elicited one of the biggest responses in model outputs. When all other parameters were held constant, reducing the non-decomposer TTE from 10% to 1% reduced total system biomass by roughly 33% (Table 6). However, when consumption of primary producers was limited to only diatoms, this trend did not hold (Table 6), indicating that the model is more sensitive to limiting the amount of primary producer biomass available for consumption by higher trophic levels. When decomposers are present in a food web, they feed additional biomass back into the ecosystem, thus causing an increase in overall system biomass (e.g. Schramski et al. 2015). Therefore, it should be expected that increasing the amount of material consumed by decomposers would, in turn, increase the total biomass of the system because decomposers are adding additional biomass to the system.

It is interesting that increasing decomposer TTE has very little impact on total system biomass in certain scenarios. When the non-decomposer TTE was very small (1%), or when diatoms were the only primary producers consumed by higher trophic levels, variation in either food web complexity or decomposer TTE elicited virtually no changes in total biomass outputs (Table 6). Model outputs reflect biomass, not population, and a small contribution of microbial biomass to total ecosystem biomass does not correlate to a small population of microorganisms. Additionally, increasing food web complexity causing irregular biomass distributions did not change when decomposer TTE was varied (Fig. 11). These results suggest that variables other than the microbial loop could play a more important role in the ecosystem dynamics of the Middle Oconee River.
CHAPTER 5
CONCLUSIONS

This project entailed the adaptation of a mechanistic metabolic theory model for part of the MOR to predict whole-ecosystem properties such as biomass and carbon export rates from the ecosystem. Existing datasets from the MOR and sufficiently similar datasets from similar rivers (e.g. body sizes, temperatures, populations, etc.) were used to build the model. The modeling effort and the model itself was used to assess whether this type of model can be accurately transferred from larger, global-scale ecosystems (e.g. Schramski et al. 2015; Woodson et al. 2018) to smaller, more localized riverine ecosystems, and more generally applied to other rivers. Further, model sensitivities to data and assumptions were explored. The ultimate goal of this effort was to build a solid foundation for a mechanistic metabolic model that can be applied to any river ecosystem as a simple, user-friendly tool for river ecosystem assessment where this model can serve as a basis for future research and refinements.

There are three main points to consider concerning the practicality of using metabolic mechanistic modeling to ascertain ecosystem properties in small scale riverine ecosystems: 1) Changes in the amount of primary producer biomass available for consumption by higher trophic levels elicited the greatest response in total system biomass, indicating a key vulnerability of MTE modeling of small sites with limited resources to collect extensive data or limited advanced knowledge of primary producer species, populations, or feeding knowledge; 2) Changes in non-decomposer TTE had the second largest impact on total system biomass; 3) Followed by food web complexity.
These findings demonstrate how critical it is to have both an approximation of total primary producer biomass within an ecosystem and an estimate of how much of that producer biomass is actually available for consumption by higher trophic levels. Lacking a clear understanding of these details can result in vastly different model outputs and a subsequently large over- or under-estimate of total system biomass production. Though increasing the complexity of the food web did not elicit the largest response in total system biomass, it did elicit some responses that highlight the importance of considering food web complexity when developing a mechanistic metabolic model for ecosystem assessment. In addition to the correlation between food web complexity and total ecosystem biomass, it also resulted in a shift in contribution to total biomass from smaller trophic levels towards higher trophic levels. Finally, increasing food web complexity elicited a shift in the relationship between individual mass and biomass towards a more complex relationship. Though variation in decomposer TTE did elicit a response in some cases, the response was minimal compared to the impacts observed when varying all other parameters. This perhaps lends support to the widely-debated idea that decomposers might play a more important role in nutrient cycling than in transferring biomass (energy) through the fluvial food web.

The mechanistic metabolic model developed in this study can be used as a tool to evaluate ecosystem functionality, to gain an initial understanding of which aspects of riverine ecosystem structure are most sensitive to change, and to inform restoration efforts. Future expansion and development of this model should especially address flow variability and associated seasonal changes in food web and community, as well as varying habitats and substrates, as these attributes are likely to alter ecosystem functioning across timescales smaller than a year and thus could impact overall biomass and energy transfer. Though this model will
require substantial ground-truthing and perhaps additional development before being generally applicable to riverine ecosystems, this study demonstrates that metabolic models, currently restricted to larger geographic scale studies, also have insightful discovery and educational merit in assessing more localized ecosystems.

Use of a mechanistic metabolic model to assess environmental health and functionality is an inherently ecosystem-based approach, and thus provides a broadly insightful and otherwise revealing analysis. As such, it is intended to be used as a complimentary tool to environmental sampling techniques that already exist. Data from routine environmental sampling can be used as model inputs, making the use of this model simplistic and easy to integrate into current assessment efforts. Further, the general approach of using a mechanistic metabolic model for ecosystem assessment is directly applicable to all ecosystems, and can therefore be considered not only for rivers, but also for other types of small, localized ecosystems.
REFERENCES


Conn, C. (In prep.). Quantifying ecological outcomes of hydrologic variability.


Katz, R. A. (2009). *Abundance and survival of common benthic biota in a river affected by water diversion during an historic drought.* (MS), University of Georgia, Athens, GA.


McKay, S. K. (2014). *Informing flow management decisions in the Middle Oconee River.* (Ph.D.), University of Georgia, Athens, GA.


Pahl, J. P. (2009). *Effects of flow alteration on the aquatic macrophyte Podostemum ceratophyllum (riverweed): local recovery potential and regional monitoring strategy.* (MS), University of Georgia, Athens, GA.


APPENDIX A

INDIVIDUAL BODY MASS DATA
<table>
<thead>
<tr>
<th>Organism</th>
<th>Common name</th>
<th>Taxa</th>
<th>Theme</th>
<th>Feeding Habit/Diet Preference</th>
<th>Body Mass (kg)</th>
<th>Source</th>
<th>Found by</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alosa sapidissima</td>
<td>American shad</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, benthic crustaceans, insects, planktonic crustaceans</td>
<td>2.50±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Anamias bremense</td>
<td>Small bullhead</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, fish, insects, crustaceans</td>
<td>1.38±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Alosa vulpes</td>
<td>White catfish</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, fish, small fish, snails</td>
<td>2.12±0.00</td>
<td>drummondjdvx</td>
<td>3</td>
</tr>
<tr>
<td>Alosa sapidissima</td>
<td>Flat bullhead</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, fish, small fish, snails</td>
<td>1.66±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Alosa sapidissima</td>
<td>Bowfin</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, fish, small fish, detritus, plants</td>
<td>1.18±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Anguilla rostrata</td>
<td>American eel</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth zooplankton, fishes, insects, benthic crustaceans</td>
<td>4.03±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ateles sagus</td>
<td>Piranha</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.76±0.01</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Anguilla rostrata</td>
<td>Carparker</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>9.67±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Chilorrhogoglogogogolabirris</td>
<td>Grass carp</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.88±0.01</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Cypinnolus solifer</td>
<td>Drumuline shiner</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.05±0.01</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Cypinnolus spilifer</td>
<td>Barbeo shiner</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.05±0.01</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Doradus cepedianus</td>
<td>Yellow shad</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>1.18±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Doradus cepedianus</td>
<td>Threadfin shad</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.58±0.01</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Erimyza saginae</td>
<td>Creek chub</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>7.36±0.01</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Erimyza saginae</td>
<td>Chan pike</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>1.80±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethroma urbanus</td>
<td>Christmas darter</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
<tr>
<td>Ethromorphus sp indicating</td>
<td>Small perch</td>
<td>fish</td>
<td>Ectotherm</td>
<td>Forth fish, small crustaceans, small fish</td>
<td>2.00±0.00</td>
<td>annamurlavys.org</td>
<td>3</td>
</tr>
</tbody>
</table>
| Ethromorphus sp indicating | Small perch  | fish    | Ectotherm      | Forth fish, small crustaceans, small fish      | 2.00±0 “Found by” column: (1) Nelson and Scott (1962), (2) Grubaugh and Wallace (1995), (3) Evans (1994)
<table>
<thead>
<tr>
<th>Organism</th>
<th>Common name</th>
<th>Taxa</th>
<th>Feeding Habits/Diet Preference</th>
<th>Body Mass (kg)</th>
<th>Source</th>
<th>Found by</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratitis sp.</td>
<td>insect</td>
<td>extinct</td>
<td>Ectotherm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chromatoides sp.</td>
<td>midge fly</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>2.000-9</td>
<td>calculated from Beke et al. 2009</td>
<td>2</td>
</tr>
<tr>
<td>Chlorodenalai (Tassyadina) sp.</td>
<td>midge</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>2.000-9</td>
<td>calculated from Beke et al. 2009</td>
<td>2</td>
</tr>
<tr>
<td>Corydalis humulus</td>
<td>eastern doborfly</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>2.000-9</td>
<td>calculated from Beke et al. 2009</td>
<td>2</td>
</tr>
<tr>
<td>Cryphalaena sp.</td>
<td>honey bee</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>3.30-3</td>
<td>calculated from Beke et al. 2009</td>
<td>2</td>
</tr>
<tr>
<td>Cricetulus sp. (Araneidae)</td>
<td>midge flies</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptochromis sp. &amp; cth.</td>
<td>true fly?</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>3.600-9</td>
<td>Strayer 1994</td>
<td>1</td>
</tr>
<tr>
<td>Dendrophila sp.</td>
<td>true fly</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>3.600-9</td>
<td>Strayer 1994</td>
<td>1</td>
</tr>
<tr>
<td>Dendrophila sp. long-legged fly</td>
<td>extinct</td>
<td>Ectotherm</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drosophila sp.</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>4.700-6</td>
<td>Burns 2013</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectotherm</td>
<td>Ectotherm</td>
<td>extinct</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Body Mass Data References


APPENDIX B

DIET MATRICES
### Table B.1. Linear size-structured food web with all primary producers in one trophic compartment.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>PP</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary Producers (PP)</td>
<td>N/A</td>
<td>0</td>
<td>0.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>$10^{-8}$</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>$10^{-5}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>$10^{-1}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>$10^{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>$10^{-12}$</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

### Table B.2. Generalist food web with all primary producers in one trophic compartment.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>PP</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary Producers (PP)</td>
<td>N/A</td>
<td>0</td>
<td>0.8</td>
<td>0.4</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>$10^{-8}$</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>$10^{-5}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>$10^{-1}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>$10^{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>$10^{-12}$</td>
<td>0</td>
<td>0.2</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

### Table B.3. Literature-approximated food web with all primary producers in one trophic compartment.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>PP</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary Producers (PP)</td>
<td>N/A</td>
<td>0</td>
<td>0.4</td>
<td>0.1</td>
<td>0.2</td>
<td>0.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>$10^{-8}$</td>
<td>0</td>
<td>0.2</td>
<td>0.8</td>
<td>0.35</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>$10^{-5}$</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.35</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>$10^{-1}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.3</td>
<td>0.05</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>$10^{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>$10^{-12}$</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table B.4. Linear size-structured food web with primary producers split into three trophic compartments.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>DI</th>
<th>FA</th>
<th>M</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms (DI)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.33</td>
</tr>
<tr>
<td>Filamentous algae (FA)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.33</td>
</tr>
<tr>
<td>Other Macroalgae (M)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.33</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>$10^{-8}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>$10^{-5}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>$10^{-1}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>$10^{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>$10^{-12}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table B.5. Generalist food web with primary producers split into three trophic compartments.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>DI</th>
<th>FA</th>
<th>M</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms (DI)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
<td>0.3</td>
<td>0.25</td>
<td>0.19</td>
<td>0.07</td>
</tr>
<tr>
<td>Filamentous algae (FA)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.05</td>
<td>0.04</td>
<td>0.03</td>
<td>0.07</td>
</tr>
<tr>
<td>Other Macroalgae (M)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.05</td>
<td>0.04</td>
<td>0.03</td>
<td>0.07</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>$10^{-8}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>$10^{-5}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>$10^{-1}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>$10^{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>$10^{-12}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table B.6. Literature-approximated food web with primary producers split into three trophic compartments.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>DI</th>
<th>FA</th>
<th>M</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms (DI)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.3</td>
<td>0.08</td>
<td>0.15</td>
<td>0.08</td>
<td>0.13</td>
</tr>
<tr>
<td>Filamentous algae (FA)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
<td>0.01</td>
<td>0.03</td>
<td>0.01</td>
<td>0.13</td>
</tr>
<tr>
<td>Other Macroalgae (M)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
<td>0.01</td>
<td>0.03</td>
<td>0.01</td>
<td>0.13</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>(10^{-8})</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0.8</td>
<td>0.35</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>(10^{-5})</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.35</td>
<td>0.3</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>(10^{-1})</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.3</td>
<td>0.05</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>(10^0)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>(10^{-12})</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table B.7. Linear size-structured food web; the only primary producer consumed is diatoms.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>DI</th>
<th>FA</th>
<th>M</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms (DI)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Filamentous algae (FA)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Other Macroalgae (M)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>(10^{-8})</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>(10^{-5})</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>(10^{-1})</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>(10^0)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>(10^{-12})</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table B.8. Generalist food web; the only primary producer consumed is diatoms.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>DI</th>
<th>FA</th>
<th>M</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms (DI)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.8</td>
<td>0.4</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Filamentous algae (FA)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Other Macroalgae (M)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>$10^{-8}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>$10^{-5}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.33</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>$10^{-1}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.25</td>
<td>0.2</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>$10^{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>$10^{12}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table B.9. Literature-approximated food web; the only primary producer consumed is diatoms.

<table>
<thead>
<tr>
<th>Trophic Compartment</th>
<th>Individual Mass (kg)</th>
<th>DI</th>
<th>FA</th>
<th>M</th>
<th>Z</th>
<th>I</th>
<th>SF</th>
<th>LF</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms (DI)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>0.1</td>
<td>0.2</td>
<td>0.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Filamentous algae (FA)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Other Macroalgae (M)</td>
<td>N/A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zooplankton, small insects and invertebrates (Z)</td>
<td>$10^{-8}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0.8</td>
<td>0.35</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Large insects and invertebrates (I)</td>
<td>$10^{-5}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.35</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Small fish (SF)</td>
<td>$10^{-1}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
<td>0.3</td>
<td>0.05</td>
</tr>
<tr>
<td>Large fish (LF)</td>
<td>$10^{0}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
</tr>
<tr>
<td>Decomposers (D)</td>
<td>$10^{12}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
APPENDIX C

MATLAB CODE

Code for primary producers in a single trophic compartment

```matlab
function S=compute_biomass_singlePP(dietmatrix,GPP_literature,temp_annual)

% Uses literature GPP = 0.1 kg m^-2 y^-1, and
% phytoplankton biomass = 1.89 kg m^-2 y^-1. Constant values from Woodson et
% al (2018)

k=8.62e-5; %Boltzman constant

%Constant variables used are from Woodson et al. (2018)
%set constant variables for primary producers (level 0)
Po_p=1.32e9; E_p=0.32; beta_p=1.036;
%set constant variables for zooplankton, small insects, & small inverts (level 1)
Po_z=2.16e9; E_z=0.65; beta_z=0.96;
%set constant variables for large insects and invertebrates
Po_i=2.16e9; E_i=0.65; beta_i=0.75;
%set constant variables for fish (levels 3 and 4)
Po_f=2.16e9; E_f=0.65; beta_f=0.79;
%set constant variables for decomposers (level 5) (same as for primary
%producers)
Po_d=1.32e9; E_d=0.32; beta_d=1.036;

%loop through LMEs and calculate biomass

clear Find gross prod net_prod group_mass
%load diet matrix for lme
[dietmatrix, text2, alldata] = xlsread(['dietmatrix3.xlsx']);

%parse data into matrix, trophic level, ind mass, and ecotrophic efficiency

ENDO=dietmatrix(:,1);
orgmass=dietmatrix(:,2);
dietmatrix=dietmatrix(:,3:end);
[n m]=size(dietmatrix);
group_name=text2(4:end,1);
class=text2(4:end,2);
reference=text2(1,2);

clear alldata text2;

%initialize flow matrix

flowmatrix=zeros(n,m);
flowmatrix(1,1)=1;

%recompute diet matrix as a proportion of total mass flow
dietmatrix2=dietmatrix;
```

for i=1:n-1
    for j=1:n-1
        dietmatrix2(i,j) = dietmatrix(i,j) ./ sum(dietmatrix(i,1:n-1));
    end
end

dietmatrix2(isnan(dietmatrix2)) = 0;
dietmatrix = dietmatrix2; clear dietmatrix2;

%compute flow matrix to 1e-12 tolerance
test = 1;
temp = 1;

%trophic transfer efficiencies
epsilon = ones(n,1);
for ii = 2:n
    if strcmp(class(ii), 'D')
        epsilon(ii) = 0.4; % Set decomposer trophic transfer efficiency
    else
        epsilon(ii) = 0.1; % Set non-decomposer trophic transfer efficiency
    end
end

while (abs(test) >= 1e-12)
    for i = 1:n
        for j = 2:n
            flowmatrix(i,j) = epsilon(j) .* sum(flowmatrix(:,i)) .* dietmatrix(i,j);
        end
    end
    test = (sum(flowmatrix(n,:)) - temp) / temp;
    temp = sum(flowmatrix(n,:));
end

flowmatrix = flowmatrix .* (GPP_literature); % multiply GPP (kg C m^-2 y^-1) by flow matrix

% compute ecosystem properties and production, gross production, net production, population size, and group total biomass for each trophic compartment based on Schramski et al 2015 (PNAS)
for i = 1:n
    if ENDO(i) == 0
        T(i) = 273 + temp; % ambient temperature in degK for exotherms
    else
        T(i) = 273 + 37; % 310 K for endotherms
    end
    switch char(class(i))
        case 'P'
            Pind(i) = Po_p .* (orgmass(i) ^ beta_p) .* exp(-E_p / (k * T(i))) .* PAR;
        case 'Z'
            Pind(i) = Po_z .* (orgmass(i) ^ beta_z) .* exp(-E_z / (k * T(i)));
        case 'I'
            Pind(i) = Po_i .* (orgmass(i) ^ beta_i) .* exp(-E_i / (k * T(i)));
        case 'F'
            Pind(i) = Po_f .* (orgmass(i) ^ beta_f) .* exp(-E_f / (k * T(i)));
        case 'D'
            Pind(i) = Po_d .* (orgmass(i) ^ beta_d) .* exp(-E_d / (k * T(i)));
        end
    switch char(class(i))
case 'P'
gross_prod(i)= GPP_literature; %GPP from Lamberti and Steinman 1997 (mid-range
value for GPP measured in streams of similar latitude)
  net_prod(i)=0.5*gross_prod(i);
group_massdensity(i)= 1.89; %wet biomass measured by Caitlin Conn (UGA RBC)
case {'Z', 'I', 'F', 'D'}
gross_prod(i)=sum(flowmatrix(:,i));
  net_prod(i)=0.5*gross_prod(i);
  population(i)=net_prod(i)./Pind(i);
group_massdensity(i)=population(i).*orgmass(i);
end
end

S.total_mass=sum(group_massdensity);
S.flowmatrix=flowmatrix;
S.dietmatrix=dietmatrix;
S.orgmass=orgmass';
S.class=class';
S.Pind=Pind;
S.gross_prod=gross_prod;
S.net_prod=net_prod;
S.population=population;
S.group_massdensity=group_massdensity;
S.group_name=group_name;

clear Pind gross_prod net_prod population group_massdensity T;
end
Code for primary producers split into three separate trophic compartments

```matlab
function S=compute_biomass_multPP(dietmatrix,GPP_literature,temp_annual)

%Uses literature GPP = 0.1 kg m^-2 y^-1, and
%phytoplankton biomass = 1.89 kg m^-2 y^-1. Constant values from Woodson et
%al (2018)

k=8.62e-5; %Boltzman constant

%Constant variables used are from Woodson et al. (2018)
%set constant variables for primary producers (level 0)
P_o_p=1.32e9; E_p=0.32; beta_p=1.036;
%set constant variables for zooplankton, small insects, & small inverts (level 1)
P_o_z=2.16e9; E_z=0.65; beta_z=0.96;
%set constant variables for large insects and invertebrates
P_o_i=2.16e9; E_i=0.65; beta_i=0.75;
%set constant variables for fish (levels 3 and 4)
P_o_f=2.16e9; E_f=0.65; beta_f=0.79;
%set constant variables for decomposers (level 5) (same as for primary
%producers)
P_o_d=1.32e9; E_d=0.32; beta_d=1.036;

%loop through LMEs and calculate biomass

clear Find gross Prod net Prod group mass
%load diet matrix for lme
[dietmatrix, text2, alldata] = xlsread(['dietmatrix6.xlsx']);
%parse data into matrix, trophic level, ind mass, and ecotrophic efficiency
ENDO=dietmatrix(:,1);
orgmass=dietmatrix(:,2);
dietmatrix=dietmatrix(:,3:end);
[n m]=size(dietmatrix);
group name=text2(4:end,1);
class=text2(4:end,2);
reference=text2(1,2);

clear alldata text2;
%initialize flow matrix
flowmatrix=zeros(n,m);
flowmatrix(1,1)=1;

%recompute diet matrix as a proportion of total mass flow
dietmatrix2=dietmatrix;
for i=1:n-1
    for j=1:n-1
        dietmatrix2(i,j)=dietmatrix(i,j)./sum(dietmatrix(i,1:n-1));
    end
end
dietmatrix2(isnan(dietmatrix2))=0;
```
dietmatrix=dietmatrix2; clear dietmatrix2;

%compute flow matrix to 1e-12 tolerance
test=1;
temp=1;

%determine number of primary producer trophic compartments
nPrimary=sum(strcmp(class,'P'));

%trophic transfer efficiency
epsilon=ones(n,1);
for ii=(nPrimary+1):n
    if strcmp(class(ii),'D')
        epsilon(ii)=0.4; %assign decomposer TTE
    else
        epsilon(ii)=0.1; %assign non-decomposer TTE
    end
end

%allocate GPP to primary producer classes. GPP assigned to each trophic compartment was weighted based on relative biomass
for ii=1:nPrimary
    if strcmp(group_name(ii),'diatoms')
        X = 0.0047
        flowmatrix(ii,ii)=(GPP_literature).*X/1.89;
    elseif strcmp(group_name(ii),'filamentous algae')
        X = 0.0635
        flowmatrix(ii,ii)=(GPP_literature).*X/1.89;
    else % for other primary producers
        X = 1.818
        flowmatrix(ii,ii)=(GPP_literature).*X/1.89;
    end
end
while (abs(test)>=1e-12)
    for i=1:n
        for j=(nPrimary+1):n
            if j==n
                flowmatrix(i,j)=sum(flowmatrix(:,i)).*dietmatrix(i,j);
            else
                flowmatrix(i,j)=epsilon(j).*sum(flowmatrix(:,i)).*dietmatrix(i,j);
            end
        end
        test=(sum(flowmatrix(n,:))-temp)./temp;
        temp=sum(flowmatrix(n,:));
    end
end

flowmatrix
%compute ecosystem properties ind production, gross production, net production, population size, and group total biomass for each trophic compartment based on Schramski et al 2015 (PNAS)
for i=1:n
    if ENDO(i)==0
        T(i)=273+temp; %ambient temperature in degK for exotherms
    else
        T(i)=273+37; %310 K for endotherms
    end
switch char(class(i))
    case 'P'
        \( P_{\text{ind}}(i) = P_o_p \cdot (\text{orgmass}(i)^{\beta_p}) \cdot \exp(-E_p/(k \cdot T(i))) \cdot \text{PAR}; \)
    case 'Z'
        \( P_{\text{ind}}(i) = P_o_z \cdot (\text{orgmass}(i)^{\beta_z}) \cdot \exp(-E_z/(k \cdot T(i))); \)
    case 'I'
        \( P_{\text{ind}}(i) = P_o_i \cdot (\text{orgmass}(i)^{\beta_i}) \cdot \exp(-E_i/(k \cdot T(i))); \)
    case 'F'
        \( P_{\text{ind}}(i) = P_o_f \cdot (\text{orgmass}(i)^{\beta_f}) \cdot \exp(-E_f/(k \cdot T(i))); \)
    case 'D'
        \( P_{\text{ind}}(i) = P_o_d \cdot (\text{orgmass}(i)^{\beta_d}) \cdot \exp(-E_d/(k \cdot T(i))); \)
end

switch char(class(i))
    case {'Z', 'I', 'F', 'D'}
        gross_prod(i) = sum(flowmatrix(:,i));
        net_prod(i) = 0.5 * gross_prod(i);
        population(i) = net_prod(i) / Pind(i);
        group_massdensity(i) = population(i) * orgmass(i);
    end
end

S.total_mass = sum(group_massdensity);
S.flowmatrix = flowmatrix;
S.dietmatrix = dietmatrix;
S.orgmass = orgmass';
S.class = class';
S.Pind = Pind;
S.gross_prod = gross_prod;
S.net_prod = net_prod;
S.population = population;
S.group_massdensity = group_massdensity;
S.group_name = group_name;
clear Pind gross_prod net_prod population group_massdensity T;
end